Working Group Briefing Materials

2016 CBSG Annual Meeting
Puebla, Mexico

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Puebla, Mexico
6-9 October 2016

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CBSG Annual Meeting Working Group Schedule

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Working Group Descriptions: 2016 CBSG Annual Meeting

How do we deal with conservation-reliant species?

CONVENOR: Sarah Long

AIM: The aim of this Working Group session is to discuss the prioritization and allocation of resources for conserving species that may always be reliant on some human intervention to manage threats or foster population viability.

BACKGROUND: Implicit in many definitions of recovery (including that of the US Endangered Species Act) is the assumption that threats to species can be eliminated or mitigated sufficiently such that a recovered species would be able to sustain itself without human intervention. However, if the threats are human-induced they may be difficult to halt (e.g., habitat fragmentation and loss, conflicts with human property or land use, climate change effects, etc.). So some kind of assistance or management may be necessary in perpetuity for an estimated 84% of endangered and threatened species with USFWS recovery plans (Goble et al 2012). How should this change the prioritization of species for initial listing or allocation of resources? How does this change the roles of government, non-governmental organizations, or private people in conservation?

LITERATURE CITED:

Goble, D.D., J. A. Wiens, J. M. Scott, T. D. Male, and J.A. Hall. Conservation-Reliant Species. 2012. *BioScience*. Vol.62 No.10.

How Species Distribution Models (SDMs) can improve decision-making in conservation planning

CONVENOR: Katia Maria P. M. B. Ferraz (Forest Science Department, ESALQ/USP)

AIM: To present and discuss the potential use of Species Distribution Models to support decision-making in conservation planning.

BACKGROUND: Species Distribution Models (SDMs) are an important tool often used to assess the relationship between a species, its distribution, and the environmental conditions. They integrate species occurrence records and environmental variables to develop environmental suitability maps for a species in space and time. SDMs are built for the following purposes: 1) to map and update the current species distribution, 2) to evaluate the environmental suitability of the landscape for the species occurrence, 3) to identify corridors and priority areas for conservation, 4) to identify key areas for conservation efforts, 5) to identify gaps in sampling database, 6) to identify new potential areas for species occurrence, 7) to improve the assessment of endangered species, 8) to supplement population viability analysis. When successfully used SDMs can influence policy development and support public actions for conservation and management decisions.

SDM are built before and during the workshop. They require participants provide exact GPS locations of the species. Map construction should begin a year to six months before the workshop. It is key to have a preliminary map to show at the beginning of the workshop so that it can be further discussed by all the participants, many maps are created during the workshop with participation input and discussions.

CBSG Brasil has used SDMs in the Jaguar Action Plan (2009) and the Chacoan Peccary (2016). Furthermore this tool has been fully integrated by the government authorities for the planning of endangered carnivores in Brazil. This tool can potentially be used for conservation planning of many of the species CBSG is involved with.

PROCESS: The working group will start by a presentation of the concepts involved in species distribution modeling. A brief review of the use of SDMs in workshops will be presented, emphasizing the applications of SDM for conservation planning. Opportunities on how this tool could improve species conservation planning for CBSG network will be discussed. Finally, we will brainstorm what further needs might be addressed for bridging the gap among researchers, modelers and decision-makers in favor of species conservation and how this could help the CBSG work.

Integrating human dimensions into conservation

CONVENOR: Sarah Long

AIM: The aim of this working group session is to explore how we can more systematically gather and integrate information about human dimensions into the conservation process.

BACKGROUND: Conserving species requires basic biological and ecological data relevant to the threats to a species and its biological potential for overcoming these threats. While conservation planning often factors in non-biological information, including economic costs and the potential impact on multiple stakeholders, the influence of the human dimension on conservation is often underestimated. With the growth and expansion of human populations and increasing urbanization, the conservation of species will more than likely need to occur in a human-dominated landscape. However, there is still an expectation among both scientists and citizens that species can be conserved behind fences away from people (e.g., on government land), rather than coexisting alongside people (e.g., on a patchwork of private and public lands). To achieve success in this new model, conservation planning will increasingly benefit from the integration of data from social scientists regarding perceived costs and benefits, values, and attitudes of a wide range of potential stakeholders. Beyond the input of social science, conservation planning could also benefit greatly from strategically planned education initiatives and public relations efforts.

PROCESS: The working group will begin by discussing concepts and examples of how to integrate human dimensions into the traditionally biologically driven conservation planning process. An example focal species conservation effort for this discussion could be the endangered red wolf in the southeastern United States. At the time of this writing, the recovery program for this species in North Carolina is currently under review, but there may be new recovery efforts needed for this species. The reintroductions of different wolf species in the United States, or of any predator species coexisting near people, provide a good opportunity to discuss the historical successes and challenges relating to this topic.

OUTCOMES: The group will produce a set of recommendations that describe various ways in which CBSG and other conservation planners can better integrate social sciences, human behavioral data, and the skills of non-scientists into the conservation planning process for more successful conservation outcomes.

Genetic Rescue

CONVENORS: Oliver Ryder, Dalia Conde and Johanna Staerk

BACKGROUND: In 2015 at the CBSG meeting in Al Ain, we had the first GENETIC RESCUE workshop. This year we will follow up focusing on developing a decision framework for which species we need to urgently store live cells. This may depend on many different factors, not only on species threats, population size, but access to samples and possibilities to infrastructure development. We have invited Dr. Melissa A. Kenney to help us developing this framework. Dr. Kenney is an Assistant Research Professor in Environmental Decision Analysis and Indicators at the University of Maryland, Earth System Science Interdisciplinary Center (ESSIC) and Cooperative Institute for Climate and Satellites - Maryland.

<u>Introduction to Genetic Rescue</u>

GENETIC RESCUE is defined as *an increase in population-level viability through the re-introduction of previously lost genetic material by cell-based human intervention.*

Genetic rescue involves utilizing preserved and banked tissue samples, both reproductive and somatic across a variety of technological means to add genetic diversity and/or producing viable offspring for critically endangered animals and plants. They include artificial insemination, *in vitro* fertilization, etc., along with induced stem cell development and applications of cloning technology.

<u>Rationale</u>

Genetic Rescue is the response to an extinction crisis. It has the greatest potential for impact where traditional means of species recovery by live animal transfer are not practical or possible. Emerging technologies in genetics and assisted reproduction will be crucial for some species sustainability. Numerous challenges exist in moving from proof of principle to making these technologies practicable. Two examples are methods of species choice for rescue, and another is the lack of availability of suitable samples.

SOURCES:

Full description of genetic rescue:
Definition from revive and restore
http://reviverestore.org/what-we-do/genetic-rescue/

Genetic rescue and biodiversity banking, Oliver Ryder at TEDxDeExtinction:
http://tedxtalks.ted.com/video/Genetic-rescue-and-biodiversity

The alluring simplicity and complex reality of genetic rescue
http://www.uas.alaska.edu/artssciences/naturalsciences/biology/faculty/tallmon/Tallmonetal_TREE.pdf
Cited by Edmands (2007): Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management http://onlinelibrary.wiley.com/doi/10.1111/j.1365-294X.2006.03148.x/epdf

2009 Genetic rescue guidelines with examples from Mexican wolves and Florida panthers
http://link.springer.com/article/10.1007/s10592-009-9999-5

2005 TREE Genetic restoration:' a more comprehensive perspective than 'genetic rescue
http://www.sciencedirect.com/science/article/pii/S0169534705000078

2001 TREE Restoration of genetic variation lost – the genetic rescue hypothesis
http://www.sciencedirect.com/science/article/pii/S0169534700020656

Expanding Options for Species Survival: Establishing a Global Wildlife GeneBank of Viable Cell Cultures – presentation by Oliver Ryder
http://iucncongress.ipostersessions.com/?s=D5-24-E1-A7-26-30-69-B9-F6-4F-6A-8A-0C-58-02-09

Addressing human population and behavior in the design of conservation planning processes

CONVENOR: Phil Miller

AIM: The aim of this working group session is to explore how we can better incorporate knowledge around human population growth dynamics and behavior-driven activities that threaten wildlife persistence into our species conservation planning workshops. This effort will extend the discussions on a similar topic that began at the 2015 CBSG Annual Meeting in Al Ain, UAE.

BACKGROUND: We have only rarely incorporated human demographic analysis into the risk assessment component of our conservation planning workshops. Furthermore, we do not include a detailed analysis of human activities on the landscape – and the behaviors that drive those activities – and how they impact local wildlife populations. From the perspective of developing a vision of the future for threatened wildlife populations, we need to understand how threatening activities may change in the future as human populations continue to grow. As pointed out by a growing number of conservation professionals, the real issue with human population is their mechanisms and ever-increasing rate of natural resource consumption, particularly as nations evolve along the socio-economic continuum.

Therefore, successful planning for endangered species conservation requires identifying means by which human activities can be modified to maintain viable populations. For more than 20 years, CBSG's Population and Habitat Viability Assessment (PHVA) workshops have featured recommendations that are developed in the spirit of moderating our negative impacts on species and habitats. But we have not systematically addressed the issue of increasing human population abundance and how to face the dynamic impacts of this threat.

At the 2015 CBSG Annual Meeting in Al Ain, a working group began to address this issue. The participants enthusiastically supported the general proposal to incorporate these aspects of "the human dimension" into future CBSG-facilitated species conservation workshops. We focused our subsequent discussion in the context of a potential workshop opportunity in Chile, where Humboldt penguins are impacted by a variety of human-mediated activities. Discussions among Humboldt penguin biologists and other interested parties have been ongoing after the Al Ain session.

PROCESS: The working group will begin by revisiting the discussion of concepts initiated in the 2015 Al Ain working group, and will expand ideas and concepts from that session that are most relevant to our long-term aim. We will also build on appropriate themes discussed by other working groups meeting earlier in the 2016 agenda that are addressing the larger topic of human population and species conservation. Finally, we will revisit the Chile Humboldt penguin workshop opportunity to generate a more clear vision of an expanded conservation planning process that can be promoted and facilitated by CBSG.

OUTCOMES: The group will produce a set of guidelines that describe how such an expanded process can be applied, with an emphasis on the resources required to increase its chances for successful application.

Using the tools of the Species Conservation Toolkit Initiative

CONVENORS: Jon Ballou, Bob Lacy, Taylor Callicrate

DESCRIPTION: The Species Conservation Toolkit Initiative is a partnership to ensure that the new innovations and tools needed for species risk assessment, evaluating conservation actions, and managing populations are developed, globally available, and *used effectively*. The tools in the toolkit include PMx, Vortex, Outbreak, MetaModel Manager, Vortex Adaptive Manager, and more. These are powerful tools for guiding species risk assessments and conservation planning, but it is not always easy to know how to use the many features in the software. In this working group, we will provide a short training session followed by discussion of further training needs. The specific tool(s) to be the focus of the training session will be identified by a survey of the meeting participants.

How do we deal with conservation-reliant species?

Working Group
2016 CBSG Annual Meeting
Puebla, Mexico

How do we deal with conservation-reliant species?

Sarah Long

Aim

The aim of this Working Group session is to discuss the prioritization and allocation of resources for conserving species that may always be reliant on some human intervention to manage threats or foster population viability.

Background

Implicit in many definitions of recovery (including that of the US Endangered Species Act) is the assumption that threats to species can be eliminated or mitigated sufficiently such that a recovered species would be able to sustain itself without human intervention. However, if the threats are human-induced they may be difficult to halt (e.g., habitat fragmentation and loss, conflicts with human property or land use, climate change effects, etc.). So some kind of assistance or management may be necessary in perpetuity for an estimated 84% of endangered and threatened species with USFWS recovery plans (Goble et al 2012). How should this change the prioritization of species for initial listing or allocation of resources? How does this change the roles of government, non-governmental organizations, or private people in conservation?

Literature Cited

Goble, D.D., J. A. Wiens, J. M. Scott, T. D. Male, and J.A. Hall. Conservation-Reliant Species. 2012. BioScience. Vol.62 No.10.

Conservation-reliant species and the future of conservation

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Keywords
Conservation-reliant species; endangered species; Endangered Species Act; extinction; management strategies; priority-setting; recovery plans.

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Abstract

Species threatened with extinction are the focus of mounting conservation concerns throughout the world. Thirty-seven years after passage of the U.S. Endangered Species Act in 1973, we conclude that the Act's underlying assumption—that once the recovery goals for a species are met it will no longer require continuing management—is false. Even when management actions succeed in achieving biological recovery goals, maintenance of viable populations of many species will require continuing, species-specific intervention. Such species are "conservation reliant." To assess the scope of this problem, we reviewed all recovery plans for species listed as endangered or threatened under the Act. Our analysis indicates that 84% of the species listed under the Act are conservation reliant. These species will require continuing, long-term management investments. If these listed species are representative of the larger number of species thought to be imperiled in the United States and elsewhere, the challenge facing conservation managers will be logistically, economically, and politically overwhelming. Conservation policies will need to be adapted to include ways of prioritizing actions, implementing innovative management approaches, and involving a broader spectrum of society.

Introduction

There is a broad consensus that humans have fundamentally altered the earth and placed many of its species at risk of extinction (e.g., Janzen 1998; McKibben 2006; Meyer 2006; Kareiva *et al.* 2007; Wiens 2007). Human impacts have increased over the past several decades as local has become global and the scale of human influences has multiplied (Millennium Ecosystem Assessment 2005; IPCC 2007). Not only are extinction rates increasing, but the geographic and taxonomic scope of threatened extinctions is broadening as well (Ricketts *et al.* 2005).

The growing recognition of the magnitude of human impacts on nature and of the current and looming wave of global extinctions has prompted both international and national programs to protect imperiled species (Balmford *et al.* 2005; Goble 2006). In the United States, the Endangered Species Act of 1973 established "a program for the conservation of ... endangered species and threatened species" and "the ecosystems upon which [these] species depend" (16 U.S.C. sec. 1531(b)). The Act was based on the assumption that preventing extinction is a straightforward process: identify species at risk of extinction, document the factors that imperil them, conduct research to determine the conservation measures necessary to eliminate those threats, implement those measures on a biologically relevant scale, and, when populations rebound to the point at which they are self-sustaining in the wild without the protection they are afforded under the Act, remove them from the list ("delist"), and declare them "recovered."

The expectation when the Act was drafted was that recovery would be commonplace once the appropriate actions were taken. To be sure, there have been notable successes, including the peregrine falcon

(*Falco peregrinus*), Aleutian cackling goose (*Branta hutchinsii leucopareia*), and gray whale (*Eschrichtius robustus*). But such species are the exception rather than the rule (Doremus & Pagel 2001; New & Sands 2003). On December 31, 2007, only 15 of the 1,136 listed species had met recovery goals and been removed from the list (USFWS 2009a).

In the United States, the Endangered Species Act requires that the decision to list or delist a species be based on findings on the risk the species faces from a statutory list of five threat categories: habitat loss, overutilization, disease or predation, inadequate regulatory mechanisms, and any other reason (ESA sec. 4(a)(1)(A)-(E)). The key to success under the Act, therefore, is eliminating the threat(s) that led to a species' imperilment. If these threats cannot be eliminated, continued management will be required and this management will require "existing regulatory mechanisms" to ensure that it continues for the foreseeable future. For example, although the population recovery goals for Kirtland's warbler (*Dendroica kirtlandii*) have been met since 2001, the species has not been delisted because its maintenance requires continuing and intensive management (timber stand management and control of brown-headed cowbirds, *Molothrus ater*) (Bocetti & Goble 2010). Without such management, the species would once again become imperiled.

We have previously labeled such species "conservation reliant" because they will require some form of conservation management for the foreseeable future (Scott *et al.* 2005). Conservation reliance is a continuum encompassing different degrees of management. It extends from species that occur only in captivity, through those that are maintained in the wild by releases from captive-breeding programs and those that require continuous control of predators or human disturbance, to species needing only periodic habitat management. Although the intensity and frequency of management actions required varies among species at different points on this continuum, the common characteristic is that some form of management will be required, even after the biological recovery goals for a species have been achieved or exceeded, to prevent it from sliding back toward extinction (Scott *et al.* 2005). For example, management of grizzly bears (*Ursus arctos horribilis*) in the greater Yellowstone area led to population increases and the delisting of the species as recovered under the provisions of the Endangered Species Act. When the decision was challenged, however, a federal district court held that the postdelisting management provided insufficient protection and ordered the species relisted (Federal District Court for the District of Montana 2009). In Australia, the woylie (brush-tailed bettong, *Bettongia penicillata*) was delisted in 1999 on the basis of a positive response to management, only to be relisted within a decade as populations declined, possibly in response to threats not considered in the initial listing (Australian Government Department of the Environment, Water, Heritage and the Arts 2009).

The U.S. Endangered Species Act does not recognize distinctions among species at different points on this conservation-reliance continuum; species are either listed (as threatened or endangered) or not. After a previously listed species is delisted, it receives no legal protection beyond that accorded to other species that are not (legally) imperiled. It is this lack of species-specific protection following delisting that is the source of the problem facing the Kirtland's warbler, the grizzly bear, and the other species that are conservation reliant.

If only a few of the species currently listed under the U.S. Act are conservation reliant, then the challenge is manageable. But if conservation reliance is widespread, the task for conservation managers would be overwhelming. Managing species at risk of extinction is expensive, logistically difficult, and often politically contentious (witness the controversy surrounding management of the spotted owl, *Strix occidentalis*, in the U.S. Pacific Northwest; Yaffee 1994), making it unlikely that all conservation-reliant species can receive the necessary management attention. Managers and policy makers will need to establish priorities and make hard decisions.

Methods

To evaluate the magnitude of the problem, we analyzed information from the recovery plans developed for species listed under the U.S. Endangered Species Act. We used these plans because they provide a rich and extensive body of data about the conservation-management requirements of a large number of species at risk of extinction. We reviewed the final recovery plans for 1,136 listed species (495 animals [196 invertebrates, 299 vertebrates] and 641 plants) available on December 31, 2007 (USFWS 2009b). Recovery plans synthesize the available biological information for a species and specify the actions necessary to reclassify it from endangered to threatened status ("downlist") or to remove it from the Act's protection altogether ("delist") (USFWS 1990). Our analysis follows the definition of "species" in the Act, which includes subspecies and distinct population segments of vertebrates (ESA sec. 3(14)).

We categorized a species as *conservation reliant* if the conservation-management actions identified in the narrative portion of the species' recovery plan addressed threats that will require ongoing management because they cannot be eliminated. In identifying management actions that lead to conservation reliance, we included only actions that involved active management implementation; we did not include actions that were contingent upon additional research or evaluation. Thus, we included actions that included the terms "control," "implement," "manage," or "conduct," but did not include actions preceded by the terms "assess," "monitor," "identify," "investigate," "determine," "if needed," or "if warranted."

These terms are admittedly imprecise and do not take into account differences in the magnitude or frequency of the required actions. For example, control of disturbance to an endangered plant species might require only that an area be fenced to exclude people or herbivores. Once the initial management investment is made, subsequent management might entail little more than periodically maintaining the fencing. But it would still require ongoing monitoring and maintenance, even at a low level of investment. On the other hand, conservation of another endangered plant might entail onsite monitoring and educational activities to prevent people from entering a critical area as is required for Robbins' cinquefoil (*Potentilla robbinsiana*) (USFWS 2002). Exclusion of people and pets from nesting areas of federally endangered California least terns (*Sterna antillarum browni*) or federally threatened western snowy plovers (*Charadrius alexandrinus nivosus*) necessitates fencing or posting of areas and requires continuous maintenance.

Recovery plans do not contain sufficient information to distinguish among levels of management that may be required to maintain a species. In addition, the terms that we did not include in designating a species as conservation reliant (and which therefore may define a species as nonconservation reliant) often reflect a lack of knowledge about the threats that imperil a species, so some of these species may turn out to be conservation reliant once more is known. For example, the recovery plan for the Sonoran pronghorn (*Antilocapra americana sonoriensis*) lists several management strategies that need to be "investigated" (USFWS 1998), so we did not categorize the species as conservation reliant. Some of these strategies are now being implemented as management actions (i.e., forage enhancement, supplemental watering, and captive breeding; Krausman *et al.* 2005), and it is likely that such actions will need to continue to ensure the pronghorn's persistence. Our assessment of the extent of conservation reliance among listed species thus may underestimate the actual magnitude of the problem.

The management actions identified in recovery plans can take many forms. Efforts may be focused on managing other species that negatively affect the conservation target (e.g., control of predators, nest parasites, competitors, disease vectors), actively managing habitat and ecological processes (e.g., prescribed cuts, prescribed burns, controlled releases of water from dams), supplementing resources (e.g., providing contaminant-free food for California condors, *Gymnogyps californianus*), controlling direct human impacts (e.g., excluding people from a least tern colony), or artificial recruitment (e.g., supplementing populations through release of captive-reared individuals or translocation from another site to maintain genetic diversity or augment population numbers). We grouped management actions into five conservation-management strategies, each of which includes two or more similar types of management actions: (1) control of other species, (2) control of pollutants, (3) habitat management, (4) control of use of species and/or human access, and (5) population augmentation. Because species that require multiple management strategies may have a more difficult road to recovery, we also assessed the number of conservation-management strategies required for each species. We used chi-square goodness-of-fit tests to test for differences among groups (Mead *et al.* 1993).

Results

Conservation-reliant species

Of the 1,136 listed species we evaluated, 951 (84%) are conservation reliant by our measures. The percentage of conservation-reliant species did not differ significantly among major taxonomic groups (84%, 85%, and 81% for invertebrates, plants, and vertebrates, respectively; $P = 0.94$; $\chi^2 = 0.12$, df $= 2$). Similarly, there was no statistical evidence for differences in the percentage of conservation-reliant species among vertebrate groups (mammals, 67%; birds, 96%; reptiles, 72%; amphibians, 77%; fish, 80%; $P = 0.11$; $\chi^2 = 7.64$, df $= 4$) or among invertebrate groups (insects, 100%; crustaceans, 94%; snails, 83%; clams, 72%; $P = 0.11$ $\chi^2 = 5.96$, df $= 3$).

Required management strategies

The most common management strategies listed for conservation-reliant species were control of other species, active habitat management, and artificial recruitment. Management strategies varied among taxonomic groups (Table 1). For example, active habitat management was the most frequently identified management strategy for vertebrates and plants ($P < 0.01$; $\chi^2 = 9.47$, df $= 2$), whereas artificial recruitment and pollution control were most frequently cited for invertebrates ($P < 0.01$; $\chi^2 = 11.67$ & 31.12, df $= 2$) (Table 1). The recovery plans for most species (65%) listed multiple strategies that would be required for postrecovery management (Table 2).

Table 1 Percentage of species for each conservation-management strategy

	Vertebrates	Invertebrates	Plants	**All species**
Control of other species	64%	54%	71%	**66%**
Active habitat management	62%	32%	52%	**51%**
Control of direct human impacts	49%	23%	35%	**36%**
Artificial recruitment	33%	62%	39%	**42%**
Pollution control	12%	19%	<1%	**7%**
All strategies	**81%**	**84%**	**85%**	84%

Discussion

The challenge created by the conservation reliance of threatened and endangered species is formidable. Based on our analysis, 84% of the species listed under the U.S. Endangered Species Act will need continuing management actions, even after these species have met the population and distribution goals of their recovery plans. For example, delisting of the Columbian white-tailed deer (*Odocoileus virginianus leucurus*) was predicated upon the development of land-management policies to protect its habitat on a fragmented mosaic of public and private ownership and on the assurance that this habitat would continue to be managed to meet the species' requirements (Goble 2010). This required crafting a complex management approach that included zoning and land-use ordinances, set-asides (e.g., green belts, parks), conservation easements, and agreements with landowners and public-land managers to manage their land in specific ways.

The deer, like many species at risk of extinction, occurs on landscapes that are fragmented in quality and ownership. In other situations, the natural disturbance agents that historically maintained openings necessary to the survival of species are missing or altered (Menges & Hawkes 1998). Changes in grazing regimes and elimination of American bison (*Bison bison*) migrations, for example, may have caused declines of running buffalo clover (*Trifolium stoloniferum*); the recovery plan for this species calls for mimicking these historical disturbances through ongoing habitat management (USFWS 2007).

Table 2 Percentage of conservation-reliant species with one or more conservation-management strategy

Number of conservation-management strategies	Vertebrates	Invertebrates	Plants	**All species**
1 Strategy	33%	29%	38%	**35%**
2 Strategies	29%	56%	35%	**37%**
3 Strategies	24%	10%	18%	**18%**
4 Strategies	11%	4%	9%	**9%**
5 Strategies	2%	1%	0%	**1%**

Often, threats emanate from an area larger than that occupied by the species of concern. The most common conservation-management strategy for the species we considered, for example, is control of other species (Table 1). When the threatening species occupy a wider range of habitats or larger areas than the species to be conserved, however, elimination of the threat may not be possible and control must be ongoing. The eradication of exotic foxes (*Vulpes* spp.) from the breeding islands used by the Aleutian cackling goose was instrumental to their recovery and delisting (USFWS 1990), but removal of introduced mongooses (*Herpestes* spp.), rats (*Rattus* spp.), and feral cats (*Felis catus*) from the much larger islands inhabited by the endangered Hawaiian stilt (*Himantopus mexicanus knudseni*) has proved impossible. Continuing control of nonnative predators and management of small marsh habitats throughout the islands are necessary to maintain the stilt in the wild (USFWS 2005).

The Australian experience suggests that conservation reliance is not restricted to imperiled species only in the United States. For example, control of nonnative species is a major tool in conservation management of many endemic mammals in Australia (Short & Smith 1994), and control of nonnative predators is an important element of conservation management of the woylie (Martin *et al.* 2006). Studies also suggest that postrecovery management will be required for many endangered insects (New & Sands 2003).

Nonetheless, because conservation reliance is determined in large part by the nature of the threats a species faces, it is likely to vary among countries to the extent that the types of threats vary. In China, overexploitation appears to be the primary threat to vertebrates; nonnative species were identified as a threat factor for only 3% of the listed species (Yiming & Wilcove 2005). Although the threat factors identified for endangered species in Canada are generally similar to those in the United States, overexploitation is considered a more significant threat than nonnative species (Venter *et al.* 2006).

In addition, the provisions in the U.S. Endangered Species Act requiring an explicit description of regulatory mechanisms as an element of the decision to delist a species may be a significant factor in calling attention to the problem. The statutes of other nations do not include an explicit list of threats that must be assessed in determining whether a species is imperiled. For example, neither Canada's Species at Risk Act (2002) nor Australia's Environment Protection and Biodiversity Conservation Act (1999) includes such a list of threats. Australia's Act recognizes a "conservation-dependent" category that includes species that are "the focus of a specific conservation program the cessation of which would result in the species becoming vulnerable, endangered or critically endangered" (EPBCA sec. 179(6)). Thus, a species could remain on the threatened species list even though it no longer meets the eligibility criteria, if delisting would seriously reduce the beneficial effects of management.

Conservation reliance is likely to become even more pervasive in the future. Wilcove & Master (2005) estimated that 14,000–35,000 species may currently be imperiled in the United States. These trends are not limited to the United States. Expanding human populations, the resulting degradation and fragmentation of habitats and spread of nonnative species, and the consequences of climate change will push more species toward extinction (Ricketts *et al.* 2005; Sekercioglu *et al.* 2008), swelling the ranks of conservation-reliant species. Globally, the International Union for Conservation of Nature (IUCN) Red List of species threatened with extinction continues to grow, from 16,118 species in 2007 to 17,291 species in 2009. The Intergovernmental Panel on Climate Change has projected that perhaps 20–30% of the species assessed to date are likely to have an increased risk of extinction if increases in average global warming exceed 1.5–2.5 °C (IPCC 2007). Clearly, we have seen only the tip of the iceberg.

What can be done? Part of the solution is in funding. In the United States, current funding is inadequate even to meet the conservation-management needs of those species that are currently listed (Miller *et al.* 2002). In 2003, for example, the U.S. Fish & Wildlife Service estimated that it would cost $153 million just to process the 286 candidate species then awaiting a listing decision; the total budget for all listing activities that year was only $16 million (Stokstad 2005) Things have not improved: the 2009 listing budget was actually less than the 2003 budget when adjusted for inflation (FWS 2009; www.fws.gov/budget/2009/2009%20GB/05.2%20Listing.pdf). As the ranks of conservation-reliant species continue to grow, the budgetary shortfall will only become greater. Other solutions must be sought.

We must begin by recognizing the extent and importance of conservation reliance. Presently, the listing of species and drafting of plans for their recovery revolve around the identification of threats that have caused imperilment and that must be addressed by recovery actions. Too often, the approach is based on a short-term response to an emergency. For recovery to be lasting, recovery plans should also include an evaluation of the threats that are likely to continue when recovery goals have been met. The management actions necessary to ameliorate these long-term threats should be incorporated into recovery plans at the outset. As experience with individual species increases, the recovery plans and postlisting management structure should become increasingly specific. This will reduce the chances that the extinction risk for a delisted species will increase once the legal protections of an endangered species act are removed (as with the woylie in Australia) as well as reduce the level of reliance of the species. Delisting of a species is a legal or regulatory step, not necessarily the endpoint of management.

The conservation-management actions needed to assist conservation-reliant species will also require the participation of a broad community of individuals and entities. Governments and nongovernmental conservation organizations and land trusts have been instrumental in protecting and managing places for nature, but protected areas alone will be insufficient to meet conservation goals (Wiens 2009). Management practices must be expanded to include a mix of public and private lands, balancing the priorities of differing land uses, ownerships, and conservation objectives (Walter *et al.* 2007; Freyfogle 2009). Incorporating a broader array of land uses and ownerships into the conservation agenda will depend on strong public-private partnerships. Fashioning such partnerships will require that management options be expanded beyond those available under the Endangered Species Act. One approach is to develop partnerships among federal and state agencies and nongovernmental organizations through the use of conservation-management agreements, which formalize the legal responsibilities of the conservation managers to meet the biological requirements of a species (Scott *et al.* 2005; Bocetti & Goble 2010). Incorporation of such a mechanism into the framework of the Endangered Species Act would require changes in policies and regulations, but not the law. A creative mix of regulations and incentives and a greatly expanded group of individuals involved in postrecovery management will be needed to ensure that conservation-reliant species receive adequate conservation efforts if and when they are delisted (Wilcove 2004; Parkhurst & Shogren 2006; Freyfogle 2009).

Even if new conservation partnerships are forged, the range of policy and management options is expanded, and the private sector is empowered to do more, the sheer number of current and future conservation-reliant species compels us to recognize that not all species can receive the same level of conservation attention (nor do they now). Priorities must be established for which species and ecosystems should be managed and which management practices should be employed. Prioritization approaches based on cost-effectiveness or return-on-investment (e.g., Murdoch *et al.* 2007; Briggs 2009) offer some possibilities, but other approaches should also be explored. We have not been able here to consider differences in the magnitude and duration of the conservation actions required by different conservation-reliant species, but such information should be part of a prioritization effort.

The U.S. Endangered Species Act and similar instruments in other nations have worked well. Recognizing the degree of conservation reliance among imperiled species should not be taken to mean that recovery and delisting are unattainable goals or that conservation-reliant species are beyond hope. To avoid extinction, we must recognize when and where conservation reliance is likely to occur and incorporate it into conservation planning. It is also essential to implement the targeted monitoring that will be needed to detect when management can be reduced or removed without further imperiling a species or how management actions should be adjusted in the face of unanticipated demographic responses of target species to rapid environmental change. Conservation-reliant species are yet another indication that we live in human-dominated landscapes in which maintenance of biodiversity will increasingly require increased investments of time, money, and dedication by all segments of society.

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Conservation-Reliant Species

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A species is conservation reliant *when the threats that it faces cannot be eliminated, but only managed. There are two forms of conservation reliance: population- and threat-management reliance. We provide an overview of the concept and introduce a series of articles that examine it in the context of a range of taxa, threats, and habitats. If sufficient assurances can be provided that successful population and threat management will continue, conservation-reliant species may be either delisted or kept off the endangered species list. This may be advantageous because unlisted species provide more opportunities for a broader spectrum of federal, state, tribal, and private interests to participate in conservation. Even for currently listed species, the number of conservation-reliant species—84% of* endangered *and* threatened *species with recovery plans—and the magnitude of management actions needed to sustain the species at recovered levels raise questions about society's willingness to support necessary action.*

Keywords: conservation reliant, fragmented ecosystems, conservation dependent, conservation, endangered species

Humans have been altering the Earth's ecosystems for millennia (Diamond and Veitch 1981, Pyne 1995, Flannery 2001, Jackson et al. 2001). Since the onset of the Industrial Revolution, however, the temporal and geographic scales of these modifications have increased at an accelerating rate. The cumulative impact is such that it has been proposed that the world has entered a new geological era—the Anthropocene (Crutzen and Stoermer 2000). Regardless of the descriptor, the message is simple and damning: The accumulated effects of individual and societal actions, taken locally over centuries, have transformed the composition, structure, and function of the global environment (Janzen 1998, Sanderson et al. 2002, McKibben 2006, Kareiva et al. 2007, Wiens 2007). Ecological lows have become the new baseline (Pauly 1995). Although climates have always been dynamic, and threats have always existed, recent anthropogenic threats to the integrity, diversity, and health of biodiversity are unprecedented, not only causing additional stress to ecosystems but also challenging our ability to respond (Julius and West 2008). How do we manage species and ecosystems in a world of global threats and constant change (Botkin 1990)?

One response in the United States to the endangerment and loss of species was the enactment of the Endangered Species Act (ESA). The Act's goal is to bring species at risk of extinction "to the point at which the measures provided pursuant to this Act are no longer necessary" (ESA § 3(3)). The ESA's drafters envisioned this as a logical progression: Species at risk of extinction would be listed under the Act in a process that would identify the risks the species faced, a recovery plan to address these risks would be drafted, the management tools required to conserve the species would be identified and implemented at relevant scales, the species would respond by increasing in numbers and distribution, the recovery goals would be achieved, and the species would then be delisted as *recovered*. In the interim, it would be protected by the ESA's suite of extinction-prevention tools (e.g., prohibitions on taking listed species or adversely modifying their critical habitats; Goble 2010). With recovery and delisting, the formerly listed species would achieve the ESA's goal of planned obsolescence when the Act is no longer necessary. To the extent that management would be needed, it would be provided through existing federal and state regulatory mechanisms.

The past nearly four decades has demonstrated the naivete of this vision. The path to recovery is far more winding than had been imagined. Even species that have met their biological recovery goals often require continuing, species-specific management, because existing regulatory mechanisms are seldom sufficiently specific to provide the required ongoing management (Goble 2009). For example, few species have thrived as easily as the now-delisted Aleutian cackling goose (*Branta hutchinsii leucopareia*), whose populations recovered once foxes that preyed on breeding birds and chicks were eliminated from nesting islands and for which the Migratory Bird Treaty Act's monitoring and take restrictions are sufficient. The threats that most species face cannot be eliminated, only managed. The scale of anthropogenic alteration of most ecosystems means that many imperiled species will require conservation management actions for

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the foreseeable future to maintain their targeted population levels. Adequate postdelisting management (i.e., regulatory assurances), however, is seldom possible, because for most species, no sufficiently focused and powerful regulatory mechanism is available to replace the ESA (Goble 2009, Bocetti et al. 2012 [in this issue]).

This is hardly surprising. The species listed under the ESA all became imperiled despite existing state and federal management systems. The problems remain: Most states lack regulatory systems that address nongame and plant species (Goble et al. 1999); funding is often tied to hunting and fishing license fees and remains insufficient (Jacobsen et al. 2010). Although existing management systems (e.g., the Marine Mammal Protection Act) may be sufficient for species such as the gray whale (*Eschrichtius robustus*; Goble 2009), the expectation that our work would be done once recovery goals have been met turns out to have been wishful thinking. Just how wishful was suggested by Scott and colleagues (2010), who examined the management actions required by recovery plans for species listed under the ESA. Scott and colleagues (2010) found that 84% of the species are conservation reliant, because their recovered status can be maintained only through a variety of species-specific management actions. Even if the biological recovery goals for these species are met, continuing management of the threats will be necessary. Reed and colleagues (2012 [in this issue]) provide insight into this problem by describing the challenges to recovery and to postrecovery management for one of the world's most management-dependent communities: the endemic birds of Hawaii. These species are "conservation reliant" in the sense described by Scott and colleagues (2005).

The ESA is focused on moving species to the recovery threshold. The magnitude of conservation reliance makes it clear that attention must also be given to postrecovery management (Goble 2009, Scott et al. 2010). Furthermore, species not currently listed but at risk because of declining populations or range contractions are also likely to be conservation reliant. In this context, a range of management actions may be required to preclude the need to list the species under the ESA. Although comprehensive wildlife conservation strategies developed by states with funding from the federal government provide a blueprint for sustaining nongame species and their habitats, the available state funding for these management efforts is widely viewed as insufficient (Jacobsen 2010).

Earlier, we addressed the question of conservation-reliant species in the context of the ESA (Scott et al. 2005). We did so in part by placing species along a gradient of levels of human intervention and management. At one end were those species now known only in captivity, such as the Guam kingfisher (*Todiramphus cinnamominus cinnamominus*), or sustained in the wild only through repeated releases of individuals reared in captivity, such as the California condor (*Gymnogyps californianus*). These species require the greatest degree of human intervention to achieve the basic conservation objective: the prevention of extinction. At the other end of the gradient are species such as the peregrine falcon (*Falco peregrinus*), whose recovery, once the major threat of DDT (the insecticide dichlorodiphenyltrichloroethane) had been eliminated, was secured by its ability to adapt to human-dominated environments by nesting on skyscrapers and foraging in cities on pigeons (*Columba livia*) and starlings (*Sturnus vulgaris*). The falcon thus thrives under existing federal regulations that protect all birds used in falconry and no longer requires species-specific management. The species is no longer conservation reliant. Between these extremes are a variety of species that will require differing intensities and forms of management intervention to persist in the wild. The point along this gradient at which a species becomes conservation reliant is determined by the necessity of continuing, species-specific intervention, rather than the type of intervention. The need for continuing intervention is, in turn, determined by the threats that species face. In some instances, the threats can be eliminated through appropriate actions. The key to the recovery of peregrine falcons was the banning of the pesticides that contributed to eggshell thinning and reproductive failure. For the Aleutian cackling goose, it was the removal of an introduced predator on its breeding grounds. Both species now thrive under the general provisions of the Migratory Bird Treaty Act and are no longer conservation reliant. When, however, the threat cannot be eliminated but only controlled and conservation goals can be achieved only through continuing management intervention, the species will remain conservation reliant.

In an earlier paper (Scott et al. 2005), we stated that we did not consider species either to be conservation reliant or to be delistable if they were dependent on the release of captive-reared animals or on assisted migration at the population level. We offered the California condor and the Pacific salmon (*Oncorhynchus* spp.) as examples of such species. On reflection, we now recognize that we confused the concept of *conservation reliant* with the policy decision to delist a species. By definition, all listed species are conservation reliant. The question is whether a species that has achieved recovery goals through management actions can be delisted as *recovered* without assurances that management will continue after delisting. If species-specific assurances are required, the species is conservation reliant.

The recognition that conservation reliance is a deeper and more widespread problem for listed and at-risk species than we (and others) initially thought has led us to a more nuanced perspective on this problem. In fact, two forms of conservation reliance affect species: population-management reliance and threat-management reliance. Although the ability of a species to persist is ultimately related to the characteristics and condition of both populations and the threats they face, conservation actions are often focused primarily either on managing populations or on managing threats. For example, species such as the northern Idaho ground squirrel (*Spermophilus brunneus*) live in isolated patches of habitat and may require some level of direct human intervention to move among those patches, even after local population sizes are stable (Garner et al. 2005). In contrast, other species may persist without direct population management if appropriate habitat is available. Given current land uses (and other pressures of the Anthropocene), however, human intervention may be required to maintain the habitat. As a result, it is not only species that are conservation reliant but entire ecosystems and the associated disturbance regimes (such as fire) and ecological succession pathways that define them. For example, the Karner blue butterfly (*Lycaeides melissa samuelis*), the red-cockaded woodpecker (*Picoides borealis*), and Kirtland's warbler (*Dendroica kirtlandii*) rely on periodic fire to maintain their habitat. The natural fire regimes that shaped the habitats and habitat associations of these species no longer occur, so prescribed burns must be used instead. Species such as these will continue to require threat management for the foreseeable future, even after the direct management of populations is no longer required. The two forms of conservation reliance are not independent of each other. For example, threats often influence what population actions are necessary: Where habitat encroachment has isolated small populations from each other, manipulation of the habitat may reduce habitat loss and fragmentation and may increase gene flow between the populations.

The conservation challenge is clear. The number of species that will require ongoing management is already large, and it will get larger as climate change, land-use change, human population growth, and other manifestations of the Anthropocene push more and more species to their limits. The ESA has been an effective approach for recognizing taxa that are on the brink of extinction and defining the steps needed to reverse their downward trajectory. The need for continuing intervention, even for "recovered" species, was not anticipated. We now face the conundrum that building on our conservation success will require long-term investments.

Paradoxically, continued listing under the ESA for many currently listed species may not be the best way to achieve long-term persistence. The legal restrictions imposed by the ESA may preclude some appropriate management actions. For example, landowners are often reluctant to manage their land in ways that might attract an endangered species because of the regulatory constraints imposed by the ESA (Wilcove 2004). Similarly, the paperwork and its concomitant costs in time and money are disincentives to the use of available conservation tools such as habitat conservation plans, candidate conservation agreements, and safe harbor agreements (Lin 1996, Burnham et al. 2006, Fox et al. 2006). However, delisting a species may open the door to an increasing array of unregulated threats that push it back into peril. For example, the delisting of gray wolves (*Canis lupus*) in the Northern Rocky Mountains resulted in unsustainable mortality from hunting and other pressures (Creel and Rotella 2010), which led to a judicial decision to relist the species (US District Court 2010) and a congressional decision to again delist the species through a budget rider (US Congress 2011).

To avoid such costly and contentious course reversals, a mechanism is needed to ensure that the appropriate management actions are implemented once the recovery goals for a species are met. Although no changes to the ESA are necessary to make this possible, we do need to acknowledge that continuing management is often needed after a species meets its biological recovery goals: We need a tool kit of management structures that will facilitate the transition from listed to delisted. Fortunately, examples are plentiful. The Robbins' cinquefoil (*Potentilla robbinsiana*) was delisted under a postdelisting management agreement under which the landowner (the US Forest Service) and a recreational group (the Appalachian Mountain Club) agreed to monitor and manage both the species' habitat and the threat (hikers) in order to maintain the recovered population (Goble 2009). Similarly, the Bureau of Land Management acquired nearly 3000 hectares of habitat for the Columbian white-tailed deer (*Odocoileus virginianus leucurus*) and agreed to manage its habitat through prescribed burning, grazing modifications, and restoration actions. In addition, Douglas County, Oregon, adopted a series of land-use and zoning ordinances designed to maintain habitat and corridors for the species (Goble 2009). The conservation management agreement for the grizzly bear (*Ursus arctos horribilis*) in the Greater Yellowstone Area is an example of an agreement among federal, states, and tribal land- and wildlife-management agencies that can provide a structure through which post-delisting management can be assured (USFWS 2007). Such agreements operate like candidate conservation agreements that have been used to preclude the need to list at-risk species (Lin 1996).

Bocetti and her colleagues (2012) provide an example of how a biologically and legally defensible postrecovery conservation management agreement can be developed and funded. The biggest challenges lie in finding conservation partners and obtaining funding to implement the needed management actions at ecologically relevant scales. This can be complicated on an American landscape in which two-thirds of listed and other at-risk species occur on private lands outside protected areas (Groves et al. 2000). No single mechanism can meet all needs. Instead, we envision a suite of conservation tools that can be matched to the species and landscapes that meets both the conservation threats and the diverse needs of landowners with different economic and personal interests. Funding through tax rebates, real estate transfer taxes, excise taxes, general funds, and private dollars are tools that have all been used to support wildlife and their habitats (Mangun and Shaw 1984, Smith and Shogren 2001). In addition, nongovernmental groups such as the Rocky Mountain Elk Foundation, Ducks Unlimited, Trout Unlimited, and Pheasants Forever have been formed to actively manage selected species and their habitats.

Management actions undertaken to benefit conservation-reliant species offer opportunities to accelerate the removal of species from the endangered species list and to prevent other species from becoming endangered (USFWS 2001). What is required is demonstrably effective management agreements that include management and funding commitments outside the framework of the ESA. But our focus needs to shift to abating those factors that lead to endangerment, and a conservation-reliant framework may be of assistance in doing so (Averill-Murray et al. 2012 [in this issue]). Given the criticisms of the ESA and the lower potential costs of conserving species before they are listed, understanding the ongoing management requirements of a species and responding before listing is needed has the potential to be a universal societal goal regarding species conservation. The challenge will be in creating reliable alternative funding and management structures.

The barriers to conserving and eventually delisting species are nowhere more apparent than in the Hawaiian Islands. In a thoughtful examination of our recurrent failure to implement identified recovery actions, Leonard (2008) suggested several not unrelated reasons: a lack of funding (Restani and Marzluff 2001), a lack of understanding both in the islands and on the mainland of the importance and urgent need for conservation action, and social and political barriers that reflect conflicting management goals for areas in which endangered species occur (e.g., hunting mouflon sheep [*Ovis aries orientalis*] versus maintaining the integrity, diversity, and health of palila [*Loxioides bailleui*] habitat; Banko 2009).

The consequences of failing to implement needed management actions are not trivial. The refusal to remove feral ungulates from the critical habitat of the species, despite its priority in a 1977 recovery plan and several court orders, has resulted in the continuing decline of the palila (Banko 2009). On Kauai, despite a 1984 recovery plan (Sincock et al. 1984) that called for the removal of feral ungulates from the core habitat of endangered forest birds, no action was taken until 2011. In the interim, five species went extinct (Pratt 2009) and two more species have been added to the list of endangered wildlife (USFWS 2010). The failure to act on the information in the recovery plans was a consequence of social and political pressures resulting from the perceived conflict between management intervention to recover endangered species and the continued hunting of introduced ungulates. A lack of funding also contributed to the problem.

The task we face is daunting. There are nearly 1400 listed species, and there are indications that the actual number of at-risk species is an order of magnitude or greater more (Wilcove and Master 2005). At this point, it is naive to continue to assume that funding will be available for the management needed to prevent the listing of at-risk species or to recover and manage listed species. The average expenditure for the recovery of listed species is less than a fifth of what is needed (Miller et al. 2002), and expenditures for recovery are often distributed among species for nonbiological reasons (DeShazo and Freeman 2006, Leonard 2008). Furthermore, the number of warranted but precluded decisions by the US Fish and Wildlife Service (USFWS) is increasing, and recovery has been designated a fourth-tier priority in the USFWS's guidelines for recovery planning.

Continuing business as usual, in which the majority of recovery funds are used to conserve a few iconic species while others are only monitored or simply ignored, will achieve little of lasting value. Even with increased funding, it is unlikely that we can conserve all species facing extinction, particularly as the queue gets longer. We must develop sensible ways of assigning conservation priorities in which both the magnitude of management required and the potential benefits of management and conservation actions are considered. Information about the degree of conservation reliance of a species is central to developing sensible conservation priorities.

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POLICY PERSPECTIVE

Connectivity Conservation and Endangered Species Recovery: A Study in the Challenges of Defining Conservation-Reliant Species

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Abstract

Many species listed under the US Endangered Species Act (ESA) face continuing threats and will require intervention to address those threats for decades. These species, which have been termed conservation-reliant, pose a challenge to the ESA's mandate for recovery of self-sustaining populations. Most references to conservation-reliant species by federal agencies involve the restoration of population connectivity. However, the diverse threats to connectivity faced by different species have contrasting implications in the context of the ESA's mandate. For species facing long-term threats from invasive species or climate change, restoration of natural dispersal may not be technically feasible in the foreseeable future. For other species, restoration of natural dispersal is feasible, but carries economic and political cost. Federal agencies have used a broad definition of conservation reliance to justify delisting of species in the latter group even if they remain dependent on artificial translocation. Distinguishing the two groups better informs policy by distinguishing the technical challenges posed by novel ecological stressors from normative questions such as the price society is willing to pay to protect biodiversity, and the degree to which we should grow accustomed to direct human intervention in species' life cycles as a component of conservation in the Anthropocene Epoch.

Introduction

The US Endangered Species Act (ESA) is among the world's most far-reaching and influential biodiversity protection statutes (Taylor *et al*. 2005). Listing of species as threatened or endangered under the ESA is designed to trigger an array of federal regulatory provisions that protect both the species and its habitat. Congress intended that these legal tools would reduce threats and allow a species' status to improve "to the point at which the measures provided pursuant to this Act are no longer necessary" (16 U.S.C. §1532 [3]). The species would then be removed from the ESA's list of threatened and endangered species (delisted) and primary management responsibility returned to the states.

Many of the first species to be delisted, such as the peregrine falcon (*Falco peregrinus*) and brown pelican (*Pelecanus occidentalis*), fit this pattern. These species were primarily threatened by pesticide pollutants that could be comprehensively addressed by new federal regulations. In contrast, many currently listed species face ecologically complex threats that are less amenable to regulatory remedy (Doremus & Pagel 2001). For example, as human landuse fragments natural habitats, many species have experienced a reduction in population connectivity (Soulé & Terborgh 1999). Connectivity is important to recovery because it may enhance demographic and genetic flows that support persistence of peripheral populations and long-term maintenance of a species' evolutionary potential (Lowe & Allendorf 2010).

Recovery efforts often seek to restore connectivity between core habitat areas by means of habitat restoration or restrictions on overexploitation in areas used for dispersal. This approach, because it can result in long-term amelioration in threats, is analogous to the falcon and pelican examples in fitting within the delisting framework envisioned under the ESA. Alternately, translocation (capture, transport, and release of individuals) offers an option for avoiding the socioeconomic costs of restoring connectivity in the landscape matrix where wildlife must coexist with human landuses. Such a translocation-based strategy does not create self-sustaining populations but rather relies on long-term intensive management to counteract the effect of connectivity loss on species viability. Such intensive management is a common approach for species, while they are listed as endangered or threatened (USFWS 2003, 2010). The question of whether a species can be delisted, while still dependent on such intensive management has proved more controversial.

Recent reviews have posited that most listed taxa are "conservation-reliant species" (CRS) because "preventing delisted species from again being at risk of extinction may require continuing, species-specific management" into the future (Scott *et al.* 2005, see also Scott *et al.* 2010 and Goble *et al.* 2012). The U.S. Fish and Wildlife Service (FWS) has employed the concept of CRS to justify delisting of species that still require direct manipulation of their populations to maintain a biologically secure status. This issue has most often arisen in the context of population connectivity; four of the five references to CRS in recovery planning and delisting documents have invoked CRS to justify delisting species that still require artificial translocation to maintain connectivity (Supplementary Information S3).

The question of whether delisting such species is appropriate as a legal and policy matter has received little scrutiny. In aggregate, decisions on when to delist species have far-reaching implications for the ultimate status of biodiversity. Such decisions also touch on the broader issue of whether society should grow accustomed to direct human intervention in ecosystems and species' life cycles as a necessary component of conservation in what has been termed the Anthropocene Epoch (Kareiva *et al.* 2012). The relevance of this broader question is not limited to the U.S. context. For example, Australia's endangered species listing framework follows that of the International Union for Conservation of Nature (IUCN) in defining a "conservation dependent species" as one which is the focus of a species-specific conservation measures, the cessation of which would result in the species becoming vulnerable, endangered or critically endangered within a period of 5 years (IUCN 2013).

In this article, we first review the limited guidance provided by the ESA and subsequent case law on the question of what level of connectivity restoration is appropriate before a species is delisted. We then consider examples from a range of listed species to discover commonalities that can clarify key policy questions regarding connectivity restoration for endangered species.

The legal context of conservation reliance and connectivity

The language of the ESA and much subsequent agency practice emphasize an overarching goal of recovery of species and ecosystems in the wild (16 U.S.C. §1531 [a][3], see Supporting Information S1 for references to a goal of self-sustaining populations in recovery plans). In the 2009 case *Trout Unlimited v. Lohn* (559 F.3d 946, 9th Cir. 2009), the court cited both the ESA's preamble and the act's legislative history in concluding that "the ESA's primary goal is to preserve the ability of natural populations to survive in the wild." However, the relatively few court cases that have addressed this issue have not established clear precedent as to if and when exceptions can be made so that species can be delisted while still dependent on translocation. The most relevant case involves a 2007 U.S. FWS proposal to delist the Yellowstone grizzly bear (*Ursus arctos*), a carnivore with relatively limited dispersal range (Proctor *et al.* 2004; see Supporting Information S2 for additional information on species referenced in the text). FWS asserted that the Yellowstone grizzly bear is a conservation-reliant species because it requires active management (72 FR [Federal Register] 14987; see also Supporting Information S3 for a list of uses of "conservation-reliant species" in agency documents). FWS then relied on the CRS label to justify translocation of bears if efforts to reestablish natural connectivity between Yellowstone and more northerly bear populations were unsuccessful (72 FR 14896). The delisting rule was challenged in part over its potential future dependence on translocation. Although the rule was vacated on other grounds, the Montana District Court noted that "the concerns about long-term genetic diversity" (i.e., the need for translocation) did not warrant continued listing. It is unclear whether the court reached this conclusion because genetic concerns could be satisfactorily resolved by translocation following delisting, or simply because genetic concerns would not manifest within the "foreseeable future." The Services' (FWS and National Marine Fisheries Service) currently define the "foreseeable future" as extending as far into the future as predictions based on best available data can provide a reasonable degree of confidence (USDI 2009).

This definition, although not excluding consideration of long-term genetic threats, in practice allows wide latitude to the Services on whether to address such issues.

Unlike the grizzly bear, the gray wolf (*Canis lupus*) can disperse long distances (>800 km; Boyd *et al.* 1995). Although successful reintroductions in the mid-1990s led by 2005 to abundant wolf populations in the northern Rocky Mountains, delisting of the species was delayed in Wyoming, in part because the state's wolf management plan provided the species protection from overexploitation in only a small portion of the state. To ensure adequate dispersal between Yellowstone and other wolf populations, Wyoming subsequently agreed that wolves would receive more protection during peak dispersal season in limited areas. However, environmental groups sued to block the wolf delisting rule, in part because the state could resort to translocation if sufficient natural dispersal does not occur (77 FR 55530).

FWS referenced conservation reliance several times in rulemaking processes regarding wolves (Supplementary Information S3). Initially, the proposed delisting rule for wolves in the northern Rocky Mountains asserted that "[h]uman intervention in maintaining recovered populations is necessary for many conservation-reliant species and a well-accepted practice in dealing with population concerns (Scott *et al.* 2005)" (74 FR 15178, 76 FR 61816). In response to critical public comments, the FWS qualified and seemingly contradicted its earlier assertion by stating that the northern Rocky Mountain wolf population is "not expected to need or rely on human-assisted migration often, if ever, and these populations will not become "conservation-reliant" as defined by Scott *et al.* (2005, entire)" (77 FR 55565).

FWS's treatment of connectivity requirements in wolf populations contrasts with its consideration of connectivity for the wolverine (*Gulo gulo*), a carnivore species inhabiting the northern Rocky Mountains with dispersal abilities similar to the wolf (>500 km, Flagstad *et al.* 2004). In a recent draft proposal to list the wolverine as a threatened species, FWS found loss of natural connectivity a primary reason the species merited listing (78 FR 7886). Whereas for wolves, translocation was judged as consistent with delisted status, FWS found the need for such action warrants listing of wolverines as threatened.

The influence of ecological factors on a species' connectivity requirements

Ecological factors such a species' mating system, magnitude of population fluctuations, and migratory behavior (Table 1) affect the level of connectivity required for recovery. The most commonly proposed rule of thumb for connectivity suggests that at least one genetically effective migrant (but in some cases >10 migrants; Vucetich & Waite 2000) per generation into a population is necessary to minimize loss of polymorphism and heterozygosity (Allendorf 1983; Table 1, column 1). If the species' mating system causes individuals to have widely varying reproductive contributions, many individual "census migrants" are required to ensure that one migrant is genetically effective (produces at least one offspring in the recipient population) (Table 1, column 2). For example, among gray wolves, only a single pair of dominant individuals typically breeds within each pack.

The magnitude of population fluctuations experienced by a population also affects the role of connectivity in ensuring persistence. Invertebrates, such as the Karner blue (*Lycaeides melissa samuelis*) and Fender's blue butterfly (*Icaricia icaroides fenderi*), typically have short generation times and highly variable population sizes (USFWS 2003, 2010). This causes population connectivity in the form of demographic rescue (Brown & Kodric-Brown 1977) to be critical if the overall metapopulation is to persist in a dynamic natural environment (Table 1, column 3). Lastly, a species' migratory behavior may imply that a large proportion of population must successfully move between areas on an annual or generational basis (Table 1, column 4). For example, Pacific salmon from the Columbia River spend 3–4 years in the ocean, so up to a third of the adult cohort must return to the natal river each year.

We classified species (Table 1) by these three ecological factors and by whether connectivity restoration could be achieved by one-time measures (e.g., dam removal or operational changes) or necessitated continued intervention (e.g., invasive species control). Species affected by more than one factor (e.g., species with varying reproductive contributions inhabiting fluctuating environments) are categorized based on the factor imposing the highest connectivity requirements.

Lack of connectivity is an immediate demographic threat to migratory species such as Columbia River Pacific salmon. Recovery plans for species in this group (cell with horizontal line background; Table 1) propose translocation as necessary both before and after delisting, and do not include recovery actions that would restore natural migration. Although it is technically feasible to remove or mitigate barriers to migration such as hydroelectric dams, there are often enormous economic and legal impediments to doing so. Proposals to delist such species as dependent on translocation in perpetuity are in effect proposals to reconsider the ESA's normative assumption concerning the value society places on recovery of wild, self-sustaining populations.

Table 1 Categorization of species discussed in text in terms of degree of population connectivity (i.e., dispersal rate) required for recovery and socioeconomic cost required to restore connectivity. Species affected by more than one ecological factor are categorized based on the factor imposing the highest connectivity requirements

	Degree of connectivity required for recovery, due to life history or ecological factors			
Type of intervention necessary to restore connectivity	1. Lowest—One to several genetically effective migrants per generation	2. Low—Genetically effective migration where individuals have highly varying reproductive contribution	3. Medium—Demographic rescue due to variable population size	4. High—Migratory populations
One-time intervention (dam removal, habitat restoration, and regulatory remedy)	**Grizzly bear** **Concho water snake**	**Gray wolf** **Red-cockaded woodpecker**	**Fender's blue butterfly** **Karner blue butterfly**	**Columbia river salmon**
Continuing intervention (augmentation, translocation, control of invasive species)	**Wolverine** **Many species due to climate change**	**Southern Idaho ground squirrel** **Greater sage grouse**	**Black-footed ferret**	**Peary caribou**

A second group of species (cells with vertical line background; Table 1) may be nonmigratory, but nonetheless face long-term genetic threats from loss of connectivity. With the exception of reintroductions needed to restore extirpated populations, recovery plans for these species typically do not specify translocation prior to delisting but acknowledge that translocation may be necessary in the future if adequate genetic diversity is not present. Recovery plans may choose not to include recovery actions designed to reestablish natural dispersal because of significant societal opposition to the species' presence in dispersal zones (wolves and grizzly bears) or because of the economic costs of removing barriers to natural dispersal (Concho water snake [*Nerodia paucimaculata*]; USFWS 1993).

In the examples discussed above, connectivity restoration can be achieved via controversial or costly—but technically feasible—actions such as dam modification or removal, or via restrictions on overexploitation in habitat important for natural migration. For a final category of species (cells with gray background; Table 1), loss of historic levels of population connectivity is due to threats (e.g., invasive species, altered disturbance regimes, or climate change) that are extraordinarily challenging or impossible to fully remedy given current technical knowledge. For example, invasive species may operate synergistically with altered disturbance regimes to degrade an ecosystem to the point where restoration to the previous state may become difficult or impossible (Suding *et al*. 2004). In large portions of the western United States, sagebrush (*Artemisia* spp.) has been replaced by cheat grass (*Bromus tectorum*), an exotic annual bunchgrass. This trend, in turn, may trigger a shift toward more frequent fires that inhibit sagebrush recovery and limit dispersal of sagebrush-associated species such as the southern Idaho ground squirrel (*Spermophilus brunneus endemicus*) and greater sage grouse (*Centrocercus urophasianus*) (Knick *et al*. 2003). Climate change is projected to cause contraction or shifts in suitable habitat for a large proportion of the world's species (Thomas *et al*. 2004). For example, wolverines are threatened by loss of natural connectivity as climate change causes loss of their habitat, which is associated with snow-covered areas (78 FR 7886).

Discussion

Based on a review of recovery plans for a range of species (Table 1 and Table S2), we conclude that three contrasting types of challenges confront efforts to restore connectivity between populations of listed species: 1) threats that society avoids addressing because of the socioeconomic costs of doing so, 2) threats that society avoids addressing because they are not immediate, and 3) threats for which there is no permanent resolution at any cost given current technical knowledge. Distinguishing species affected by these three classes of threats is important because it allows us to distinguish normative questions from the technical obstacles to maintaining a self-sufficient population of a species that arise from the ecological attributes of a species and its stressors. These normative questions include both economic elements (what price society is willing to pay to protect biodiversity and how future risks are weighed against current costs), and ethical elements such as whether humans have an obligation to prevent species extinction (Callicott 2009).

As the Services attempt recovery of controversial and formerly widely distributed species such as gray wolves (Bruskotter *et al.* 2013), the agencies have gradually decreased their focus on recovering self-sustaining populations, a shift justified in some instances by reference to a broad definition of conservation-reliant species (74 FR 15178). This is consistent with reviews that found that most (Scott *et al.* 2010) or all (Goble *et al.* 2012) listed species fit the definition of conservation-reliant. Scott *et al.* (2010) classified most listed species as conservation-reliant in part because they included species requiring any of several types of ongoing conservation action, including efforts to 1) control other species, 2) control pollutants, 3) manage habitat, 4) control exploitation or human access, or 5) augment populations. However, these five types of actions have contrasting implications as to whether a species' status is self-sustaining in light of the ESA's mandate. The ESA anticipated that new regulations would be necessary to remedy threats such as overexploitation and pollutants, even for otherwise self-sustaining populations (Rohlf *et al.* in press). Similarly, because the continued persistence of almost all species requires regulatory limitations on human actions that destroy their habitat, the need for such protections should not preclude considering a population as self-sustaining. In contrast, a species that requires repeated population augmentation or intensive control of invasive competitor or predator species or disease does conflict with the paradigm of listing as a temporary stage followed by recovery of self-sustaining populations.

We agree with Scott *et al.* (2010) that conservation reliance is "a continuum encompassing different degrees of management," and acknowledge that some examples straddle the border between species that are or are not potentially self-sustaining in the wild. For example, although delisted populations of Karner blue and Fender's blue butterfly may not be dependent on translocation, they will require continued prescribed fire or fire surrogates to maintain suitable habitat. Because prescribed burning might not be necessary if conservation areas were sufficiently large to accommodate natural disturbance regimes (Pickett & Thompson 1978), such populations could become self-sustaining in the absence of humans. In most landscapes, however, disruption of natural disturbance processes can be remedied only by continued intervention to maintain fire-dependent ecosystems. Because prescribed fire is typically not a "species-specific" intervention (as specified in Scott *et al.* 2005's definition of CRS), but rather an ecosystem restoration tool, it is consistent with the ESA's mandate for conserving the ecosystems upon which listed species depend.

When the Services interpret the ESA's mandate using a definition of conservation-reliant species that include most or all listed species, they presuppose that costly or politically difficult obstacles to a species' self-sufficiency need not be fully addressed to delist species if these species could be secure given continued intensive management. Removing self-sufficiency from the threshold for considering a species recovered has several undesirable consequences. If natural dispersal is achievable (e.g., for highly vagile species such as the gray wolf or wolverine), delisting of populations still dependent on translocation rather than natural dispersal lowers the likelihood that delisted populations will meet other common recovery standards such as resiliency, redundancy, and representation (Shaffer & Stein 2000). Populations that require intensive management actions such as translocation by definition have lower resilience than those that are self-sustaining without such measures (Redford *et al.* 2011). Conversely, broad-scale connectivity is likely to increase the resilience of species to climate change by increasing adaptive potential (Lowe & Allendorf 2010).

The ESA of 1973 went beyond previous versions of the act in extending legal protections to vertebrate species facing extinction in only a portion of their range (Carroll *et al.* 2010). This had the overall effect of raising the threshold for recovery away from the earlier focus on preserving relict populations toward a more ambitious goal of geographically widespread recovery of self-sustaining populations and the ecosystems on which species depend. Species that are well-distributed outside of core habitat (e.g., in dispersal corridors) are more likely to achieve the representation goals suggested by the ESA's protection for species imperiled in a "significant portion of [their] range" (Carroll *et al.* 2010).

We advocate use of a narrower and more explicit definition of conservation reliant species, which would be limited to those species that lack the ability to persist in the wild in the absence of direct and ongoing human manipulation of individuals or their environment (Rohlf *et al.* in press). This definition distinguishes those species which would persist and even thrive if humans were to vanish from the landscape (e.g., gray wolf) from those whose only hope of persistence lies in human intervention (e.g., black-footed ferret threatened by introduced plague).

The complex question of whether species permanently threatened by invasives, altered disturbance regimes, and climate change should be eventually delisted or remain under long-term federal management involves both normative and technical issues. Ultimately, resolution of the normative issues hinges on resolving contrasting visions of the meaning of ecological recovery in the Anthropocene Epoch. A definition of conservation-reliant species that clearly distinguishes technical from values-based judgments will allow society to better address the normative debate over what cost should be borne to protect biodiversity, while separately addressing the urgent biological challenges that novel stressors such as climate change and invasive species pose for ecosystem and species restoration.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

S1. Examples of references to the goal of self-sustaining populations in recovery planning documents.

S2. Table of attributes of species mentioned in text that provide examples of consideration of connectivity in recovery planning.

S3. Use of the term "conservation-reliant species" by the US Fish and Wildlife Service in recovery and delisting documents.

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How Species Distribution Models (SDMs) can improve decision-making in conservation planning

Working Group
2016 CBSG Annual Meeting
Puebla, Mexico

How Species Distribution Models (SDMs) can improve decision-making in conservation planning

CONVENORS: Katia Maria P. M. B. Ferraz (Forest Science Department, ESALQ/USP)

AIM: To present and discuss the potential use of Species Distribution Models to support decision-making in conservation planning.

BACKGROUND: Species Distribution Models (SDMs) are an important tool often used to assess the relationship between a species, its distribution, and the environmental conditions. They integrate species occurrence records and environmental variables to develop environmental suitability maps for a species in space and time. SDMs are built for the following purposes: 1) to map and update the current species distribution, 2) to evaluate the environmental suitability of the landscape for the species occurrence, 3) to identify corridors and priority areas for conservation, 4) to identify key areas for conservation efforts, 5) to identify gaps in sampling database, 6) to identify new potential areas for species occurrence, and 7) to improve the assessment of endangered species. 8) to supplement Population viability analysis. When successfully used SDMs can influence policy development and support public actions for conservation and management decisions.

SDM are built before and during the workshop. They require participants provide exact GPS locations of the species. Map construction should begin a year to six months before the workshop. It is key to have a preliminary map to show at the beginning of the workshop so that it can be further discussed by all the participants, many maps are created during the workshop with participation input and discussions.

CBSG Brasil has used SDMs in the Jaguar Action Plan (2009) and the Chacoan Peccary (2016). Furthermore this tool has been fully integrated by the Government authorities for the planning of endangered Carnivores in Brazil. This tool can potentially be used for conservation planning of many of the species CBSG is involved with.

PROCESS: The working group will start by a presentation of the concepts involved in species distribution modeling. A brief review of the use of SDMs in workshops will be presented, emphasizing the applications of SDM for conservation planning. Opportunities on how this tool could improve species conservation planning for CBSG network will be discussed. Finally, we will brainstorm what further needs might be addressed for bridging the gap among researchers, modelers and decision-makers in favor of species conservation and how this could help the CBSG work.

Species Distribution Models: Ecological Explanation and Prediction Across Space and Time

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climate change, invasions, niche, predict, presence-only, spatial

Abstract

Species distribution models (SDMs) are numerical tools that combine observations of species occurrence or abundance with environmental estimates. They are used to gain ecological and evolutionary insights and to predict distributions across landscapes, sometimes requiring extrapolation in space and time. SDMs are now widely used across terrestrial, freshwater, and marine realms. Differences in methods between disciplines reflect both differences in species mobility and in "established use." Model realism and robustness is influenced by selection of relevant predictors and modeling method, consideration of scale, how the interplay between environmental and geographic factors is handled, and the extent of extrapolation. Current linkages between SDM practice and ecological theory are often weak, hindering progress. Remaining challenges include: improvement of methods for modeling presence-only data and for model selection and evaluation; accounting for biotic interactions; and assessing model uncertainty.

INTRODUCTION

Throughout the centuries humans have observed and recorded consistent relationships between species distributions and the physical environment. Whilst early scientific writings were largely qualitative (Grinnell 1904), numerical models are now widely used both for describing patterns and making predictions. These numerical techniques support a rich diversity of applications, arguably with varying degrees of success. Published examples indicate that species distribution models (SDMs) can perform well in characterizing the natural distributions of species (within their current range), particularly when well-designed survey data and functionally relevant predictors are analyzed with an appropriately specified model. In such a setting, models can provide useful ecological insight and strong predictive capability. By contrast, applications that fit models for species not substantially in equilibrium with their environment, that extrapolate in time or space, and/or use inadequate data are much more challenging, and results are more equivocal.

Our aim is to review the history and current status of the SDM literature, exploring applications spanning biological realms and scientific disciplines. We define an SDM as a model that relates species distribution data (occurrence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations (for key steps, see Sidebar, Basics of Species Distribution Modeling). The model can be used to provide understanding and/or to predict the species' distribution across a landscape. Names for such models vary widely. What we term SDMs have also been called (sometimes with different emphases and meanings): bioclimatic models, climate envelopes, ecological niche models (ENMs), habitat models, resource selection functions (RSFs), range maps, and—more loosely—correlative models or spatial models. We include these, but exclude models that are mechanistic or process-based (see Kearney & Porter 2009 for a review), or that predict community-level features such as community composition and species turnover or richness (see Ferrier & Guisan 2006 for a review).

Reviews of SDM literature include those of Guisan & Zimmermann (2000), Stauffer (2002), Guisan & Thuiller (2005), Richards et al. (2007), and Schröder (2008). Several books have either been recently published or are in preparation (Franklin 2009; A.T. Peterson & A. Guisan, personal communication). Instructional texts and training opportunities in species modeling are now available, including online texts (Pearson 2007) and university courses and workshops.

In light of these resources, we provide only a brief review of the technical aspects of SDMs and do not give methodological advice, concentrating instead on historical and cross-disciplinary features. In particular, we probe the motivations and concepts inherent in different approaches, attempting to identify commonalities that are widely relevant, regardless of discipline boundaries. We explore the diverse uses of SDMs (across environments, spatial and temporal scales, and modeling techniques), including earlier emphases on understanding ecological relationships

BASICS OF SPECIES DISTRIBUTION MODELING

Key steps in good modeling practice include the following: gathering relevant data; assessing its adequacy (the accuracy and comprehensiveness of the species data; the relevance and completeness of the predictors); deciding how to deal with correlated predictor variables; selecting an appropriate modeling algorithm; fitting the model to the training data; evaluating the model including the realism of fitted response functions, the model's fit to data, characteristics of residuals, and predictive performance on test data; mapping predictions to geographic space; selecting a threshold if continuous predictions need reduction to a binary map; and iterating the process to improve the model in light of knowledge gained throughout the process (Elith & Leathwick 2009).

and the more recent focus on prediction. Finally, we identify and examine several emerging issues. Our limit of 120 references means that many interesting and relevant pieces of work inform our review but are not explicitly mentioned, so we also provide a **Supplemental Literature Cited** (follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**) for download, listing useful papers for each topic.

Supplemental Material

THE SPECIES MODELING LANDSCAPE: ITS DEVELOPMENT AND DIVERSITY

Conceptual and Technical Underpinnings

Broadly speaking, contemporary SDMs combine concepts from ecological and natural history traditions with more recent developments in statistics and information technology. The ecological roots of SDMs belong in those early studies that described biological patterns in terms of their relationships with geographical and/or environmental gradients (e.g., Grinnell 1904, Murray 1866, Schimper 1903). Moreover, research that highlighted the individualistic responses of species to their environment (e.g., for vegetation, see Whittaker 1956; and for birds, see MacArthur 1958) provided the strong conceptual argument for modeling individual species rather than communities.

Modern quantitative modeling and mapping of species distributions emerged when two parallel streams of research activity converged. On the one hand, field-based ecological studies of species-habitat associations, at first reliant largely on linear multiple regression and discriminant function analyses (Capen 1981, Stauffer 2002), benefitted from new regression methods that provided coherent treatments for the error distributions of presence-absence and abundance data. Generalized linear models (GLMs) enabled pioneering regression-based SDMs that had much more sophistication and realism than was possible earlier (e.g., see Austin's work in 1970s and 1980s, cited in Austin 1985). The key structural features of GLMs (non-normal error distributions, additive terms, nonlinear fitted functions) continue to be useful and are part of many current methods including RSFs (Manly et al. 2002) and maximum entropy models (MaxEnt; Phillips et al. 2006).

In parallel, rapid methodological advances in physical geography provided new data and information systems. New methods allowed robust and detailed preparation of digital models of the Earth's surface elevation, interpolation of climate parameters, and remote sensing of surface conditions in both marine and terrestrial environments (see **Supplemental Literature Cited**). These greatly enhanced SDM capabilities by providing estimates of environmental conditions across entire landscapes, including retrospectively at surveyed locations. Alongside these advances, the development of geographic information systems (GIS) provided important tools for storing and manipulating both species records and environmental data (see Foody 2008; and Swenson 2008, who include accessible introductions to GIS). The gains are easily taken for granted, but stand in stark contrast to the resources available to early ecologists who usually only had simple measurements of location (e.g., latitude, longitude, and elevation or depth), and sometimes of local site conditions (e.g., slope, drainage, geology).

Early approaches to modeling species distributions within GIS used simple geographic envelopes, convex hulls, and environmental matching (e.g., Nix 1986; and see Section below, Methods for Modeling). SDMs as we think of them today emerged when the new statistical methods from field-based habitat studies were linked with GIS-based environmental layers. In one of the earliest applications of this integrated approach, Ferrier (1984, cited in Ferrier et al. 2002) applied GLMs (logistic regression) to predict the distribution of the Rufous scrub-bird using known locality records for the species, and remotely mapped and modeled environmental variables.

Models across Terrestrial, Freshwater, and Marine Environments

Spatial autocorrelation: when the values of variables sampled at nearby locations are not independent from each other

Species distributions have been modeled for terrestrial, freshwater and marine environments, and across species from many biological groups (see **Supplemental Literature Cited**). Terrestrial vascular plant analyses were prevalent in early years and are still common, along with studies of terrestrial animals (including invertebrates); marine and freshwater applications were relatively rare until the past 5–10 years, and soil-based organisms are still only infrequently modeled.

SDMs from these diverse fields display commonalities and contrasts, with differences in mobility between species prompting some major differences in modeling approach. When a species is sessile it is relatively easy to characterize its environment, even including the wider influence of landscape (e.g., the water flowing into a site can be modeled using topographic information). By contrast, mobile species tend to intermittently use resources that are patchily distributed across a landscape. Defining the environments sampled by such species at any given location can be challenging, particularly for some combinations of mobility and life-history characteristics. Models for mobile species with small home ranges are often fitted using methods similar to those for sessile organisms, perhaps with focal predictors summarizing information from the near-neighboring landscape (Ferrier et al. 2002). In contrast, models for highly mobile species (e.g., diadromous fish) need to include movement or access-related descriptors (e.g., stream-based distance to coast; Leathwick et al. 2008). RSFs or related techniques are useful for species where the important distinction is between locations that are "available" (can be reached by the animal, used or not) versus those that are "used" (for example, habitat selection studies for birds; Jones 2001).

Detection of mobile species can be problematic. In aquatic studies, observations are often treated as probabilities of capture and analyzed using similar methods as for sessile species, sometimes including temporal predictors to accommodate seasonal variation in catchability/presence (Venables & Dichmont 2004). Alternatively, specialized modeling techniques have been developed to account for imperfect detection (e.g., MacKenzie et al. 2002, Royle et al. 2004).

Historic differences in the way data are collected also create different emphases across disciplines. Plant quadrats are usually regarded as statistically independent samples provided they are sufficiently geographically separated. Continuous tow sampling is used for some marine organisms, resulting in loss of independence between samples located along the same tow. Similar problems exist for terrestrial transect samples and for samples from contiguous stream reaches. Such data have prompted use of mixed models or other methods for dealing with pseudoreplication and spatial autocorrelation (Dormann et al. 2007, and **Supplemental Literature Cited**).

Spatial Scale

Scale is relevant to the distributions of both species and environments, and comprises both grain and extent. The extent (or domain) usually reflects the purpose of the analysis. For instance, macroecological and global change studies tend to be continental to global in scope (e.g., Araújo & New 2007), whereas studies targeting detailed ecological understanding or conservation planning tend toward local to regional extents (Fleishman et al. 2001, Ferrier et al. 2002). Grain usually describes properties of the data or analysis—often the predictor variables and their grid cell size or polygon size, but also the spatial accuracy and precision of the species records (Dungan et al. 2002, Tobalske 2002). Grain should be consistent with the information content of the data, though in practice this is not always feasible, e.g., grids sometimes have to be defined at finer resolutions than the underlying data for consistency across predictors. A number of researchers have addressed the implications of using coarse- versus fine-scale data in SDMs (e.g., Ferrier & Watson 1997 and **Supplemental Literature Cited**), generally indicating that effects depend on the spatial accuracy of the data, characteristics of the terrain and species, and the intended application.

Conceptually there is no single natural scale at which ecological patterns should be studied (Levin 1992). Rather, the appropriate scale is dictated by the study goals, the system, and available data. Some species modelers emphasize notions of hierarchy in conceptualizing the influences of environment on species distributions (Allen & Starr 1982, Cushman & McGarigal 2002, Pearson & Dawson 2003). In terrestrial systems climate dominates distributions at the global scale (coarsest grain, largest extent), whereas at meso- and toposcales (a few to hundreds of kilometers) topography and rock type create the finer-scale variations in climate, nutrient availability, and water flows that influence species (e.g., Mackey & Lindenmayer 2001). Similarly, in freshwater ecosystems, hierarchical scales from watersheds to reaches to microhabitats all affect distributions (e.g., Poff 1997). Alternatively, scale can be considered from the species' viewpoint using the concept of selection orders (selection of microsite, patch, home range, population block, and geographic range) and focusing on the ways in which mobile animals interact with the spatial arrangement of environments (Addicott et al. 1987).

Although these are long-standing concepts, there is as yet little consensus on how to deal with scale disparities when fitting SDMs. Several methods, mostly from landscape ecology, focus on describing scales of pattern in ecological data. These include lacunarity, spectral analysis, and wavelet-coefficient regression (Saunders et al. 2005 and **Supplemental Literature Cited**). They provide useful tools for evaluating the inherent structure in data but their use for prediction seems underdeveloped. More commonly, analysts impose scales through data choice or model structure. Many do this unconsciously, using predictors likely to both vary and have effects on biota at markedly different spatial scales, but without explicit testing or discussion of the effect that this has on their results. Some deliberately construct a set of scale-dependent predictors to represent factors affecting the distribution of the target species at more than one spatial scale (Beever et al. 2006). Alternatively, several recent analyses explicitly create models with hierarchical structure, e.g., with different predictors separated into submodels, so that relationships at disparate scales can be modeled and perhaps combined (Mackey & Lindenmayer 2001). Some Bayesian approaches allow explicit hierarchies and can include process-related elements that might operate across scales (Latimer et al. 2006). Alternatively, hierarchical regression models ("mixed models") allow nested structures of data (Beever et al. 2006), and hierarchical canonical variance partitioning can be used to provide a structured decomposition of variance across scales (Cushman & McGarigal 2002). Unfortunately, the relative merits of these different approaches appear untested both theoretically and practically, and it remains unclear whether more complex hierarchical approaches achieve as much or more than a well-constructed set of predictors used in a sensibly fitted nonhierarchical model. There is ample opportunity to progress knowledge on this topic, particularly with a coherent treatment of theory, data requirements, and model structure.

Supplemental Material

The Interplay of Geographic and Environmental Space

One important concept central to SDMs is the distinction between geographic and environmental space. Whereas geographic space is defined by two-dimensional map coordinates or three-dimensional digital elevation models, environmental space is potentially multi-dimensional, defined by some set of environmental predictors (**Figure 1**). When an SDM is fitted using solely environmental predictors it models variation in occurrence or abundance of a species in environmental space. Any calculation of predictions for new sites is also based on the species' locations in environmental rather than geographic space. Importantly, such a model is effectively ignorant of geographic proximity even when predictions are mapped into geographic space. Mapped

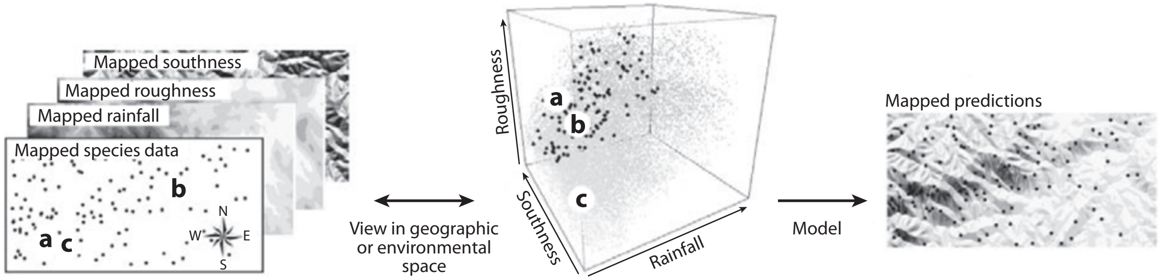

Figure 1

The relationship between mapped species and environmental data (*left*), environmental space (*center*), and mapped predictions from a model only using environmental predictors (*right*). Note that inter-site distances in geographic space might be quite different from those in environmental space—*a* and *c* are close geographically, but not environmentally. The patterning in the predictions reflects the spatial autocorrelation of the environmental predictors.

predictions show clustering and appear spatially informed, but in SDMs with solely environmental predictors this simply reflects the spatial autocorrelation of environment (**Figure 1**).

We note, as an aside, that some SDMs are purely geographic. Examples include geographic range maps, convex hulls, kernel density estimators, kriging, and models of species richness in geographic space. Their use sometimes indicates a belief that geographic processes are dominant over environmental ones, or reflects extremely limited availability of environmental predictors or species data. At most scales and for most species, however, evidence points to the importance of environment in structuring distributions, meaning that inclusion of environment in SDMs is important.

Spatial autocorrelation is an important aspect of the interplay between environmental and geographic space. Geographic clumping of species can result from their response to spatially autocorrelated environmental factors and/or the effects of factors operating primarily in geographic space (Legendre 1993). Where the distribution of a species is largely determined by environmental factors, a properly specified model fitted using an adequate set of predictors will display minimal spatial autocorrelation in its residuals.

Strong residual geographic patterning generally indicates that either key environmental predictors are missing (Leathwick & Whitehead 2001), the model is mis-specified (e.g., only linear terms where nonlinear are required), or geographic factors are influential (Dormann et al. 2007, Miller et al. 2007). The latter include glaciation, fire, contagious disease, connectivity, movement, dispersal, or biotic interactions. For these, the model might require additional relevant predictors, geographic variables and/or realistic estimates of dispersal distances or movement (Ferrier et al. 2002; see **Supplemental Literature Cited**). Alternatively, some modelers enhance SDMs with process-based information to jointly characterize the environmental and spatial influences on distribution (e.g., Rouget & Richardson 2003, Schurr et al. 2007; and see below). Geographic influences in aquatic environments are particularly challenging to model: marine currents can directionally impede dispersal, and in river networks dispersal is generally restricted to the river network and effective distances are strongly influenced by flow directions.

Testing for spatial patterns both in the raw data and model residuals should be part of any SDM study. Methods include use of Moran's I or Geary's c to measure the amount of spatial autocorrelation, addition of local proximity variables to an environmental model to test for residual spatial structure, or use of LISA (local indicator of spatial autocorrelation) to estimate the contribution of each sampling unit to the overall measure of spatial autocorrelation (Dormann et al. 2007, Miller et al. 2007, Rangel et al. 2006).

Alternatively, some approaches explicitly model spatial autocorrelation effects within the modeling process (Rangel et al. 2006). Overall these are used relatively infrequently, although they receive some emphasis in macroecology. One technique is to fit a surface characterizing the geographic pattern (e.g., a trend surface), which is then used as a predictor in the model, sometimes with other environmental predictors used to model the remaining variation (Rangel et al. 2006). Although this describes and controls for geographic pattern it is not fully integrated into the modeling process, and it introduces the risk of confusing geographic effects with spatially autocorrelated environmental terms. More integrated and coherent methods are reviewed in papers detailed in the **Supplemental Literature Cited**; these include autoregressive methods, geostatistical methods based around kriging, generalized linear mixed models, generalized estimating equations, and geographically weighted regression. Currently these methods are more difficult to implement than standard techniques so they are under-utilized, but they have appealing properties and further development might promote their wider use.

Supplemental Material

None of the methods reviewed here provide a strong basis for distinguishing between spatial and environmental effects, though a careful interpretation of the model and its predictions might provide useful insights. Erroneous use of geographic terms to correct for either missing environmental predictors or wrongly specified models is likely to result in poor predictive ability, especially when extrapolating to new regions or times (Dormann et al. 2007, and see below).

Using Models for Explanation versus Prediction

Trends in SDM usage reveal subtle but important shifts in intention. Many early studies had a strong ecological focus, seeking insight, even if indirectly, into the causal drivers of species distributions (Mac Nally 2000). SDMs are still regularly used for such purposes, particularly in quantitative ecological studies (Leathwick & Austin 2001) and evolutionary biology (Graham et al. 2004b). With growing sophistication of modeling algorithms, greater availability of spatially extensive environmental data, and strong demand for mapped products for conservation and land management, an increasing number of papers now focus on predicting distributions (e.g., Hamazaki 2002, and **Supplemental Literature Cited**). Ecological understanding is, of course, still critical to such applications, particularly in the selection of predictors and models and the interpretation of results.

Prediction is used in two main ways. First, predictions are made to new sites within the range of environments sampled by the training data and within the same general time frame as that in which the sampling occurred. We call this model-based interpolation to unsampled sites. Typical applications include global analyses of species distributions, mapping within a region for conservation planning or resource management, and identifying suitable habitat for rare species (Guisan & Thuiller 2005). Such interpolation is usually reliable enough for effective decision making provided that the data and model are reasonable, and any correlations between predictor variables are stable across the geographical domain for which predictions are made.

Training data: those data (species records and predictors) used to fit the model

Second, models are also used to predict to new and unsampled geographic domains and/or future or past climates. The environments in these new times and places need to be carefully assessed, particularly for new combinations of predictor values or for predictor values outside their original ranges in the training data. Prediction to new geographic regions is a special case and has been termed transferability, but often without clear information on the environmental similarities and differences between the model fitting and prediction regions (see **Supplemental Literature Cited**). Prediction to new environments is generally termed extrapolation or forecasting (Araújo & New 2007, Miller et al. 2004). It is inherently risky because no observations of species occurrence are available from the training data to directly support the predictions (see sidebar, Using Models

USING MODELS FOR EXTRAPOLATION

Key assumptions of SDMs are that species are at equilibrium with their environments, and that relevant environmental gradients have been adequately sampled. Use in non-equilibrium settings (e.g., invasions, climate change) usually involves species records unrepresentative of new conditions, and prediction to novel environments. Critics have identified several problems with SDMs and extrapolation, including: different (combinations of) environmental factors may limit distributions or biotic interactions may change substantially in the new context; outcomes will be influenced by genetic variability, phenotypic plasticity and evolutionary changes; dispersal pathways are difficult to predict (De Marco et al. 2008, Dormann 2007, Midgley et al. 2006). However, correlative models currently remain one of few practical approaches for forecasting or hindcasting distributions. We expect that SDMs have a contribution, providing methods and results are rigorously assessed.

Several approaches can improve the use of models for extrapolation, and reduce or expose errors. Differences between the sampled and prediction spaces can be quantified (e.g., similarity measures, Williams et al. 2007; **Figure 2**); species data can be weighted to represent the invasion process or the sample bias of records (Phillips et al. 2009); dispersal can be incorporated using estimates of dispersal rates (Midgley et al. 2006), models of dispersal (Schurr et al. 2007), or by linking SDMs to cellular automata (Iverson et al. 2009); evolutionary change might be estimable and included in models (Hoffmann & Kellermann 2006). Predictions can be tested through retrospectives (Araújo et al. 2005). Differences between models can be reduced by consensus (Pearson et al. 2006), used for discovering why predictions differ (Elith & Graham 2009), or quantified to inform risk analyses and decision making. Alternatively, SDMs can be linked with landscape, population, and physiological models representing processes of change (Kearney & Porter 2009, Keith et al. 2008). Substantial challenges remain, especially those related to how biotic interactions are likely to change and how they can be modeled.

for Extrapolation). As an aside, it is worth recognizing that some researchers exclude interpolation from their definition of prediction, reserving prediction for extrapolation to new conditions or solely for inference from causal models (Berteaux et al. 2006).

A focus on prediction rather than explanation has implications for the way that models are fitted and evaluated. Models for prediction need to balance specific fit to the training data against the generality that enables reliable prediction to new cases. Information criteria such as AIC (Akaike's Information Criterion) address this balance by trading off explained variation against model complexity. Alternatively, data mining and machine learning methods use cross-validation or related methods to test model performance on held out data, both within the model-fitting process, and for model evaluation (Hastie et al. 2009). We anticipate expanding interest in machine learning methods for prediction. The special case of extrapolation needs more attention, so that robust model fitting and testing methods can be developed.

The Need for Functionally Relevant Predictors

Some SDM studies include many candidate predictors, motivated by their ready availability and a belief that the model will identify those that are important. By contrast, a number of modelers have argued strongly for use only of predictors that are ecologically relevant to the target species. Mac Nally (2000) comments: "Statistical tinkering, which really (is) what the entire domain of model selection is about, can never be a substitute for intelligent prior selection of independent variables that may influence the dependent variable. . . . The variable-selection process will be substantially improved—and, therefore, the inferences too—if that process involves building upon existing knowledge and theory."

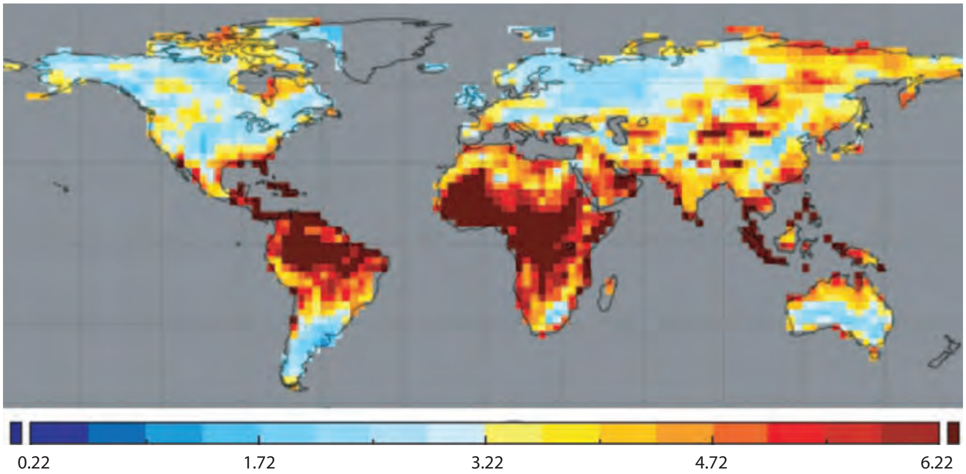

Figure 2

Dissimilarities between 2000 A.D. climates and those (within 500 km of a target site) estimated for 2100 A.D. using multimodel ensembles for the A2 scenario of the IPCC fourth assessment report. High dissimilarities (*red*) indicate the risk of regionally novel climates (from Williams et al. 2007, used with permission).

Austin and Smith (1989, cited in Austin 2002) provide an early example of a deliberate and rigorous approach to predictor selection, distinguishing between resource, direct and indirect gradients. Indirect gradients in terrestrial studies are represented by (distal) predictors such as elevation, which rarely directly affect species distributions. Instead, they are correlated, and sometimes only loosely, with more functionally relevant (proximal) predictors such as temperature, rainfall and solar radiation. In marine systems depth is an indirect proxy for several proximal predictors: temperature and its variability, salinity, light, pressure, and the availability of elements (e.g., calcium).

Use of more ecologically relevant predictors is increasingly possible as interpolated estimates of climate factors and remotely sensed data are more readily available. Franklin (2009, Chapter 5) reviews these predictors comprehensively. Terrestrial examples include Box's analysis of global plant distributions (Box 1981), Zimmermann & Kienast's (1999) use of growing degree days for modeling Swiss tree distribution, and several studies using water balance models of varying sophistication to estimate water availability (see Austin 2007 for a review). Leathwick et al. (2008) constructed functionally relevant predictors of freshwater fish distributions, including estimates of catchment-driven variability in local flow, and access to and from the sea for migratory species. Maravelias & Reid (1997) used surface and seafloor temperature, salinity, and zooplankton availability to predict herring abundance. Remote sensing also offers data that can be adapted to represent proximal predictors—for instance, for approximating habitat complexity for birds (Vierling et al. 2008; St-Louis et al. 2009). Despite these advances, many studies appear to use only data that are readily at hand, failing to explain the relevance of selected predictors, and likely missing important ecological drivers.

While it is logical that ecologically relevant predictors are necessary for explanation and insight, it could be argued that any predictors will suffice if prediction is the sole aim. Multiple lines of evidence suggest otherwise. Predictions show patterned residuals when variables are inadequate, and can be improved substantially by using more proximal predictors (Leathwick & Whitehead 2001), and small data sets and model selection difficulties mean that models can select irrelevant variables (Mac Nally 2000, Steyerberg et al. 1999). Extrapolation in space or time will be particularly error-prone if only distal predictors are used, because the correlations between these and the proximal drivers vary both in space and time (Austin 2002).

Methods for Modeling: Mathematical Form and Fitting Procedures

Many methods are used to fit SDMs (Franklin 2009). Although those chosen for particular studies often reflect the nature of the data and/or the question being addressed, some differences between disciplines appear to be driven by "accepted usage," for example, the continued use of GLMs in marine studies and the common use of artificial neural nets (ANNs) for freshwater fish. Historically, the methods used to analyze data sets gathered with intention and design have tended to differ from those using collated records of species records (presence-only data compiled largely opportunistically), but methods are now increasingly convergent. Here we present only a few main points related to analytical approaches; see the **Supplemental Literature Cited** for further reading.

Supplemental Material

Techniques for modeling very sparse data include convex or alpha hulls (Burgman & Fox 2003), and—where expert opinion is considered more reliable than species records—maps drawn by hand, GIS overlays (combinations of mapped data), or habitat suitability indices (HSIs) (Elith & Leathwick 2009, Franklin 2009).

Some of the earliest numerical SDMs used environmental envelope models to describe the species' range in relation to a set of predictors (Box 1981, Nix 1986). These define the hyper-rectangle that bounds species records in multi-dimensional environmental space, weighting each predictor equally. Such models can be combined with spatially comprehensive environmental data to map likely occurrences, and methods exist for dealing with outliers, e.g., by quantifying percentiles of the distribution. Related techniques (detailed in Franklin 2009) use distance metrics such as the Gower metric or Mahalanobis distance to predict the environmental similarity between records of occurrence and unvisited sites.

Regression-based models extend envelope and similarity approaches by modeling variation in species occurrence or abundance within the occupied environmental space, and selecting predictors according to their observed importance. GLMs were commonly used in early analyses of presence-absence and count data, often with simple additive combinations of linear terms. As the common occurrence of nonlinear species' responses to environment was recognized (Austin et al. 1990), more studies included quadratic, cubic, or other parametric transforms. Generalized additive models (GAMs) are similar to GLMs but use data-defined, scatter plot smoothers to describe nonlinear responses. They have provided useful additional flexibility for fitting ecologically realistic relationships in SDMs.

Regression methods are widely used by ecologists; they can be extended to model complex data types including abundance data with many zeros, records with imperfect detection of presence, and structured samples of data such as sites nested within forest fragments (see **Supplemental Literature Cited**). More generally, many SDM methods are regression-like, assuming that a species' occurrence or abundance can be modeled using additive combinations of predictors, and sometimes also including manually selected terms representing interactions between predictors. Bayesian alternatives are also available (Latimer et al. 2006), bringing sophisticated model-fitting abilities that can incorporate process-based information (e.g., rates of spread; Hooten et al. 2007). However these can require specialized mathematics and programming, and this currently hinders wider uptake despite apparent advantages.

As SDM applications focused more on prediction, researchers looked to methods developed especially for prediction, including those in the machine learning and data mining communities. Examples include ANNs (Olden et al. 2008), multivariate adaptive regression splines (Moisen

& Frescino 2002), classification and regression trees and ensembles of trees (random forests: Prasad et al. 2006; boosted regression trees: Elith et al. 2008), genetic algorithms (Stockwell & Peters 1999), support vector machines (Drake et al. 2006), and maximum entropy models (Phillips et al. 2006). Some of these provide well-controlled variable selection and coefficient estimation, and several are capable of automatically detecting and fitting interactions between predictors. As a consequence their predictive performance may exceed that of more conventional techniques (Elith et al. 2006). While the complex and sometimes "black-box" nature of these techniques has perhaps limited their use, particularly for studies focusing on ecological insight, tools for visualizing and summarizing these models in ways relevant to ecologists are increasingly available. The other immediate constraint to uptake of machine learning techniques is that they are rarely taught in ecological courses, but we expect that to change rapidly in coming years.

Phylogeography: the spatial arrangements of genetic lineages, especially within and among closely related species

Modeling into the Past or the Future

SDMs always have some degree of temporal dimension or reference reflecting their use of species and environmental data gathered over particular time periods (Schröder & Seppelt 2006). However, whereas traditional applications of SDM generally assume a constant and current time frame (even if integrated over some months or years), numerous studies now include temporal change. These target questions relating to recent changes in distributions from disturbances including fire and land use change, the spatial and environmental correlates of speciation events, hybrid zones, paleo-distributions and phylogeography, and forecasts of invasions and distributions under climate change. A key distinction is between those applications requiring predictions in a time period matching that of the training data, compared with those using a model of the current distribution of a species to either hindcast or forecast distributions at some other point in time.

SDMs can explicitly include time as a predictor in the model. For instance, the **Supplemental Literature Cited** lists examples using time-varying food resources in an RSF for grizzly bears, and estimates of time since disturbance for modeling pioneer species in a fire-prone landscape. Models also use retrospective data, e.g., combining historical survey and remnant vegetation records to model pre-clearing vegetation distribution, or modeling pollen records with paleoclimatic data.

SDMs with an evolutionary focus evaluate spatial patterns of inter- and intra-specific variation (see Kozak et al. 2008, Richards et al. 2007, Swenson 2008 for reviews). For instance, the **Supplemental Literature Cited** presents examples that use phylogenetic data and climate envelopes to explore speciation mechanisms in frogs, assess the role of climate in maintaining the location of hybrid zones in birds, and explore species delimitation in salamanders.

Those applications using models to make predictions for time frames substantially different from those of the training data generally require extrapolation in environmental space (see sidebar, Using Models for Extrapolation). Models of the biotic repercussions of global warming and land-use changes require forecasting (Araújo & New 2007, Fitzpatrick et al. 2007, Thuiller et al. 2005), and hindcasting is used for exploring the effects of climate on evolutionary patterns (Kitchener & Dugmore 2000, Kozak et al. 2008, Ruegg et al. 2006). However, understanding and assessing the uncertainties inherent in model predictions for these applications is particularly problematic.

THE SPECIES MODELING LANDSCAPE: HOTSPOTS, RARITIES, AND DIRECTIONS OF CHANGE

Here we identify areas undergoing either rapid development or receiving particularly strong interest, and also explore some less commonly researched topics.

Linking Ecological Theory and Distribution Modeling

Although good linkage between model assumptions and underlying theories and concepts might be reasonably expected in any scientific discipline, several researchers have criticized the SDM community for its lack of theoretical grounding (e.g., Austin 2002, Jiménez-Valverde et al. 2008). In a penetrating critique Huston (2002) states, "[C]ontinued development of rigorous statistical approaches to analyzing habitat data, assisted by the spread of easy computation . . . has been unaccompanied . . . by corresponding development of rigorous logic." Consequences include poorly informed use of models, slow improvement in the ecological realism of methods, and limited uptake of SDM methods and results by other disciplines in which they could be relevant. For instance, recent commentaries by macroecologists and biogeographers (Gaston et al. 2008, Sagarin et al. 2006) point to many interesting theoretical questions about species ranges, but barely refer to insights from the SDM literature, possibly because SDM practitioners largely fail to explicitly identify the broader relevance of their work.

One exception to this general neglect of theoretical issues is a recent debate on the relationship between SDMs and the species niche (see sidebar, The Name Niche Modeling). Unfortunately, this discussion has been plagued by semantic, conceptual, and technical difficulties, and has yet to reach consensus. In common with Austin (2002), Huston (2002) and others, we believe that a more wide-ranging approach to linking theory, data, and models would bring substantial benefits. Important issues additional to niche concepts include the degree of equilibrium in species distributions; how to identify, construct and test functionally relevant predictors; whether current, predominantly

THE NAME NICHE MODELING

Early efforts to relate SDMs to the niche concept were cautious, acknowledging limitations in both data and models. For instance, to Booth et al. (1988), natural distribution data described only the "realized niche," i.e., the competition-mediated distribution. Similarly, Austin et al. (1990) and Austin (2002) described their probabilistic models of eucalypt distribution as an approximation to the "qualitative environmental realized niche," perhaps with sink habitats also included.

Peterson and Soberon have argued for conceptual distinctions between ecological niche models (ENMs) and SDMs, restricting "SDM" to those models containing biotic or accessibility predictors and/or being limited in spatial extent (Peterson 2006). Whilst the links between their framework (Soberon 2007), data types, and models are not yet entirely clear, it appears that they include all environment-based models in their definition of ENMs, particularly (though it's not clear whether exclusively) if absence data are not used. They imply that ENMs get closer to modeling the fundamental niche, but we find this interpretation problematic. In particular, they fail to explain how the methods they class as ENMs technically overcome the well recognized difficulty in describing the fundamental niche from landscape observations of species occurrence.

Other attempts to define what is being modeled have not achieved consensus, partly because definitions of niches are not consistent, and data, methods, and scales overwhelmingly variable (Soberon 2007, Franklin 2009). Araújo & Guisan (2006) question whether the distinction between fundamental and realized niche is useful for these models, given ambiguities in the original formulation of the niche concept. In our view, a more realistic stance is to retain a healthy skepticism about which components of the niche are represented by predictions from an SDM. This is more likely to promote careful analysis of the adequacy of the data used for modeling, while also allowing for uncertainties in predictions and providing impetus for refining understanding through collecting better data, conducting ecological experiments, and testing new ways to model dispersal limitations, effects of competitors, and so on. Use of neutral terminology to describe species distributional models (SDM rather than ENM) seems preferable.

additive, modeling methods are ecologically realistic (see, for instance, multiplicative models: McCune 2006); how to deal with interspecific interactions; and how to understand and model the interplay of geographic and environmental drivers of species distributions across different spatial and temporal scales.

Pseudoabsence: a location at which predictors are sampled, variably viewed as a sample of the "background" or sampling universe, or an implied absence

When Absence Is Not Known

Presence-only data consist of records describing known occurrences (presence) of species, but lacking information about known absences. One example is the radiotelemetry data collected in wildlife studies. Analysis of these data with use-availability models has received steady attention over recent years (Pearce & Boyce 2006). Alternatively, museum records are now often utilized for evolutionary biology, macroecology, conservation, invasive species, and climate change modeling, using the millions of records compiled in electronic form from natural history collections (Graham et al. 2004a). Despite their limitations, use of such data is often justified by the lack of systematic survey data, coupled with widespread demand for mapped predictions.

Modelers are still coming to terms with how best to model presence-only data. Where analytical methods were once restricted to envelopes and distance measures, comparison of presence records with background or pseudoabsence points is now common (e.g., using GARP, ENFA, MaxEnt, and regression methods). Reviews and comparisons include Franklin (2009) and Elith et al. (2006). Attitudes to the value of presence-only data are remarkably variable. Some acknowledge that their predictions would be more robust if presence-absence or abundance data were available—a view that, if accepted, has substantial implications for the type of data that ecologists should aim to collect. An advantage of presence-absence data is that it conveys valuable information about surveyed locations (enabling analyses of biases) and prevalence (Phillips et al. 2009). Others argue that absence records introduce confounding information because they can indicate either habitat that is unsuitable or habitat that is suitable but is unoccupied, perhaps because of inaccessibility. This idea is commonly linked to the concept of modeling potential distributions (Jiménez-Valverde et al. 2008). Absence data are also sometimes viewed as misleading because the species or environment is not at equilibrium (e.g., invasions, climate change) or the species not easily detected. Interpretation of the meaning of background data or pseudoabsence data also varies. In general, the literature lacks robust discussion of the interplay between these disparate views and ecological and statistical theory. Progress in these topics, and on methods for detecting and dealing with sample bias and for evaluating presence-only models, could bring substantial benefits.

Modeling Responses Other than the Mean

Most methods for modeling presence-absence or abundance data estimate the center of the conditional distribution of the response, or the mean. Some argue that a more complete summary of the quantiles of the conditional distribution is useful (Austin 2007, Huston 2002). Upper quantiles, those near the maximum response, have received the most attention, based on the assumption that they better represent the response of the species to a predictor when other variables are not limiting (Huston 2002). They can reveal biases or missing predictors, and arguably can indicate the potential rather than the actual distribution (Cade et al. 2005). Low quantiles might also be relevant—for example, to estimate the lowest recruitment level for a species (Planque & Buffaz 2008). Interesting recent applications (see **Supplemental Literature Cited**) include freshwater, marine, and phylogenetic studies. So far, ecological examples are limited to parametric or nonparametric regression and gaussian responses, but methods are emerging that use tree ensembles and k-nearest neighbors and/or allow for differing response types (see **Supplemental Literature Cited**).

Supplemental Material

Biotic Interactions

Very few SDM studies explicitly include predictors describing biological interactions (Guisan & Thuiller 2005). In one early study, Austin & Cunningham (1981) included terms describing the presence of conspecifics in models of eucalypts, whilst acknowledging the possibility that variation attributed to conspecifics might reflect some missing but unknown environmental predictors. This typifies the difficulty in making inferences about the relative importance of jointly fitted abiotic and biotic predictors (Guisan & Thuiller 2005), because in most data sets environmental effects are confounded with those of competitors and mutualists. One exception is provided by Leathwick & Austin (2001) who treated geographic disjunctions in New Zealand's *Nothofagus* forests as a "natural removal experiment." Their SDMs indicated high levels of competitive interaction, with this effect varying depending on environmental conditions.

Given these difficulties, most practitioners use abiotic predictors alone. In models for understanding or interpolation-style prediction, the consequences may not be too severe, except where the presence of a host species is critical (e.g., Wharton & Kriticos 2004) and not predicted by the available covariates. However, for extrapolation (e.g., global warming, invasions), the effects of competitors, mutualists, and conspecific attractions might have far-reaching effects, especially where novel combinations of species are likely to occur (see sidebar, Using Models for Extrapolation). This is one of the more difficult aspects of SDMs, and we anticipate that its resolution will most likely require development of methods with capabilities beyond those available in current methods.

Integrating Pattern and Process

Several groups are now exploring how to better represent ecological processes within correlative models (see Schröder & Seppelt 2006 for a review), particularly for nonequilibrial situations. For example, Rouget & Richardson (2003) modeled the abundance of an invader allowing effects of propagule pressure; Hooten et al. (2007) modeled spread of the Eurasian collared dove using a hierachical Bayesian model incorporating density-dependent growth and dispersal, and Iverson et al. (2009) modeled emerald ash borer movement within predicted distributional ranges of trees. Others suggest combining SDMs with different types of models that allow inclusion of mechanistic, population, and landscape change effects (Drielsma & Ferrier 2009, Kearney et al. 2008, Keith et al. 2008).

Model Selection

Early SDMs generally used statistical techniques based on p-values for model selection, but a recent shift has seen much greater emphasis on AIC and multimodel inference (Burnham & Anderson 2002). This shift has been useful for reducing reliance on the "truth" of a model selected by stepwise procedures and for understanding the error tendencies of conventional selection approaches (Whittingham et al. 2006). However, though this type of multimodel inference is useful for exploring model-based uncertainty, whether it is the best way to reliably predict an outcome is unclear. Other model averaging techniques from computer science use a range of approaches to concurrently develop a set of models that together predict well (Hastie et al. 2009). Research comparing the conceptual bases and performance of various model averaging approaches including regression/AIC, Bayesian methods, and machine learning model ensembles (e.g., bagged or boosted trees, Prasad et al. 2006) could be profitable.

There are also interesting alternative approaches to selecting a single final model. The different information criteria provide a range of trade-offs between model complexity and predictive performance and can be used within cross-validation to select a model (Hastie et al. 2009). Some methods focus on simultaneous selection of variables and parameter estimation, for example, by shrinking coefficient estimates (e.g., see Reineking & Schröder 2006 on ridge regression and the lasso). These provide alternative methods for selecting a final regression model that are generally more reliable than stepwise methods. In machine learning these ideas of model selection and tuning are termed "regularization," i.e., making the fitted surface more regular or smooth by controlling overfitting (e.g., used in MaxEnt, Phillips et al. 2006). Use of these alternative model selection methods in ecology are still relatively rare, but likely to increase.

Model Evaluation

Although the need for robust model evaluation is widely acknowledged, there are diverse opinions on what properties of a model are important and how to test them appropriately (see **Supplemental Literature Cited**). Where modelers aim to explain patterns or generate hypotheses (e.g., in evolutionary biology and classical ecological studies), results are generally assessed using statistical tests of model fit and comparison with existing knowledge. In contrast, when prediction is the aim, evaluation targets predictive ability and current practice usually involves testing predictive performance using data resampling (split samples, cross-validation, bootstrapping) or, more rarely, independent data sets. Most summaries of performance are based on a relatively small set of statistics including kappa, area under the receiver operating characteristic curve (AUC) and correlation coefficients. Several researchers have attempted to understand the relative performance of these tests including their sensitivity to data characteristics, but progress toward adoption of a comprehensive toolbox of evaluation measures is slow and impeded by arguments about the general validity of some statistics. Instead, it would be more constructive to identify the proper place of each statistic in the broad realm of what needs testing. The machine learning and weather-forecasting communities have developed expertise in testing predictive performance and use some statistics rarely considered in ecology (Caruana & Niculescu-Mizil 2006, Pearce & Ferrier 2000; see also **Supplemental Literature Cited**). SDM evaluation would benefit from identifying useful techniques in other fields, and from more research focus on topics such as how to analyze spatial patterns in errors, how to deal with uncertainties, and how to assess model performance in the context of the intended application, including decision making. More use of artificial data (Austin 2007) and more experimental verification of modeled relationships (e.g., Wright et al. 2006) could also yield valuable insights.

Supplemental Material

Uncertainty

Use of SDM for applications such as conservation planning and biosecurity creates an imperative for considering errors and their relative costs. Uncertainty in SDMs results both from data deficiencies (e.g., missing covariates, and samples of species occurrences that are small, biased, or lacking absences) and from errors in specification of the model (Barry & Elith 2006). A few papers provide taxonomies of uncertainty as a basis for assessing errors, and suggest general treatments. Heikkinen et al. (2006) review various aspects of SDMs that contribute to uncertainty; Hortal et al. (2008) provide a commentary on biodiversity data and its uncertainties; and Burgman et al. (2005) review treatments of uncertainty in landscape ecology. Relatively few studies address uncertainty in SDMs and its effects on the model, predictions, and related decision making (but see **Supplemental Literature Cited**). Model uncertainty has received most attention, particularly in the context of model averaging or consensus, but also for providing mapped uncertainty estimates. Studies on data errors include assessments of the influence of errors and biases in species records, and in predictors such as digital elevation models and their products. These extend beyond the uncertainty that can be estimated from standard errors of parameters in a regression model, or from bootstrapped estimates of uncertainty. Modelers can attempt to reduce uncertainty, and/or characterize it and explore its effects on decision making. Because problems related to uncertainty are difficult to deal with they are often ignored, but we anticipate increasing recognition of their importance, particularly in management applications.

CONCLUDING THOUGHTS

Reflection on the broad scope of both past and current SDM writings reveals a rich diversity of biological and environmental settings, philosophical and analytical approaches, and research and management applications. Our summary of this multifaceted and developing field may disappoint those looking for specific advice or a more methodologically oriented review—we regard a number of emerging books and teaching resources as better able to fill these needs. Our emphasis reflects the belief that further advances in SDM are more likely to come from better integration of theory, concepts, and practice than from improved methods per se. Our hope is that this review will encourage more deliberate exploration across discipline boundaries, the informed and creative use of a breadth of approaches, and planned endeavors to fill important knowledge gaps. This expanded focus should, in turn, improve the ability of SDMs to make their contribution to delivering the type of information required for managing the Earth's dwindling biological resources.

SUMMARY POINTS

1. Modern SDMs represent the convergence of site-based ecology and advances in GIS and spatial data technologies. They are applied across terrestrial, freshwater, and marine environments, at widely varying spatial and temporal scales, and to gain ecological and evolutionary insight and predict distributions. Differences in mobility between species motivate some of the most marked differences in modeling approach.
2. Species distributions reflect the interplay of geographic and environmental processes. Using ecologically relevant environmental variables and addressing residual geographic patterning are both important.
3. Prediction takes two forms: interpolation and extrapolation. The latter violates several statistical and ecological assumptions of SDMs, so hindcasting (evolutionary questions) and forecasting (climate change and invasive species models) require special care.
4. Development of stronger links between ecological theory and concepts and SDM practice would be beneficial for developing more robust and consistent use of these techniques.

FUTURE ISSUES

1. Methods are required for dealing with uncertainty: characterizing it, reducing it, or assessing its influence on decisions.
2. Model selection and evaluation methods are likely to expand and incorporate new techniques from statistics, weather forecasting, and machine learning.

3. The use of presence-only data will continue, so methods for dealing with biases and evaluating results need more development.
4. Cycles of development, implementation, and evaluation (including experimental testing) would provide insights, strengthen links to theory, and contribute important information for developing ecologically relevant predictors.
5. Many applications could benefit from advances in modeling biotic interactions and other ecological processes.
6. If SDMs are to be used for extrapolation, more assessments of whether they are fit for purpose are required. We need carefully targeted studies addressing performance across different spatial and temporal scales and degrees of equilibrium, in the context of the nature of actions that will flow from the predictions.

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Review

Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes

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ABSTRACT

Limited conservation resources mean that management decisions are often made on the basis of scarce biological information. Species distribution models (SDMs) are increasingly proposed as a way to improve the representation of biodiversity features in conservation planning, but the extent to which SDMs are used in conservation planning is unclear. We reviewed the peer-reviewed and grey conservation planning literature to explore if and how SDMs are used in conservation prioritisations. We use text mining to analyse 641 peer-reviewed conservation prioritisation articles published between 2006 and 2012 and find that only 10% of articles specifically mention SDMs in the abstract, title, and/or keywords. We use topic modelling of all peer-reviewed articles plus a detailed review of a random sample of 40 peer-reviewed and grey literature plans to evaluate factors that might influence whether decision-makers use SDMs to inform prioritisations. Our results reveal that habitat maps, expert-elicited species distributions, or metrics representing landscape processes (e.g. connectivity surfaces) are used more often than SDMs as biodiversity surrogates in prioritisations. We find four main reasons for using such alternatives in place of SDMs: (i) insufficient species occurrence data (particularly for threatened species); (ii) lack of biologically-meaningful predictor data relevant to the spatial scale of planning; (iii) low concern about uncertainty in biodiversity data; and (iv) a focus on accounting for ecological, evolutionary, and cumulative threatening processes that requires alternative data to be collected. Our results suggest that SDMs are perceived as best-suited to dealing with traditional reserve selection objectives and accounting for uncertainties such as future climate change or mapping accuracy. The majority of planners in both the grey and peer-reviewed literature appear to trade off the benefits of using SDMs for the benefits of including information on multiple threats and processes. We suggest that increasing the complexity of species distribution modelling methods might have little impact on their use in conservation planning without a corresponding increase in research aiming at better incorporation of a range of ecological, evolutionary, and threatening processes.

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Contents

1. Introduction

Limited funding for addressing global biodiversity declines means that prioritisation of geographic regions and conservation actions is unavoidable (Bottrill et al., 2009). In systematic conservation planning, ecological features (e.g., species and habitat types) are identified; costs, constraints, and possible threat mitigation actions are considered; and decisions are subsequently derived on where and when to implement actions (Margules and Pressey, 2000; Moilanen et al., 2009). Only rarely is complete, up-to-date spatial coverage of conservation feature data available (Rondinini et al., 2006). Species distribution models (SDMs, also referred to as ecological niche models) map relationships between species distributions and environmental conditions, and are one way to project the spatial distributions of species to regions lacking biodiversity observations (Elith and Leathwick, 2009b; Guisan and Thuiller, 2005). The use of SDMs to aid conservation decision-making is increasingly recommended in the peer-reviewed literature (Bailey and Thompson, 2009; Elith and Leathwick, 2009a; Guisan et al., 2013; Phillips et al., 2006). This is because of their ability to provide biological information for a relatively low cost compared with broad-scale field surveys or models of population dynamics parameterised using long-term datasets. But how well do SDMs inform decisions within the conservation planning process? Here, we assess how often SDMs are used to inform ecological features for conservation planning, and evaluate the factors that might lead to decision-makers using alternative approaches to inform conservation prioritisations.

Until recently, the main role of systematic conservation planning was to design reserve networks to protect biodiversity *in situ* (Margules and Pressey, 2000). Typically the objective was either to minimise resources expended whilst meeting a given set of quantitative conservation targets (the minimum-set problem), or to maximise some measure of "benefit" (in a simple case, this might be the number of targets met for our assets), given a fixed budget or amount of resources that can be expended (Wilson et al., 2009). Conservation targets might be all or a subset of the features in a geographical area, or a proportion of population size or geographical extent (Pressey et al., 2003).

Increasingly, planners and scientists have sought to accommodate multiple socio-economic and biodiversity considerations, as well as information on threats, in conservation planning. For example, the decision-support tool Marxan with Zones improves on traditional reserve selection tools through the addition of user-defined zones and the ability to specify costs and targets for each zone (Watts et al., 2009), as well as incorporate predictions about how effective alternative actions in each zone might be for achieving conservation or socio-economic objectives (Makino et al., 2013). These advances have allowed planners to account for factors such as the feasibility of managing or protecting species in landscapes predominantly used for agriculture (Tulloch et al., 2014) or fishing (Makino et al., 2013). In addition, a number of decision-support tools (e.g., Zonation (Moilanen et al., 2012) and Marxan (Ball et al., 2009)), can now incorporate maps that predict changes in distributions of species or habitats in response to a particular threat (Tulloch et al., 2015).

With an increase in our capacity to solve complex objectives using systematic conservation planning tools, however, comes an increase in the data required to inform prioritisations (Guillera-Arroita et al., 2015). Collecting data is time-consuming and sometimes costly, and thus planners are faced with deciding which data are most critical to achieving their goals. A variety of approaches are possible for depicting the distributions of ecological features and informing the "benefits" to biodiversity of applying a conservation action in any one place, including point occurrence data, range maps, expert knowledge maps, or predictive model outputs such as those generated by SDMs (Elith and Leathwick, 2009b; Franklin, 2010; Peterson et al., 2011). In addition to these species-focused data, planners might wish to incorporate data on the distributions of other landscape or socio-economic features that could be important for ensuring additional objectives related to economic production (e.g. fishing areas) or ecosystem health (e.g. connectivity and productivity). Alternatively, planners faced with choosing between multiple threats to manage might want to better understand the likely outcomes for their target species of alternative threat mitigation actions (Auerbach et al., 2014).

There are five main considerations that planners face when choosing feature data to prioritise conservation decisions (Beale and Lennon, 2012; Elith et al., 2002; Loiselle et al., 2003; Rondinini et al., 2006; Sinclair et al., 2010): (i) the quality of available data and associated ability to parameterise complex models; (ii) the spatial scale of the problem; (iii) how much uncertainty the conservation planner is willing to tolerate; (iv) the importance of ecological and evolutionary processes; and (v) constraints, such as time, planning costs, computational ability, and the social-economic environment of the planning landscape (see also Guisan et al., 2013; Wilson et al., 2005). All of these issues have important impacts on prioritisation outcomes (Table 1; Wilson et al., 2005), but they can rarely be dealt with simultaneously; rather, planners are forced to trade-off some as less important than others. For instance, planners focused primarily on constraints such as time or budget might use readily-accessible point-based occurrence data (such as that in biodiversity atlases), but incomplete distribution data and spatial biases in sampling effort often result in fragmented distribution maps and underestimation of species distributions (Balmford et al., 2005; Boakes et al., 2010; Tulloch and Szabo, 2012). This can bias estimates of the benefits of conservation action towards well-surveyed locations, and limit the efficiency of conservation planning due to missed opportunities (Graham and Hijmans, 2006; Rondinini et al., 2006). In contrast, planners focused on prioritising across large spatial scales by projecting scarce occurrence data could develop highly uncertain or poorly-parameterised SDMs, which might lead to overconfident decisions and wasted conservation funding (Carvalho et al., 2011). In

Table 1
Data types used to map distributions of biodiversity features in conservation planning, and the potential issues associated with outputs. Assumptions and potential errors of each data type are classified according to frequency of occurrence, assigned to categories (due to vagueness in literature) of black = almost always, grey = sometimes, white = rarely or never. See Table S3 in Supporting information for examples from detailed review.

Data type[a]	Output used	Key assumptions								Potential errors when used in conservation planning					Examples from detailed review
		All species occurrences recorded	Counts reflect true abundance	Commission and omission errors negligible	Distribution data not spatially biased	Species detectability[b] = 1 or constant	Drivers of suitable habitat adequately characterised	Habitats adequately represent distributions of target species	Any variation in detectability is adequately captured by covariates	Omission errors – *missed opportunities*	Commission errors – *choose unsuitable areas that do not contain target species*	Under-estimate (or fail to estimate) abundance – *missed opportunities, choose areas with low suitability*	Spatial sampling bias – *prioritise more intensively sampled areas*	Variable detectability or missing covariates confound detectability and occupancy – *biased SDM and prioritisation*	
Dots on map (counts, point presences and/or absences)	Raw														SDM: 11 Non-SDM: 16
Species range maps (expert-drawn or other, e.g. IUCN Red List maps)	Presence/ absence map; Species richness														SDM: 2 Non-SDM: 10
SDM: presence-only (e.g. MaxEnt, GARP)	Relative P(occurrence) or threshold conversion to presence/ absence									c	d				SDM: 7 Non-SDM: 0
SDM: presence-absence (single survey per site; e.g. GLM, GAM, BRT, Random Forests)	P(occurrence) or threshold conversion to presence/ absence									c	d				SDM: 4 Non-SDM: 0
SDM: presence-absence (repeat surveys per site; e.g. occupancy models)	P(occurrence), threshold conversion to presence/ absence									c	d				SDM: 0 Non-SDM: 0
SDM: abundance data	Prediction of abundance									c	d				SDM: 2 Non-SDM: 0
HSI: Expert-derived habitat suitability index	Relative suitability ranking/ score, or binary distribution														SDM: 0 Non-SDM: 8
Process map (surrogate): models of environmental or evolutionary drivers of species' distributions (e.g. potential nest sites, productivity, biomass, surface hydrography, climate)	Quantification of resource availability and physiological conditions														SDM: 4 Non-SDM: 19
Pressure map (surrogate): models or remote-sensing maps indicating human pressure (e.g. land cover)	Quantification of ecosystem condition (e.g. degradation/ conversion)														SDM: 3 Non-SDM: 20
Simple habitat maps (e.g. satellite-derived vegetation, bathymetry)	Threshold conversion to presence/ absence									c	d				SDM: 8 Non-SDM: 29
Lists (expert or historical) or other expert species-specific knowledge	Expert opinion on priority locations (e.g. Important Bird Areas) or priority species (e.g. vulnerability scores)														SDM: 4 Non-SDM: 19

[a] Many publications either did not specify the type of input data, or were vague. Further interrogation of supporting informati on was carried out where possible.
[b] Detectability refers to the probability that a species will be detected at a site, given that it is present.
[c] Threshold set too high.
[d] Threshold set too low.

these cases, actions might be carried out in areas where the conservation feature is wrongly thought to exist (errors of commission, or false presences), or no management might be undertaken where the feature exists and requires immediate action (errors of omission, or false absences; Elith and Graham, 2009; Guisan et al., 2013). Finally, choosing a complex and highly-parameterised model with high-resolution predictor or population-level data might result in more accurate predictions of species distributions for conservation decision-making (Arponen et al., 2012). However, such models have an increased chance of problems such as model over-fitting, making extrapolation to other regions or timeframes challenging (Merow et al., 2014; Randin et al., 2006; Wenger and Olden, 2012). In these cases, collecting and processing the necessary data and calibrating complex models could also delay decisions, increase costs, and divert conservation attention away from learning about threats or socio-economic values (Grantham et al., 2009).

Knowing when and why conservation planners choose different biodiversity feature data inputs for informing decisions would provide insight into which data are most useful for solving which objectives. Despite a significant body of knowledge on SDMs having been assembled more than a decade ago, and repeated calls for the use of SDMs in conservation prioritisation problems (Araujo and Guisan, 2006; Guisan and Thuiller, 2005; Hernandez et al., 2006; Liu et al., 2005; Loiselle et al., 2003; Phillips et al., 2006; Rondinini et al., 2006; Wilson et al., 2005), there has been no evaluation of how often SDMs are applied to inform feature distributions in conservation prioritisations. Here, we conduct a review of the peer-reviewed and grey literature (e.g., conservation plans, agency reports), to explore if and how SDMs are used in conservation planning applications for native flora and fauna species at risk. We compare cases where SDMs are and are not used to investigate reasons for choosing SDMs to inform biodiversity features targeted for conservation action. We then evaluate the extent to which SDM-prioritisations versus non-SDM prioritisations address issues of spatial scale, uncertainty, and the ability to represent ecological, evolutionary and threatening processes, which have been identified as affecting conservation planning outcomes (Rondinini et al., 2006). Finally, we explore in what ways SDMs can inform conservation decisions, and provide recommendations that could increase appropriate use of models, readily-available conservation prioritisation tools, and alternative threat prioritisation approaches for informing conservation planning decisions.

2. Methods for the review

We sampled the peer-reviewed literature by searching the Web of Science, using the key words "conservation plan*" or "land use plan*" or "regional plan*" (to select articles addressing conservation; $n =$ 7493 articles) plus additional filter key words of "priorit*" or "reserve selection" or "resource allocation*" (to restrict outputs to articles prioritising actions or areas), and including only papers published from 2006 to 2012 (final $n = 660$ articles). We included only publications since 2006 for three reasons: (i) 2006 represents the beginning of an exponential rise in published papers on the topic "species distribution model*"(Guisan et al., 2013); (ii) a significant level of scientific knowledge on SDM techniques had recently become available in 2006 (Araujo and Guisan, 2006; Guisan and Thuiller, 2005; Hernandez et al., 2006; Liu et al., 2005; Phillips et al., 2006); and (iii) articles providing recommendations about the sensitivity and usefulness of different data types in conservation planning had also become available at that time (Loiselle et al., 2003; Rondinini et al., 2006; Wilson et al., 2005).

We first performed a text mining analysis on all of the 660 articles to explore differences between prioritisations applying SDMs and those using alternative methods of mapping feature distributions. To do this, we classified articles as "SDM-prioritisations" (60 articles), or "non-SDM prioritisations" (581 articles; see Appendix S1 for details). Nineteen articles did not fit into either category (mainly technology conference abstracts) and were excluded from the analysis. For each classification of articles, we exported all titles, abstracts, and keywords, and cleaned the dataset to standardise spelling and remove unwanted symbols (e.g. numbers, dates) using the text mining "tm 0.6–2" package in R (Feinerer and Hornik, 2015). These data were then transformed into a document term matrix, with one entry in the matrix per article. We performed topic modelling in R using package "topicmodels 0.2–2" (Grün and Hornik, 2011), by applying a latent dirichlet allocation (LDA) model with the variational expectation-maximisation (VEM) algorithm and Gibbs sampling to a response variable of the document term matrix for either SDM- or non-SDM-prioritisations. We set the target number of topics to 20, after running sensitivity analyses with different numbers of topics, and finding that 20 topics was a good balance between specificity and redundancy (Westgate et al., 2015). For each prioritisation classification (SDM or non-SDM), the outputs for each model were a classification of each article to the single topic that best represented the text of the abstract, title and keywords, and a list of terms that represented each of the 20 topics. With the term list, we summarised the topic themes and used these to compare which themes predominate each type of prioritisation. Finally, to explore if SDM-prioritisations have a greater impact in the scientific literature than non-SDM prioritisations, we compared the citation rates of papers in

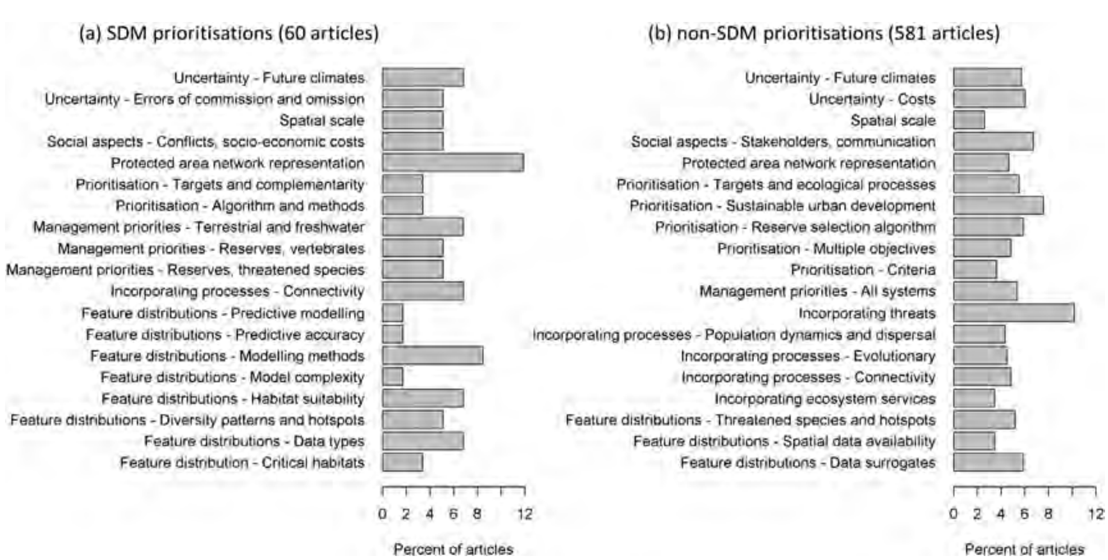

Fig. 1. Results of topic analysis of 641 conservation prioritisation articles classified into (a) only SDM prioritisations, and (b) non-SDM prioritisations. These show different priorities for papers that (a) include SDMs (mostly focused on having adequate species representation in planning, accounting for future uncertainty and multiple data types, and considering habitat suitability), compared with (b) papers that do not mention SDMs (focused more on socio-economic aspects of conservation planning and on incorporating processes).

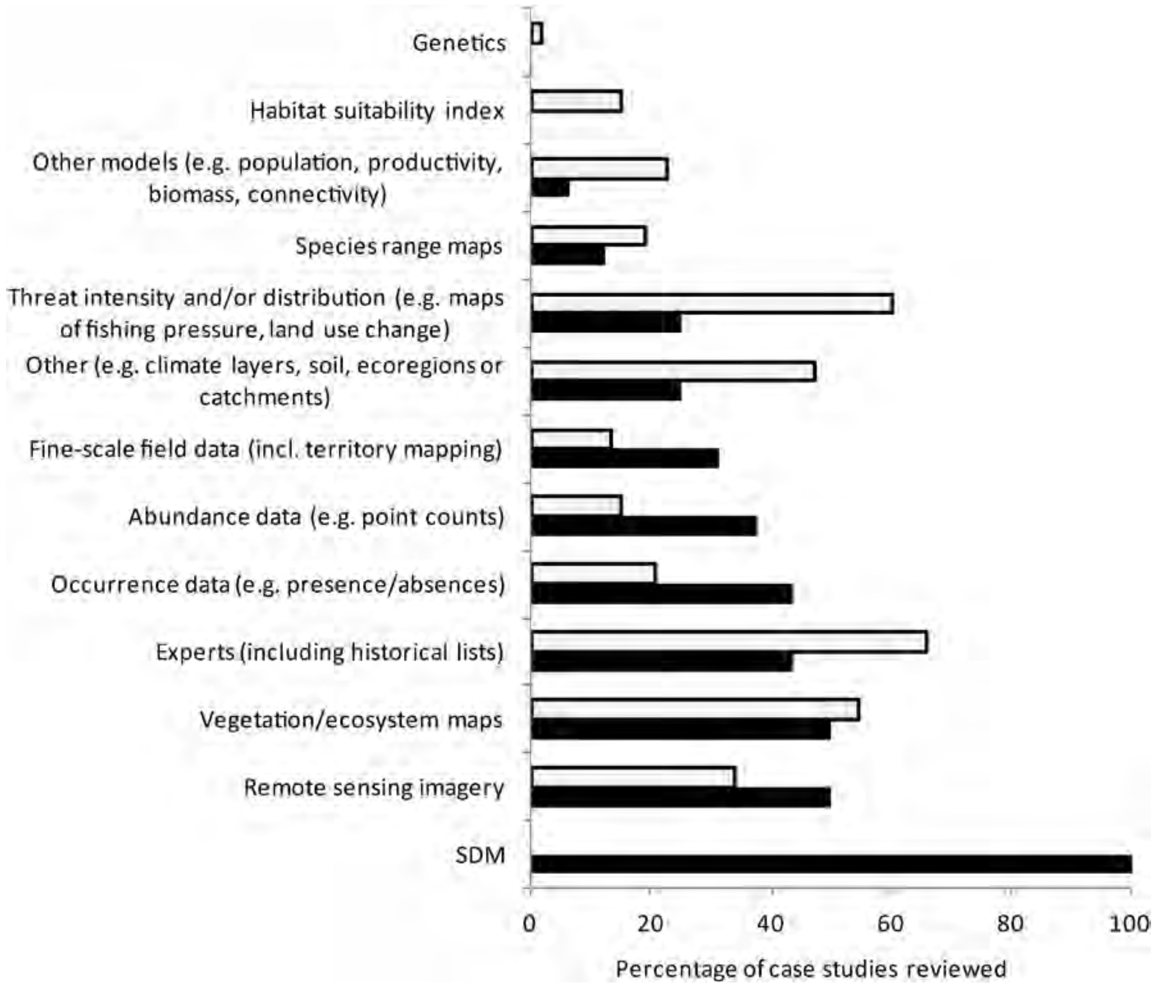

Fig. 2. Type of feature data used in 68 conservation planning prioritisations from peer-reviewed and grey literature that we reviewed, ordered by how often they were used in literature that did not use SDMs (open bars) compared with SDM-focused prioritisation literature (dark bars). Note: percentages do not add up to 100 as most prioritisations used more than one data type.

each classification using an unpaired two-sample t-test assuming unequal variances.

Next, we carried out a more detailed analysis of a selection of the 641 articles. Forty peer-reviewed articles (two marine, two freshwater, 31 terrestrial and five multi-system e.g. land-sea prioritisations) were randomly selected from the 10 journals with the most articles satisfying these criteria, plus the following additional specifications: (i) each selected article addressed conservation decisions for multiple biodiversity features, and (ii) was related to a definable prioritisation action (see Supplementary material for further details of the selection process).

Twenty-eight conservation plans (non-peer-reviewed: 16 terrestrial and 12 marine) were also selected using internet searches. Terrestrial locations were chosen to represent one of each of the hotspots defined by Myers and colleagues (Myers et al., 2000) and the additional hotspots identified by Conservation International (http://www.conservation.org/where/priority_areas/hotspots/Pages/hotspots_main.aspx, Accessed 4 December 2013). Marine locations corresponded to the twelve marine biogeographic realms of the world (Spalding et al., 2007). We were not able to find conservation plans that fit our criteria for all hotspots between the years 2006 and 2012, so we expanded the search of grey literature to allow for conservation plans from any year after 2000.

For each journal article and conservation plan, we identified the type of feature data used for prioritisation, and where SDMs were used, the SDM methodology, complexity, and model settings. We then investigated whether articles using or not using SDMs focused on different conservation planning issues related to biodiversity feature data accuracy and representativeness, which had been identified as important issues by highly-cited papers prior to the publication of the articles in our review (Elith et al., 2002; Loiselle et al., 2003; Rondinini et al., 2006; Wilson et al., 2005). Using a three-point nominal scale (Did not discuss, Discussed but did not address explicitly, Addressed explicitly in methodology), we qualitatively categorised each article as considering or not considering: (i) Scale (e.g. how might spatial resolution and planning extent affect feature data accuracy and representativeness?); (ii) Uncertainty in feature data distribution (e.g. how accurate is a species' map or point occurrence location?), (iii) Uncertainty due to bias (e.g. in expert experience, or in the choice of sampling unrepresentative locations or study taxa), (iv) Model uncertainty (e.g. which of several alternative models is the 'true' representation of a species' distribution?); and (v) Ability to represent ecological, evolutionary and threatening processes (e.g. how might connectivity and the ability of species to disperse across fragmented landscapes be incorporated into planning?). We also investigated whether each article discussed what might have been achieved if the authors had better data/time/resources, or what they needed to improve analyses or outcomes. Additional information was collected on the type of conservation planning, study area and target species/ecosystems, the prioritisation objective and the prioritisation method.

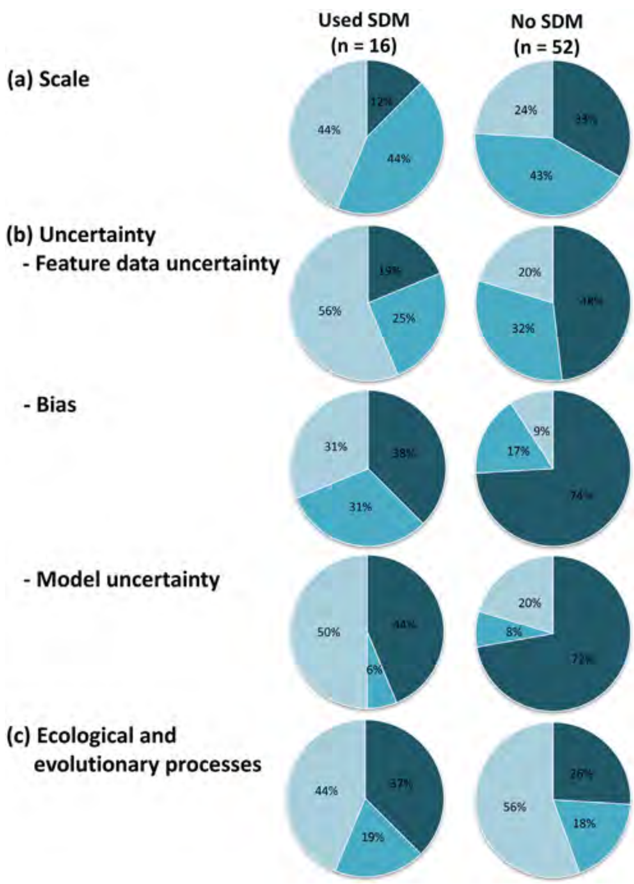

Fig. 3. Results of review into how issues related to using alternative kinds of feature data in conservation planning are dealt with in peer-reviewed and grey conservation planning literature that either used SDMs to derive feature data (16 studies) or used alternative non-SDM approaches (52 studies). Showing percentage of studies dealing with issues of (a) spatial scale, (b) uncertainty: in feature data distribution, due to bias, or in the model, and (c) ability to represent ecological, evolutionary and threatening processes. The dark blue percentage represents not discussed, medium blue represents mentioned but not dealt with, and light blue indicates the article dealt explicitly with the issue (e.g. within the methodology).

3. How prevalent are SDMs in the conservation prioritisation literature?

Text analysis suggested that only 10% of conservation planning research between 2006 and 2012 referred to SDMs (60 versus 581 prioritisations). Reviewing a sample of these articles in more detail revealed a slightly higher ratio of SDM- to non-SDM prioritisations (23% of 68 articles used SDMs). This discrepancy is due to the fact that not all peer-reviewed studies specify the modelling approach in the abstract, title, or keywords. Topic modelling of all 641 conservation prioritisation articles supported a primary emphasis on methodological aspects of predicting feature distributions in SDM prioritisations — the topics of 30% of these articles were predictive accuracy, data uncertainty, model complexity, and comparing modelling methods (Fig. 1a). In comparison, topic models of non-SDM prioritisations indicated that managing and accounting for threats to biodiversity features (including identifying hotspots where multiple threats or threatened species overlap) was the predominant focus (28% of all non-SDM articles were classified into these topics compared with 5% of SDM-prioritisations; Fig. 1b). Although non-SDM prioritisations had higher total numbers of citations and citation rates compared with SDM prioritisations, these differences were not significant (t-test; average citations: $t = 0.51$, $df = 88$, $P = 0.30$; total citations: $t = 0.88$, $df = 88$, $P = 0.19$), due to the high variance in citations for non-SDM articles (ranging from 0 to 616 citations compared with a range of 1 to 185 for SDM prioritisations; Fig. S1 in Supporting information).

Instead of using SDMs, over 35% of non-SDM prioritisations used an alternative form of statistical modelling to either predict the distributions of species across space, or to predict non-spatial or non-species aspects of biodiversity. In the first instance, 15% of non-SDM prioritisations applied habitat suitability indices (HSIs; Fig. 2), in which the attributes of multiple spatial layers representing different aspects of habitat quality are incorporated into a function that produces higher index values in areas where all required attributes for a species are met (e.g., best land cover type, elevation, slope, soils) (Bhagabati et al., 2012; Smith and Leader-Williams, 2006; Stralberg et al., 2011; Underwood et al., 2011). In the second instance, 22% of non-SDM prioritisations (and only one SDM-prioritisation) developed predictive models that were not intended to project the likely distribution of individual species across space (Fig. 2). These alternative models focused on fundamental processes (Fig. 1), and included extinction risk models such as population viability analysis (Keel, 2005; Loyola et al., 2008), least-cost path models representing the ability of species to disperse across a fragmented landscape (Keel, 2005), and models of productivity (Morgan et al., 2005), biomass (Adams et al., 2011) or ecosystem services such as carbon storage and water purification (Bhagabati et al., 2012).

In addition to biodiversity feature data, our detailed review revealed that more than 60% of non-SDM prioritisations incorporated threat-specific input data compared with only 25% of SDM prioritisations (Fig. 2). Most often this was achieved with maps that described the likelihood or intensity of specific current and future threatening processes (Tulloch et al., 2015), such as agriculture (Lombard et al., 2010; Smith and Leader-Williams, 2006), fishing (Adams et al., 2011; Balanced Seas, 2011), planned infrastructure and urban development (Francis and Hamm, 2011; Gordon et al., 2009; Thorne et al., 2009), fire (Leroux et al., 2007), or oil spills (The Nature Conservancy, 2010). Alternatively, articles mapped historical land and sea change through spatial models of habitat quality or condition (assessing level of current threats e.g. using InVEST; Bhagabati et al., 2012) or maps of landscape transformation such as human footprint mapping (Adams et al., 2011; Beier et al., 2009; CEPF (Critical Ecosystem Partnership Fund), 2003; Pourebrahim et al., 2011; Terribile et al., 2009; Wilson et al., 2010). Threat-based models were either used to identify areas of high biodiversity and low threat where development could be avoided (e.g. through protected area designation) (Gordon et al., 2009; Underwood et al., 2011), or to identify places high in diversity but also high in stress, as important for conservation action (e.g. through cumulative threat mapping and hotspot analysis) (Francis and Hamm, 2011; Roura-Pascual et al., 2010; Underwood et al., 2011). Finally, non-spatial representations of threat impacts were also applied in 5% of non-SDM prioritisations, most often species extinction risk or vulnerability assessments for particular threatening processes (Kramer and Kramer, 2002; Loyola et al., 2008).

Across all prioritisations, the most commonly-used form of non-SDM data for informing biodiversity feature distributions was expert knowledge (61% of all studies combined; Fig. 2). Experts can be a useful substitute for SDMs when species data are scarce (Murray et al., 2009). Conservation planners are likely to be constrained by data availability in poorly-surveyed regions, and experts fill knowledge gaps in various ways (Table 1). Firstly, they help with defining species distributions by: (i) drawing coarse species range maps (Kramer and Kramer, 2002; Von Hase et al., 2003); (ii) refining existing distribution maps or extrapolating small point location datasets using specialist information (Gordon et al., 2009; Pawar et al., 2007; Tognelli et al., 2008); and (iii) providing guidance on the selection of ecologically relevant landscape characteristics or model predictors to develop HSIs and SDMs (Beier et al., 2009). Experts were also useful for informing conservation feature data in

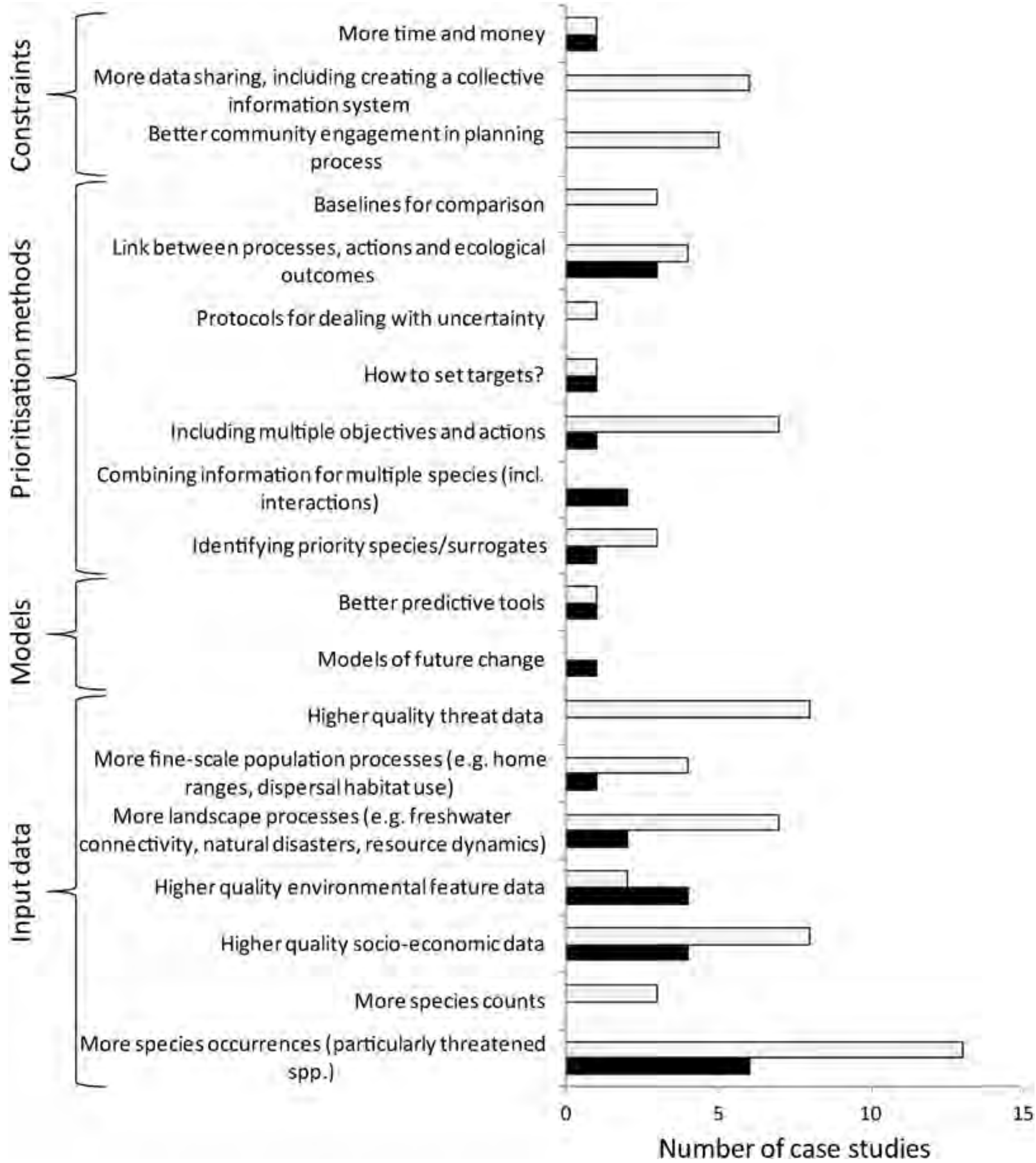

Fig. 4. Factors that scientists and conservation planners mentioned they need improved for better conservation planning (a 'wish list'), in the non-SDM prioritisation literature (open bars; 16 publications) compared with prioritisation literature that used SDMs (dark bars; 52 publications), grouped into broad categories of the prioritisation process.

non-SDM prioritisations, particularly by: (i) providing specialist knowledge on parameters for state-and-transition or population viability models (Forbis et al., 2006); and (ii) providing details on threats to, and extinction risks of, species (e.g., IUCN, 2008). In both SDM- and non-SDM prioritisations, experts were also used to select appropriate features (e.g. surrogate taxa) for prioritisation (Peralvo et al., 2007), to provide additional maps of important environmental features (e.g. habitat trees) for which continuous datasets across the study landscape were not available (Beaudry et al., 2011; Lombard et al., 2010), or to contribute actively to the final prioritisation, either through weighting of decision criteria in multi-criteria decision analysis (Pourebrahim et al., 2011; Roura-Pascual et al., 2010), or in some cases, choosing where to place conservation versus alternative conflicting land uses in a consensus process (Recatalá Boix and Zinck, 2008).

4. Why are alternative approaches used in place of SDMs to inform conservation?

By combining topic modelling with detailed reviews of randomly sampled conservation planning articles, our review revealed several important distinctions between SDM- and non-SDM prioritisations (Figs. 1 to 4). These were: (i) differences in the quantity of species occurrence data; (ii) different spatial scales of planning for SDM- compared with non-SDM-prioritisations; (iii) a tendency to focus on data uncertainty and its challenges in SDM-based analyses; and (iv) a fundamental difference in the goals of the majority of SDM-prioritisations compared with non-SDM prioritisations. These distinctions lead to differences in the kinds of feature data selected for informing conservation planning. Here we expand on what these differences mean for decisions about input data for conservation planning.

4.1. Data quantity and quality

Our review revealed considerable variation in the quantity and quality of data used to inform conservation priorities. Prioritisations that relied on SDMs generally targeted fewer biodiversity features (mean of 345 ± 169 S.E. versus 1214 ± 865 for SDM and non-SDM prioritisations, respectively) and had more spatially-explicit occurrence records per species compared to non-SDM prioritisations (mean of 1499 ± 1035 S.E. versus 128 ± 19 for SDM and non-SDM prioritisations,

Table 2
Reasons for not using SDMs in conservation planning revealed in our review, with examples of peer-reviewed and grey literature (citations in italics refer to publications external to our strategic review results).

Reason	Alternative approaches used in reviewed articles	Examples from peer-reviewed literature	Example from grey literature
Too expensive			
SDMs are relatively expensive to produce compared with 'cheaper' proxies or surrogates, as a range of other data types are required for their application (species feature data, covariate data such as habitat maps), each of which involve trade-offs in accuracy and costs of data collection.	Experts; ecosystem-based maps	Lombard et al. (2010)	Clark and Lombard (2007)
Time constraints			
Lack of data for covariates or for species — need to make immediate decisions with limited data.	Vegetation maps; remote-sensed data; experts	Francis and Hamm (2011), Lombard et al. (2010)	Clark and Lombard (2007)
Data biased: planning at a large scale			
Spatial limitations of data mean that SDMs are too uncertain (i.e. spatial bias) — afraid of over-extrapolating scarce data and assuming species are present when they are not, which can lead to wasted funding	Point occurrence data matched with vegetation/ecosystem maps or remote-sensing; experts; habitat suitability indices	Beier et al. (2009), Gordon et al. (2009), Greenwald and Bradley (2008), Stralberg et al. (2011), Underwood et al. (2011)	Critical Ecosystem Partnership Fund (CEPF) (2005), Williams (2006)
Data insufficient: planning at a large scale			
Spatial limitations of data mean that SDMs are not possible for all features — afraid of under-estimating species distributions and assuming species are absent when they are not, which can lead to unprotected species ranges.	Vegetation/ecosystem maps or remote-sensing; range maps; experts	Tognelli et al. (2008), *Wilson et al. (2010)*	Critical Ecosystem Partnership Fund (CEPF) (2000, 2003), Eastern African Marine Ecoregion Programme (2004), NZ Government (2000), Ong et al. (2002), Smith and Leader-Williams (2006)
Planning at a small scale			
All existing localities of a species are known and restricted (when planning in a very small area or across islands)	Point data	Rottenberg and Parker (2003)	Avon Catchment Council (2007)
Environmental or species occurrence data not at fine enough resolution to match the planning scale.	Point data; experts; habitat suitability indices	Beaudry et al. (2011), Beier et al. (2009), Lombard et al. (2010)	Gobierno de Chile (2002)
Complex systems: interacting species			
Require more complex models as complexity of species interactions and limitations of existing models make it difficult to determine how threats and environments influence species with static SDMs	Mass-balance ecosystem models of energy/foraging; simulation-based optimisation procedures from artificial intelligence	Ciannelli et al. (2004), *Chadès et al. (2012)*	The Nature Conservancy (2010)
Characteristics of target species			
Variable (and often large) ranges of target species that are nomadic, migratory, resource-driven, and/or highly mobile. Other techniques used in place of SDMs.	Satellite tracking and capture-mark-recapture model (for species with large ranges e.g. migratory sea birds); spatially-linked time-series approaches incorporating seasonal and interannual variability (e.g. sea otter and pacific walrus distributions are reliant on variability in prey populations and sea ice availability)	*Iwamura et al. (2013)*	Department of Sustainability Environment Water Population and Communities (2011)
SDMs too simplistic, need for population processes			
Population modelling (using demography data) more important than distribution modelling	Integrated occurrence-mortality model	*Falcucci et al. (2009)*, *Franklin et al. (2014)*	The Nature Conservancy (2010)
Ecosystem rather than species approach			
For many communities (e.g., corals, sponges, vegetation), methods are needed to map the entire ecosystem rather than individual species. Alternative methods to SDMs available.	Remote-sensing maps	Cameron et al. (2008), Chomitz et al. (2006), Game et al. (2008), Roura-Pascual et al. (2010)	Keel (2005), Reimaan National Planning Team (2008), The Nature Conservancy (2010)

respectively). This difference was not significant due to variation across studies (single-factor ANOVA; $F = 1.59$, d.f. $= 1,16$, $P = 0.22$), but nevertheless suggests that available data drives decisions to include SDMs in prioritisations (Table 2). However, several SDM-prioritisations also had small sample sizes due to a paucity of unique locality data. In one study, more than 90% of the 4083 species in the plant database had less than four unique localities, and only 1.9% of the species (78 species) had 10 or more unique localities (Peralvo et al., 2007). Despite literature highlighting the dangers of over-fitting SDMs, only half of the SDM-prioritisations satisfied the recommended ratio of 1 predictor per 10 observations (Harrell, 2001), with an average ratio of predictors to observations of 1:4. In such cases, specific implementations of SDMs, such as ensembles of small models, whereby multiple models are fitted using a range of SDM algorithms (ESM; Breiner et al. in press; Lomba et al., 2010), could be used to develop a consensus prediction (e.g. by averaging; Araujo and New, 2007; Marini et al., 2009). Alternatively, modellers

Table 3
Two recent examples of on-ground conservation planning initiatives that used SDMs to deal with different issues of conservation input data.

Planning Organisation	California Landscape Conservation Cooperative (CALCC)	Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO)
Scientific partners	Arizona State University; Conservation Biology Institute; University of California Riverside; US Fish and Wildlife Service	National Research Center for Carnivore Conservation (CENAP); University of São Paulo, Luiz de Queiroz College of Agriculture
Example plan	Decision support for climate change adaptation and fire management strategies for at risk species in southern California; http://californialcc.org/projects/decision-support-climate-change-adaptation-and-fire-management-strategies-risk-species	Jaguar National Action Plan (NAP); http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/plano-de-acao/1344-plano-de-acao-para-conservacao-da-onca-pintada.html
Summary of goals	1) Integrate fire risk models, SDMs and population models with scenarios of future climate and land cover to project how effects of climate and land use changes impact threatened species in fire-prone ecosystems. 2) Identify and prioritise potential management responses to climate change.	1) Recognise suitable areas for current jaguar occurrence. 2) Use SDMs for conservation planning. 3) Delineate areas for jaguar conservation units (hereafter JCUs). 4) Design corridors among priority areas. 5) Prioritise JCUs.
Model complexity	1) MaxEnt: Presence-only data inputs. 2) Multiple models per species compared.	1) MaxEnt: Presence-only data inputs. 2) Functionally relevant variables for species selected to improve model certainty. 3) Land use data included to account for current constraints on distributions (Ferraz et al., 2012). 4) Multiple models per species compared.
Scale	Downscaled climate data to account for finer-scale topographic effects using spatial and statistical interpolation methods.	1) Considered environmental heterogeneity as the species distribution is wide-ranging. 2) Multiple models produced, scaled at different extents (biome-level) to improve model accuracy across heterogeneous planning landscape: different biomes have different driving factors for distributions (i.e. land use in south, elevation in north).
Uncertainty	1) Multiple models per species: Selected using statistical tests of predictive ability. 2) Models thresholded to discriminate between suitable/unsuitable habitat: Areas with predicted suitability below threshold considered unsuitable. 3) Scenarios: Modelled current and future distributions under current and future urbanisation threats. 3) Sensitivity analyses. 4) Incorporated uncertainty explicitly into prioritisation: Probabilistic models used in optimisation.	1) Rigorous criteria for selecting presence data: Used only current data (within fixed time period), avoiding historical data, discarding uncertain presences (imprecise coordinates, interviews, clustered data etc). 2) Expert validation: Experts picked best model (with no previous information about variables or procedures to avoid bias selection), and validated occurrence data (independent database used to validate suitable and unsuitable areas). 3) Models thresholded: 3 models (thresholded using different values from Maxent output) submitted for experts (species and biome specialists) to answer question: "which model best explains the current species distribution, according to what you know/expect?" 4) Model selection based on congruence of expert opinion.
Processes	1) Incorporated threats: Dynamic habitat maps representing alternative scenarios of climate change and urban growth coupled with population models and simulated stochastic fire regimes (Bonebrake et al., 2014). 2) Incorporated viability: Link a population model with dynamic bioclimate envelopes (RAMAS® GIS (Akçakaya, 2002) to investigate expected changes in population abundances with future change, and learn how much assisted colonisation is necessary to minimise risk of decline in populations (Franklin et al., 2014).	1) Used static map of dispersal barriers: Connectivity modelling incorporated using a cost surface (Morato et al., 2014). 2) Incorporated viability: Population viability initially included through estimates of smallest continuous area necessary to preserve a viable population of 50 individuals (Morato et al., 2014), converted to scores per landscape unit.
Constraints	Costs not considered explicitly but partners willing to share all outputs with future planners. Commons Cataloged Datasets for public use. Produced decision-support tool for public use: http://climate.calcommons.org/project/decision-support-climate-change-adaptation-and-fire-management-strategies-risk-species	Consider costs of protected areas after prioritisation only. Intending full systematic conservation planning exercise with explicit consideration of costs using decision-support tool Marxan.

could filter predictors to include only biologically meaningful variables (e.g. historical land management in addition to specialised habitat use predictors), thereby providing information compatible to the current species distribution (which sometimes differs completely from the historical distribution). This was done, for example, by researchers developing the National Carnivore Conservation Plans in Brazil (Table 3).

Trade-offs between data accessibility, representativeness, and cost were apparent in both SDM- and non-SDM prioritisations. Three of the most expensive data types to collect – genetics, fine-scale territory mapping, and new field surveys – were rarely used (Fig. 2), despite awareness of their usefulness in providing important information about environmental and demographic drivers of species distributions (Scoble and Lowe, 2010). Furthermore, despite all prioritisations mentioning the need to protect or manage species, more than 40% of non-SDM prioritisations did not use species-specific occurrence or abundance data or predictive models based on these data. In many cases authors stated that species-specific data were insufficient, unavailable, or too difficult to collect (Fig. 4), although only 12–18% of SDM- and non-SDM-prioritisations specifically mentioned the costs of feature data (Critical Ecosystem Partnership Fund (CEPF), 2003, 2005; Williams, 2006). Instead, 92% of non-SDM prioritisations used alternatives to georeferenced points such as range maps, coarse-scale habitat classifications, or threat maps (Table 2, Fig. 2). Proxies for georeferenced species distribution data are relatively low-cost and readily available, but may result in commission or omission errors, due to a lack of knowledge of the true relationship between target species and the proxies used (Table 1) (Tulloch et al., 2015). Such proxies are best used in combination with expert knowledge or fine-scale ecological data on habitat or resource requirements that might be used to avoid prioritising places unlikely to support the species (Tognelli et al., 2008).

4.2. Scale of planning

The spatial scale (both resolution and extent) at which planning and data collection are conducted, and at which feature data (including SDMs) are developed, influences our ability to make fine-scale decisions through feature data accuracy (Guisan et al., 2007; Thuiller et al., 2004), and influences our ability to make broad-scale decisions through feature data generalisability. The planning extents of both SDM- and non-SDM-prioritisations varied from very small (10 km^2: Avon Catchment Council, 2007) to global (Terribile et al., 2009). The average planning area for non-SDM prioritisations (mean = 15,078,456 km^2 ± 12,362,240 S.E.) was 62 times larger than for SDM prioritisations (mean = 239,364 km^2 ± 133,186 S.E). In many studies it appears that consistent distribution data for target species were not available at these large scales (Fig. 4).

Regardless of whether SDMs were used, spatial scale was the most-discussed issue of all of the five conservation planning feature data considerations that we explored in our detailed review (88% and 77% of SDM- and non-SDM-prioritisations, respectively; Fig. 3). Despite a high level of awareness across all studies, almost double the number of SDM-prioritisations explicitly accounted for scale issues compared with non-SDM prioritisations (44% versus 24%, respectively; Fig. 3). Trade-offs in the level of feature data detail and resolution allowable given computational limitations, mean that planners have two choices when choosing the scale at which to develop feature data layers and conduct planning: (i) plan across a broad extent to allow the entire distribution of all target features (sometimes at a national scale) to be prioritised (Leroux et al., 2007; Possingham et al., 2005), with possible loss of resolution and feature accuracy at fine scales; or (ii) increase resolution to a finer scale, trading off the ability to plan across a broad extent. Both approaches can be used with SDMs, or with non-SDM-based approaches that apply other forms of grid-based data such as remotely-sensed habitat or point occurrences. For example, the most popular approach for dealing with scale in SDM-prioritisations was a simple method of rescaling the resolution of grid-based data from predictor variables to reflect the scale of occurrence data or other spatial data (e.g. climate grids) employed in the prioritisation (Game et al., 2008; Guisan et al., 2007; Leroux et al., 2007; Possingham et al., 2005). However, inappropriate choice of scale can significantly alter the set of areas that are identified for conservation or development (Hermoso and Kennard, 2012), and small-extent or resolution models may not be applicable to other regions (McAlpine et al., 2008). An alternative approach for rescaling grid-based data (including SDMs) is to rescale feature data cell size to match the resolution of planning units (Araujo et al., 2005; Bombi and D'Amen, 2012). This is also problematic due to the difficulty of deciding how to aggregate multiple probability values, in addition to trying to quantify and use a measure of variation within the new resolution to avoid loss of information (Tulloch et al., 2013b). The most effective method for dealing with the question of what scale is most appropriate for planning is to construct a hierarchical model that explicitly links ecological and decision scales (Dudaniec et al., 2013; McMahon and Diez, 2007). For example, a hierarchical model could represent a species' fine-resolution use of tree hollows plus its regional-scale use of vegetation corridors, allowing regional planning decisions to account for the scale of the species' needs as well as those of the planners (Beaudry et al., 2011). Because different levels (or resolutions) of data are required to compare the utility of analyses at different scales, this method is also the most complex and data intensive.

The higher proportion of SDM prioritisations explicitly addressing scale choices suggests that SDMs may be better-suited to deal with the challenges of planning at the appropriate scale. This may be because there are fewer options available to conservation planners to deal with issues of scale if they have not utilised grid-based data such as SDMs and remote-sensing. One option might be to accept that different biodiversity data represent different scales of habitat use, and to compare the results of prioritisation scenarios using alternative biodiversity data inputs such as simple regional-scale range and habitat maps versus local-scale habitat resources, to identify conservation locations that are robust to scale. Alternatively, planners could set up scenarios in which the total extent of prioritisation is varied (e.g. National Carnivore Conservation Plans in Brazil; Table 3), thus explicitly accounting for the impact of selecting different spatial scales on the results of prioritisations (Pascual-Hortal and Saura, 2007).

4.3. Uncertainty

Conservation planners face multiple forms of uncertainty, predominantly (i) data uncertainty (typically related to data collection methods and resulting accuracy); (ii) uncertainty in the choice of model chosen to extrapolate data; and (iii) uncertainty in future conditions of the planning landscape (making it difficult to decide if current distributions and decisions will apply in the future). Topic modelling revealed differences in which of these uncertainties was a focus in SDM- versus non-SDM conservation planning articles. Similar proportions (~6%) of SDM- and non-SDM prioritisations focused on uncertainty in the future, specifically related to the threat of climate change (Fig. 1). Another 10% of SDM prioritisations focused on issues of biodiversity feature data accuracy and model uncertainty (predominantly related to commission and omission errors), whilst instead, non-SDM prioritisations focused more on uncertainty in management costs and alternative future threats such as urban development (14% of studies; Fig. 1).

Our detailed review showed that SDM prioritisations explicitly characterise and account for feature data uncertainty between 31 and 56% of the time (depending on whether this uncertainty relates to bias, data, or models), almost triple that of non-SDM prioritisations (Fig. 3b). Higher proportions of SDM prioritisations dealing with uncertainty and bias compared with non-SDM prioritisations suggests that SDM prioritisations have a greater capacity and/or a higher need to deal with uncertainty than those relying on alternative data sources. Failure to correct for data uncertainties in SDMs can, for example, produce SDMs that reflect sampling effort rather than true species distributions when geographic bias is correlated with bias in environmental space (Reddy and Dávalos, 2003). This can result in prioritisations incorrectly assigning high conservation value to areas that have been more intensively sampled (typically developed areas such as cities and roads). Similarly, temporal bias in distribution data can lead to prioritisation of areas that are no longer suitable for a species (e.g., when historic occurrence records fall within areas that have since been developed).

To deal with data uncertainties, both non-SDM- and SDM prioritisations relied only on recent and accurate field data provided by specialists (e.g., GPS location, signs, direct observations), or excluded species with incomplete distributional data or collection bias, modelling only focal species deemed to have 'complete' data (Stralberg et al., 2009; Williams, 2006). Using rigorous criteria to filter existing databases may reduce historical collection bias (e.g. National Carnivore Conservation Plans in Brazil; Table 3), and almost all SDM-prioritisations mentioned some kind of data filtering process (compared with <50% of non-SDM prioritisations). However, data filtering on its own is insufficient for dealing with the multiple uncertainties of conservation planning. Prioritisations may still be prone to spatial bias due to accessibility issues, or species bias due to surveyor preferences (Table 1). Furthermore, choosing surrogate or focal species by data availability instead of by an objective evaluation of the species' contribution towards conservation objectives can result in inefficient plans if excluded species provide higher benefits through complementary information (Tulloch et al., 2013a).

A number of approaches for dealing with uncertainty were specific to SDM-prioritisations. To deal with data uncertainty, SDM-prioritisations can compare errors in species distributions introduced by using alternative inputs such as presence-only instead of presence-absence data (Table 1) (Brotons et al., 2004; Hastie and Fithian, 2013; Lobo et al., 2010; Phillips and Elith, 2013), or explicitly model source(s) of error and bias during SDM development (e.g., by accounting for detectability or spatial sampling bias (McClintock et al., 2010; Phillips et al., 2009; Wintle et al., 2005). To deal with model uncertainty, one third of SDM prioritisations used sensitivity analysis to systematically vary model parameters or model structure to quantify their relative influence on model outcomes (Roura-Pascual et al., 2010). This allows one to identify the uncertainties that have the most influence on model outputs, identify redundant predictor variables, and evaluate which factors influence the selection of particular sites for reservation (Cariboni et al., 2007; Saltelli et al., 2006). Information-theoretic approaches were also used to deal with model uncertainty, in which a range of alternative models are fitted with one algorithm (e.g. GLM) and the best-supported models are combined (e.g. weighted average), allowing uncertainty related to different candidate models to be evaluated and accounted for when making predictions.

The best way to deal with uncertainty is to accept it and incorporate it explicitly into prioritisation approaches, through the use of information-gap decision theory (Moilanen et al., 2006b) or decision-support tools that allow probabilistic data to be included in site or action selection (e.g. Marxan with Probability, Zonation; Game et al., 2008). For instance, the California Landscape Conservation Cooperative used probabilistic model outputs in decision-support tools to allow uncertainty in species' distributions to be explicitly incorporated into decision-making (Table 3). These tools allow planners to account for potential errors in feature data distributions (e.g. probability of misclassification for remote sensing imagery or of species not occurring in a predicted location for SDMs) when selecting priority locations, and result in more areas being selected for reservation and increased total cost of action, but with reduced risk (Tulloch et al., 2013b). Such tools were rarely applied, but were more common in SDM- (Beaudry et al., 2011) compared with non-SDM prioritisations. Most SDM-prioritisations instead modified SDM outputs using a threshold, converting probabilistic data into values of 0 (unsuitable) and 1 (suitable), so that data could be used in non-probabilistic prioritisation approaches (e.g. Marxan). Although this binarisation is perceived to deal with uncertainty, threshold-setting can introduce misclassifications, and leads to loss of information (Table 1) (Guillera-Arroita et al., 2015).

4.4. Conservation goals: representation versus processes

Topic modelling revealed that, compared with non-SDM prioritisations, SDM-prioritisations often focused on reserve selection and current protected area representation of biodiversity features, with the words "reserve" and "protect" appearing in 41% of SDM-prioritisations (7 themes) compared with 28% of non-SDM prioritisations (4 themes). In contrast, non-SDM prioritisations were more focused on threats and evolutionary and ecological processes, such as connectivity and dispersal (25% versus 7% of non-SDM and SDM-prioritisations, respectively).

Only 53% of SDM-prioritisations compared with 74% of non-SDM prioritisations in our detailed review (Fig. 3c) acknowledged that dealing with ecological and evolutionary processes, such as demography, physiology, or dispersal, is important for making good conservation decisions. Priority areas for conservation investment are more likely to have long-term biodiversity benefits when processes responsible for maintaining and generating biodiversity are considered in their identification (Klein et al., 2009).

The most popular way to consider ecological processes in SDM-prioritisations was to incorporate a layer that directly mapped the occurrence of one or more processes involved in maintaining natural system functions (generally a map of connectivity, dispersal potential or barriers), which adjusts the conservation value of a location in the prioritisation (Gordon et al., 2009; Marini et al., 2009; Pascual-Hortal and Saura, 2007; Roura-Pascual et al., 2010). There was a wider range of alternative but generally less complex approaches to incorporating ecological and evolutionary processes in non-SDM prioritisations. Firstly, many studies used a surrogate or indicator species to represent a process. Several conservation plans did this; for example, in The Maputaland Conservation Planning System and Conservation Assessment (Smith and Leader-Williams, 2006), a map of elephant distribution was used to represent herbivory processes, and in the Alaskan Marine Arctic Conservation Action Plan (The Nature Conservancy, 2010), maps of benthic communities were used as process indicators of overall changes in the ecosystem. Non-SDM prioritisations also included a wide variety of layers representing ecological or evolutionary processes (Critical Ecosystem Partnership Fund (CEPF), 2005; Williams, 2006). In addition to general landscape connectivity surfaces built used least-cost distance models (Keel, 2005), other process maps were used to target particular taxon needs – for example, to ensure 'viability' of migratory species or species with large geographic ranges (Morgan et al., 2005; Williams, 2006), to maintain seed dispersal (Smith and Leader-Williams, 2006), or to connect feeding/breeding grounds (Birdlife International, 2005).

There was a clear dichotomy in the choice of non-SDM prioritisations to focus on including feature input data that accounted for threatening processes versus SDM-prioritisations that focused more on accounting for variability in biodiversity distributions (Fig. 1). After experts, data on the impacts (e.g., species' extinction risk) and distributions of threats (including intensity, frequency, and/or seasonality) were the most-commonly applied feature data source in non-SDM prioritisations (Fig. 2), most likely due to their ability to directly inform decision-makers about where specific actions might be taken. Prioritisations that incorporated threat mapping (e.g., human footprint, urbanisation, roads) and avoided SDMs appeared to accept the trade-off of having higher uncertainty in whether the species of concern were present in areas prioritised for action (accepting false positives), so that they could be more certain that actions were located in the areas where threats were acting or were likely to be present in the future. Assuming areas under threat, or where ecological processes occur, have high conservation value allows feature data such as threat maps or maps of rivers or fire regimes to act as surrogates for biodiversity information when data are scarce; however, this approach has the disadvantage of only informing on the process, rather than on biodiversity outcomes from managing the process (Tulloch et al., 2015). Both SDM- and non-SDM prioritisations acknowledged this trade-off between collecting species and threat data and the need for better information linking outcomes to actions (Fig. 4), e.g. "it would be better to incorporate data on how each threat specifically affects each species of concern. To accomplish such an analysis would require a tremendous effort that would likely be time and cost prohibitive" (Underwood et al., 2011).

Despite recent methodological and conceptual advances to modify SDMs to explicitly incorporate processes, such as spatially-explicit metapopulation models (Akcakaya and Regan, 2002; Keith et al., 2008; Naujokaitis-Lewis et al., 2013) that link individual models of habitat suitability, habitat dynamics, and population dynamics, and eco-physiological SDMs (Kearney and Porter, 2009) that incorporate physiological parameters to better understand processes limiting species' distributions (also see Table 3), none of the SDM prioritisations we reviewed considered these complex approaches. These models require more detailed input data, but are able to predict population processes such as extinction and colonisation, instead of probabilities of occurrence. They can also improve conservation outcomes through taking a dynamic rather than a static approach (Santika et al., 2015). The decision to include more process-based and dynamic approaches into prioritisations depends on objectives as well as the system. This includes considerations such as the availability of demographic data for the modelled species (which are generally only available for a few well-studied species), prevalence or importance of migratory or nomadic species, and whether the environment is relatively stable (e.g. boom-bust arid-zone systems; Greenville et al., 2014). Although there is clearly a desire to deal explicitly with modelling ecological, evolutionary, and threatening processes (Fig. 3), the larger proportion of non-SDM prioritisations in our review that did so suggests that the complexity of most approaches was beyond the capacity of many SDM prioritisations. For instance, the Alaskan Marine Arctic Conservation Plan (The Nature Conservancy, 2010) stated that population modelling (involving collection of life history data, capture-mark-recapture modelling, and satellite tracking of species) was more important than distribution modelling for their prioritisation process, likely due to the widespread nature of marine migratory target species and their threats (e.g. over-harvesting). Traditional, correlative SDMs are largely phenomenological and only implicitly incorporate threats and ecological and evolutionary processes. By not explicitly incorporating threats and processes, the predictive performance and ecological realism of these models are limited, bringing into question their ability to capture alternative goals such as ensuring population viability.

5. Ways forward

SDMs developed using ecologically relevant predictor variables (Austin, 2007) can help elucidate the factors that determine species distributions. Such information is invaluable for estimating effects of alternative conservation actions or how robust current protected areas are to potential environmental changes (Araújo et al., 2011; Kujala et al., 2013). However, there are many ways to prioritise threat mitigation for biodiversity. Choosing the most appropriate type of conservation input data and outputs (Table 1) should therefore start by evaluating the decision context, and the trade-offs and risks of using alternative data inputs or models for informing conservation decisions (Addison et al., 2013; Guisan et al., 2013; Tulloch et al., 2015). This will ensure that feature data choices are appropriate for the intended applications and objectives (Coutts and Yokomizo, 2014; Elith et al., 2010; Field et al., 2005; Roura-Pascual et al., 2010).

Our review suggests that there are many situations in which SDMs will not be appropriate to address conservation objectives. Firstly, if the objective is to conserve all the locations of a rare species for which the spatial distribution of all populations is largely known, then a SDM for that species would not be necessary (e.g., spiders in Durokoppin Nature Reserve: Avon Catchment Council, 2007) (Table 2). Secondly, if the objective is to conserve and protect ecological and evolutionary processes, or to mitigate multiple threats, which appears to be of concern to the majority of planners (Fig. 2), ecosystem-level maps and models of connectivity, productivity, threats, and the likely responses to their mitigation actions, may be more cost-effective than species-level SDMs (although in theory, SDMs could also be used to map these processes). Thirdly, if the objective is to conserve population processes, population-level models are required that may or may not involve spatially explicit information (e.g., the Alaskan Marine Arctic Conservation Action Plan; The Nature Conservancy, 2010) (Table 2). Coupling SDMs with population models might be useful in this situation, however, as this approach allows one to model effects of environmental change, catastrophes, and harvesting on abundance through time (i.e. extinction risk).

In our review, both scientists and practitioners consistently iterated the need to improve knowledge of species distributions, as well as the link between ecological and threatening processes and conservation outcomes (e.g. Austin and Van Niel, 2011) (Fig. 4). Determining the processes and ecological mechanisms that underlie biodiversity patterns can, however, be costly. The time, expertise, and computational resources required to produce individual SDMs linked to population and threatening processes, especially for plans at broad spatial scales that might have thousands of species within the planning region (Table 2), is likely to be outside the limitations of many budgets. In the case of species with few occurrence data, one option for reducing the costs and time required to build SDMs for every target species in a landscape is to build 'habitat models' that predict the distribution of species based only on the location of suitable habitat (e.g., Beaudry et al., 2011). For example, building an SDM predicting the distribution of a critical limiting food or nesting resource might allow planners to infer the presence or absence of a range of fauna reliant on that habitat (Delean et al., 2013). Statistical models of habitat distribution have been shown to perform as well as or better than models based on sparse species occurrences (Early et al., 2008).

Most distribution data are uncertain, leading to potential for inefficient conservation outcomes. We, therefore, recommend better use of existing approaches to account for uncertainty in conservation planning (Table S4), particularly by prioritisations not relying on SDMs. This might include evaluating the accuracy of habitat or threat maps prior to use (Beier et al., 2009; Smith et al., 2007), and using probabilistic data outputs in prioritisation approaches that explicitly account for uncertainty (e.g., Moilanen et al., 2006b; Tulloch et al., 2013b). A priori analysis of the expected improvement in the decisions made (either in cost-effectiveness, or accuracy due to reduced uncertainty) might also assist planners in understanding the benefits of incorporating additional data sources in conservation planning and threat management (Maxwell et al., 2015; Moilanen et al., 2006a; Runting et al., 2013). With such analyses, practitioners will then be in a better position to determine whether conservation outcomes could be more improved by e.g., (i) collecting demographic data and building population dynamic SDMs, (ii) incorporating maps of functional connectivity or future catastrophic change, or (iii) incorporating information on the likely effectiveness of threat mitigation actions. By applying this type of 'value-of-information' analysis, planners might evaluate how alternative information sources reduce uncertainty in conservation planning outcomes and refine prioritisations of where and when to act.

If data linking threats, species occurrences, or population trends to management actions are not available or are not cost-effective to incorporate in decision-making, and experts must be relied upon, there are alternatives to the practice of using experts to draw individual species distributions or derive habitat quality maps (Table 1). Experts can be beneficially used in two ways, depending on whether goals are focused more on incorporating non-biodiversity values or threat information. In the first instance, experts can select the most appropriate management locations through a participatory decision-making process that uses available data to map landscape-level attributes, socio-economic values, and history. In the second instance, a priority threat management process could be applied, which informs where and how actions will be most efficient by eliciting probabilistic information on the impacts of threats and their mitigation feasibility directly from experts (Carwardine et al., 2012). Whilst still applying the systematic conservation planning principles of comprehensiveness and representativeness, this new way of thinking allows threats to be managed at large scales without the requirement of spatially-explicit species distribution data (Chadès et al., 2015).

6. Conclusions

Our review indicates that conservation planners routinely select simple maps of processes and habitats to represent conservation features over more complex SDMs that might better account for uncertainty in biodiversity feature data but take more time to produce. Considering the value of alternative conservation feature data types for informing the planning goal, will help conservation planners choose the most appropriate data, given constraints such as planners' willingness to accept risk, the planning scale, time and funding (Runting et al., 2013; Tulloch et al., 2014). Although this kind of "value-of information" analysis is not routinely done, we believe it will lead to more robust conservation decisions through better use of available biological information. If planners are concerned about the choice of planning scale, or about feature data uncertainty, our review shows that SDMs are well-suited to explore such issues, with a range of approaches available to rescale or restructure models and assess alternative choices. If planners are concerned about accounting for ecological, evolutionary, and/or threatening processes, our review indicates that they frequently ignore issues of data and model uncertainty and accept inaccurate or biased proxies such as habitat maps and expert knowledge, so that time and money can be spent gathering often costly data that will inform on processes (e.g. dispersal rates or population genetics). Despite the benefits of incorporating even very simple probabilistic data to explicitly account for distribution, model, or landscape uncertainty in prioritisations, such approaches are still largely unexplored by many conservation planners. We recommend that in all cases, incorporating probabilistic outputs of SDMs or other inputs (e.g. remote sensing) directly into prioritisations will ensure that planners do not miss valuable conservation opportunities. We also suggest that increasing the complexity of SDM methods might have little impact on their use in conservation planning without a corresponding increase in research aiming at better incorporation of key ecological, evolutionary, and threatening processes.

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Appendix A. Supplementary data

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IDEA AND PERSPECTIVE

Predicting species distributions for conservation decisions

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Abstract

Species distribution models (SDMs) are increasingly proposed to support conservation decision making. However, evidence of SDMs supporting solutions for on-ground conservation problems is still scarce in the scientific literature. Here, we show that successful examples exist but are still largely hidden in the grey literature, and thus less accessible for analysis and learning. Furthermore, the decision framework within which SDMs are used is rarely made explicit. Using case studies from biological invasions, identification of critical habitats, reserve selection and translocation of endangered species, we propose that SDMs may be tailored to suit a range of decision-making contexts when used within a structured and transparent decision-making process. To construct appropriate SDMs to more effectively guide conservation actions, modellers need to better understand the decision process, and decision makers need to provide feedback to modellers regarding the actual use of SDMs to support conservation decisions. This could be facilitated by individuals or institutions playing the role of 'translators' between modellers and decision makers. We encourage species distribution modellers to get involved in real decision-making processes that will benefit from their technical input; this strategy has the potential to better bridge theory and practice, and contribute to improve both scientific knowledge and conservation outcomes.

Keywords

Biological invasions, conservation planning, critical habitats, environmental suitability, reserve selection, species distribution model, structured decision making, translocation.

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SETTING THE SCENE: SPECIES DISTRIBUTION MODELS FOR CONSERVATION APPLICATIONS

Species ranges are shifting, contracting, expanding and fragmenting in response to global environmental change (Chen *et al.* 2011). The emergence of global-scale bioinformatic databases has provided new opportunities to analyse species occurrence data in support of conservation efforts (Jetz *et al.* 2012) and has paved the way toward more systematic and evidence-based conservation approaches (Margules & Pressey 2000; Sutherland *et al.* 2004). However, records of observed species occurrence typically provide information on only a subset of sites occupied by a species (Rondinini *et al.* 2006). They do not provide information on sites that have not been surveyed, or that may be colonised in the future following climate change (Hoegh-Guldberg *et al.* 2008) or biological invasions (Thuiller *et al.* 2005; Baxter & Possingham 2011; Giljohann *et al.* 2011). However, this information is important for making robust conservation management decisions and can be provided by predictions of species occurrences derived from environmental suitability models that combine biological records with spatial environmental data.

Species distribution models (SDMs; also commonly referred to as ecological niche models, ENMs, amongst other names; see Appendix S1) are currently the main tools used to derive spatially explicit predictions of environmental suitability for species (Guisan & Thuiller 2005; Elith & Leathwick 2009; Franklin 2010; Peterson *et al.* 2011). They typically achieve this through identification of statistical

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relationships between species observations and environmental descriptors, although more mechanistic modelling approaches, and approaches involving expert opinion, also exist (Appendix S1). SDMs have the potential to play a critical role in supporting spatial conservation decision making (Margules & Pressey 2000; Addison *et al.* 2013; Appendix S2), but their applicability and relative utility across the breadth of conservation contexts remains unclear, as does the extent of their adoption in aid of conservation decision making.

The last decade has seen a surge in the development of SDMs (Fig. 1a, Appendix S3). However, despite large numbers of SDM-based studies published in the peer-reviewed literature, and widespread claims of applicability to conservation problems (Guisan & Thuiller 2005; Rodriguez *et al.* 2007; Cayuela *et al.* 2009; Elith & Leathwick 2009; Franklin 2010; Peterson *et al.* 2011), evidence of the practical utility of these models in real-world conservation management remains surprisingly sparse. An indicative assessment of keywords in ISI suggests that < 1% of published papers using SDMs are specifically targeted at conservation decisions (Fig. 1b, Appendix S3). A recent review of SDMs used in tropical regions (Cayuela *et al.* 2009) similarly concluded that < 5% of studies addressed conservation prioritisation. Furthermore, in the few published applications of SDMs to conservation decision making (e.g. Brown *et al.* 2000; Soberón *et al.* 2001; Ferrier *et al.* 2002; Leathwick *et al.* 2008), the importance of their contribution to the decision-making process and implementation of actions is often unclear (but see Pheloung *et al.* 1999). The bulk of the peer-reviewed literature clearly lacks the perspective of practitioners and decision makers on how SDMs can contribute to solving environmental problems, despite SDM construction often being justified based on their potential utility for decision making. As a result, there are a wide variety of tools published, but little guidance on how SDMs – and other models (Addison *et al.* 2013) – could be used to support decision making in relation to clear conservation objectives (Possingham *et al.* 2001). More practice-oriented assessments of the use of models to support conservation are urgently needed.

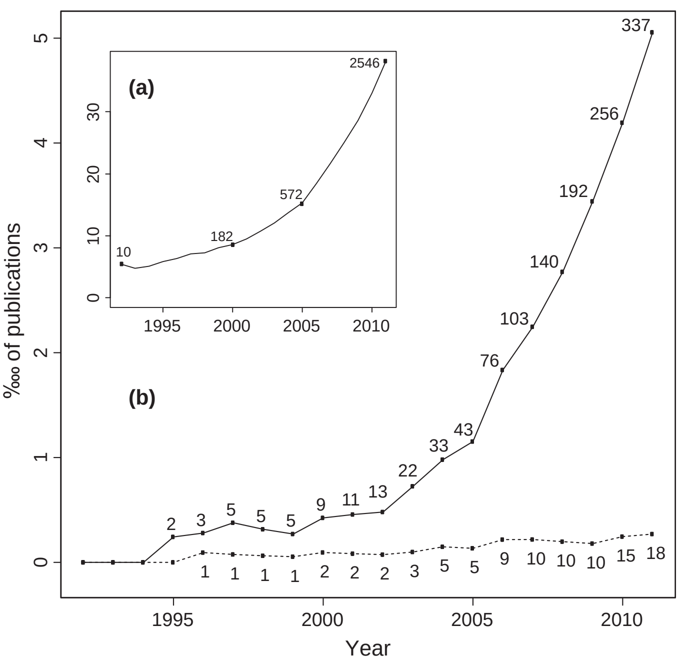

Figure 1 Cumulative trends over the last 20 years extracted from the Web of Science (WoS), showing the increasing number of peer-reviewed papers related to SDMs (keyword search). Curves are drawn as proportions (‱) of the cumulative number of papers published in the WoS category 'Ecology'. The cumulative number of papers for each year is indicated on the curves. (a) All SDM papers. (b) Only SDM papers in the four important conservation domains (biological invasions, critical habitat, reserve selection, translocation) discussed in the paper, without (solid line) or with (dashed line) the keyword 'decision'. For choice of keywords see Appendix S3.

Here, we investigate instances outside the peer-review literature where SDMs have been used to guide conservation decisions, how they were constructed when used, and how they could be used more effectively in the future. We do not propose a review of SDMs, or their use in conservation, nor do we undertake an exhaustive quantitative assessment of the grey literature, which is difficult to access in many countries. Rather, based on chosen examples in different countries (including developed and developing ones), we emphasise the importance of clearly articulating the decision context to determine where and how SDMs may be useful. We examine how closer consideration of the decision-making context and better collaboration with decision makers may encourage the development and use of SDMs for guiding decisions. Our primary focus is on statistical SDMs, as they are the most frequently and readily applied, although other approaches, such as mechanistic SDMs (Kearney & Porter 2009), may also provide input for conservation decision making.

FROM PROBLEMS TO DECISIONS: HOW CAN SDM CONTRIBUTE TO DECISION MAKING?

The potential of SDMs to guide conservation actions is best assessed by first considering the full decision-making process, a step rarely taken. Structured decision making (Gregory *et al.* 2012; Fig. 2) provides a rigorous framework for this process and is increasingly proposed to address environmental problems (Wintle *et al.* 2011; Addison *et al.* 2013). This approach is usually sequential (Possingham *et al.* 2001), with potential roles for SDMs at most stages of the decision process (Fig. 2, Table 1), as outlined below.

Identifying a problem

The need to make a conservation decision arises from the identification of a conservation problem (Fig. 2a). SDMs could play a role by highlighting likely shifts of suitable habitat for a species due to climate change (Araujo *et al.* 2011), or by identifying areas likely to be invaded by a pest species (Thuiller *et al.* 2005; Araujo *et al.* 2011), and therefore allow the identification of potential conflict areas if species may not be able to migrate across human-modified landscapes, or if the native communities at threat of being invaded shelter threatened species (e.g. Vicente *et al.* 2011).

Defining the objectives

Once a problem is identified, the definition of conservation objectives is usually the realm of decision makers and stakeholders. However, scientific input may be used to ensure objectives are realistic, given the current, or projected, state of the environment. SDMs may be used as a frame of reference for setting objectives retrospectively from the identified problem, or interactively by refining conservation objectives within an adaptive framework (Runge *et al.*

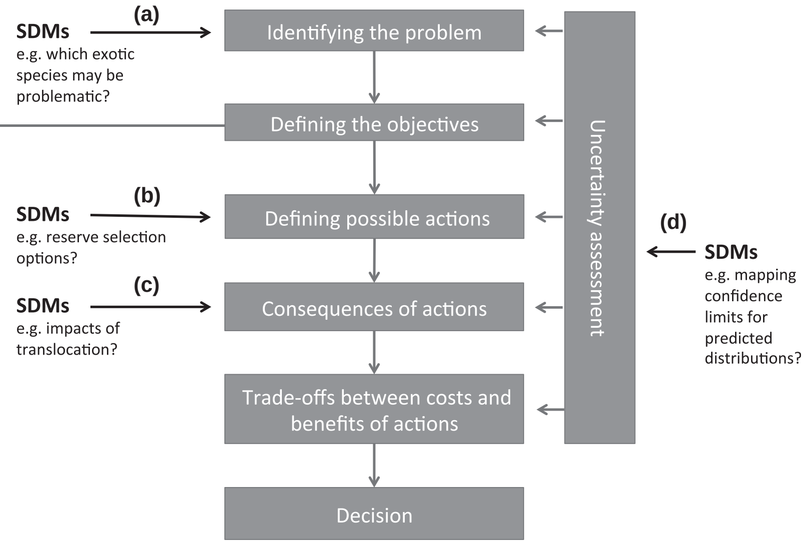

Figure 2 A structured decision-making process (Gregory *et al.* 2012) with indication of potential entry points for the use of SDMs. See main text and Table 1 for details. The black arrows indicate where SDMs can contribute to steps in the decision-making process.

Table 1 Examples of ways to increase the utility of SDMs within four conservation domains and the structured decision analysis process (DAP). The first five rows correspond to specific DAP steps, whereas the final three rows describe general issues requiring consideration.

	Biological invasions	Critical habitat	Reserve selection	Translocation
Problem identification	A new invader is likely to impact particular habitats.	Particular habitat patches drive species' extinction vulnerabilities.	Inappropriate habitat protection leads to higher extinction vulnerabilities.	The rate of climate change may exceed species' capacity to respond.
Defining the objectives	Reduce harmful impacts by prevention or mitigation of invasion.	Provide adequate habitat protection for threatened species.	Provide adequate habitat protection for threatened species.	Increase persistence probabilities of climate vulnerable species.
Defining possible actions	When and where to carry out quarantine, surveillance, eradication, containment or local control.	Strengthen protection, acquire new reserves, foster migration, translocation.	Acquire reserves, private landowner incentives, restoration, reserve management.	Translocate species, manage dispersal corridors, passive migration management.
Consequences of actions	Estimating the extent to which potential impacts may be prevented or mitigated through actions.	Estimating extent of opportunity costs for other habitat uses, estimation of extinction risk.	Estimating which subset of at risk taxa may be conserved.	Selecting subset of at risk taxa for action, risk of creating invasion problem.
Trade-off analysis	Cost efficiency of surveillance and management vs. risk of adverse impacts.	Social and economic conflict over land use.	Social and economic conflict over land use.	Cost-benefit and potential conflicts of placing species in novel environments.
Decision that can be informed by SDM	Predicting areas of potential occupancy to target surveillance and management.	Determining most favourable habitats.	Model diversity at a landscape level to set priorities.	Identify target locations for managed relocation.
How SDM uncertainty influences decisions	Under-prediction may miss critical surveillance, over-prediction may waste management resources.	Distribution model error misidentifies optimal habitats leading to excess opportunity costs or species extinction.	Uncertain suitable environments may lead to suboptimal reserve selection.	Spatial scale constraints limit the specificity of targeting locations.
Key issues for integrating science and management	Biotic interactions may play a strong role in determining environmental suitability in novel habitats.	Careful integration of population persistence processes into management decision.	Project regional diversity hotspots under global change models.	Apply SDMs to assess future distributions for species targeted for dispersal assistance.

2011). For example, initial objectives may be set based on low quality data but through the course of subsequent conservation and research actions, better quality data may inform an SDM and lead to changes in the initial objectives. It is essential that the outcomes of any subsequent action (see the following two points) be evaluated against the objectives (Chauvenet *et al.* 2012).

Defining possible alternative actions

The definition of feasible actions (Fig. 2b) may be informed by SDMs. For example, when making decisions about where to translocate a threatened species (Chauvenet *et al.* 2012) or where to target control of an invasive species (Baxter & Possingham 2011), SDMs may be used to identify candidate locations as alternative actions that may subsequently be evaluated in greater detail. Information about the costs of management actions, logistical constraints (e.g. distance) or conflicting conservation priorities (e.g. various land ownerships) for example will ultimately determine the feasibility of different actions, but the SDM provides a suite of options.

Evaluating the consequences of alternative actions

Species distribution models can be used to evaluate the implementation of alternative actions (Fig. 2c) in terms of predicting resultant changes to species' distributions, or to the quality of habitat. For example, use of SDMs has been proposed to assess alternative reserve designs and their role in conserving biodiversity under current and possible future climates (Hannah *et al.* 2007).

Assessing the trade-offs between benefits and costs of actions

This important step builds on the identified consequences of actions (Fig. 2). SDMs can be used to quantify benefits to be traded off against costs of actions, such as in prioritising competing wetland bird management options ranging from adding artificial habitat features to controlling disease outbreaks and changing pond inundation regimes (Sebastian-Gonzalez *et al.* 2011), or in optimising various control actions for invasive species across space (Giljohann *et al.* 2011).

Assessing and dealing with uncertainty

All conservation decisions are made in the presence of some uncertainty, and most involve the implicit or explicit specification of an acceptable level of risk (Fig. 2d). Assessment of risk includes estimation of the differential cost to biodiversity of errors associated with under-protection vs. over-protection (Schwartz 2012). In particular, the type (Barry & Elith 2006) and magnitude (Carvalho *et al.* 2011) of uncertainty that are acceptable need to be based on the needs of decision makers, and incorporated into the definition of the objectives (Richardson *et al.* 2009; Fig. 2a). SDMs enable the quantification of some types of uncertainties in the spatial predictions of environmental suitability (Barry & Elith 2006), and these can be explicitly incorporated in conservation prioritisation processes (Moilanen *et al.* 2006). However, some other types of uncertainties are not directly retrievable from SDMs (Appendix S1) but need to be recognised and where possible considered. When deciding whether to invest in reducing uncertainty, it is useful to consider whether the uncertainty is reducible (Barry & Elith 2006) and whether a reduction in uncertainty might lead to decisions that yield better management outcomes (Regan *et al.* 2005), a concept generally known as value of information (Runge *et al.* 2011).

EXAMPLES OF USING SDM FOR GUIDING CONSERVATION DECISIONS

Despite the numerous potential conservation applications proposed for SDMs, examples where SDMs have explicitly guided decisions relating to the management of natural resources are difficult to find in the scientific literature. We searched the grey literature (partially based on our own linkages with practitioners) and found various examples of the practical use of SDMs to guide decisions in different conservation domains, with differences in use intensity. We discuss four areas where SDMs have been used to guide management decisions: the use of climate-matching SDMs in some invasive species risk assessments (Managing biological invasions), the use of SDMs to guide the legal identification of critical habitats for threatened species (Identifying and protecting critical habitats), the use of SDMs in regional conservation planning (Reserve selection) and the use of SDMs for informing translocation of threatened or captive-bred populations (Translocation) (Table 1, Fig. 3).

Managing biological invasions

In some countries, SDMs are commonly used to guide decisions about invasive species management. For instance, Australia has implemented advanced detection, prevention and impact mitigation programmes that include SDMs. Pre-border weed risk assessment encourages the use of SDMs to aid decisions about whether to allow the import of new plant species (Pheloung *et al.* 1999; see *Defining possible actions*, Fig. 2b). Post-border weed risk assessments use maps of potential distributions, developed using SDMs, to assist in the identification of potentially widespread, high impact, invaders and to apportion control costs among potentially affected regions. SDMs are systematically used to contribute to the classification of species as weeds of national significance (NTA 2007). At the regional scale, such an approach recently contributed to the official listing of gamba grass (*Andropogon gayanus*) as a weed in the Northern Territory of Australia (NTA 2009; Fig. 3a). In Mexico, SDMs were used to predict the potential impact of the invasive cactus moth (*Cactoblastis cactorum*) on native cacti (*Opuntia* spp) to facilitate planning and mitigation of future impacts (Soberón *et al.* 2001).

Identifying and protecting critical habitats

Critical habitats are typically defined as habitats necessary for the persistence, or long-term recovery, of threatened species (Greenwald *et al.* 2012), and their identification is required by law in some countries (e.g. Canada, USA, Australia). SDMs are one tool for differentiating habitat quality at a range-wide scale, and can be combined with other sources of information, such as population dynamics, to define critical habitat (Heinrichs *et al.* 2010). In Canada, hybrid SDM-population dynamics models were used to determine critical habitat for the Ord's kangaroo rat (*Dipodomys ordii*; Heinrichs *et al.* 2010). In Catalonia (Spain), SDMs were used to identify critical habitats for four threatened bird species to guide land-use decisions in a farmland area affected by a large-scale irrigation plan. In the latter case, SDMs were first developed by scientists (Brotons *et al.* 2004), explained to practitioners (CTFC 2008) and finally influenced policy and were considered in a legal decree in the framework of the Natura 2000 network management plan (DMAH 2010; Fig. 3b; see Appendix S4). In Australia, the Victorian State Government developed SDMs for use in regulating vegetation-clearing applications (DEPI 2013).

Reserve selection

The delineation and establishment of protected areas often forms the cornerstone on which conservation plans are built (Margules & Pressey 2000). An early example of the use of SDMs in systematic conservation planning involved the development of SDMs for over

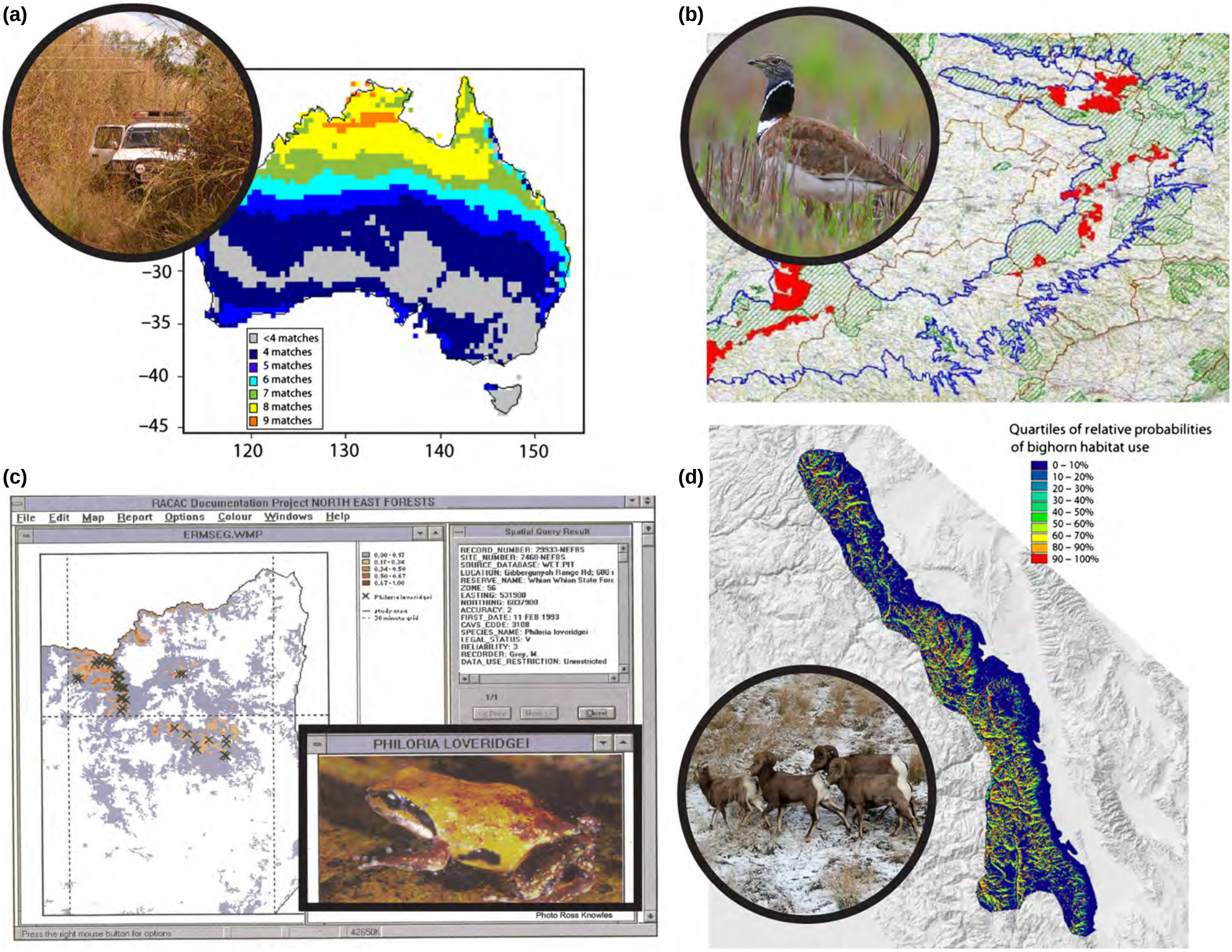

Figure 3 Four examples of maps used in conservation decision making based on SDMs. (a) Declaration of gamba grass (Andropogon gayanus, picture by Samantha Setterfield) as a weed using the weed risk assessment process in the Northern Territory of Australia (NTA 2009). (b) Identifying critical habitats (red) for three endangered bird species in Catalonia, Spain, as used in a legal decree (DMAH 2010) (picture of Tetrax tetra by Blake Matheson). (c) E-RMS tool windows and spatial query result for an endangered frog (Philoria loveridgei), as used in the conservation planning project for northeast New South Wales forests (Brown *et al.* 2000). (d) Identification of habitat use by the Bighorn sheep (Ovis canadensis sierra, picture by Lynette Schimming) in the Sierra Nevada, California, based on historical records only (NPS Seki 2011); SDM were not used to plan current translocation efforts but to predict the future distribution of potential translocation sites (Johnson *et al.* 2007).

2300 species of plants and animals throughout the northeast forests of New South Wales, Australia (results first presented in a report in 1994, cited in Brown *et al.* 2000; Ferrier *et al.* 2002). This region was the focus of a long-running conflict between the needs of commercial forest harvesting and the protection of exceptionally high biodiversity. The SDM outputs were integrated with data on other conservation and timber values in an environmental decision-support system by a team of negotiators representing all relevant government agencies and non-government stakeholders (see example in Fig. 3c). The aim was to identify areas of high conservation value for exclusion from logging, thereby resulting in major additions to the regional network of protected areas (Ferrier *et al.* 2002). This SDM application also provides an early demonstration of various approaches to evaluating and quantifying some sources of uncertainty in predictions (e.g. through expert ecological appraisal, cross-validation, and independent field testing), and to communicating this uncertainty to decision makers (e.g. through mapping of confidence limits for predicted distributions). In another example in Madagascar, SDMs for large numbers of species in the main biodiversity groups (mammals, birds, reptiles, amphibians, freshwater fishes, invertebrates, plants) were developed by scientists and managers, and used to define priority areas for conservation (Kremen *et al.* 2008) using the Zonation software (Moilanen *et al.* 2009). These were then combined with other 'priority areas' using the Marxan software (Watts *et al.* 2009) and put on the map of 'potential sites for conservation'. Following a legal decree (*Arrêté Interministériel* n18633/2008/MEFT/MEM, renewed in 2013), no mining and forestry activities can be permitted in these priority areas for conservation as long as the decree remains in force (Appendix S5).

Translocation

The active transport of species by humans has been proposed as a measure to mitigate the threats species face under present or future conditions (Richardson *et al.* 2009; Chauvenet *et al.* 2012). SDMs can potentially inform the translocation decision process at three key stages. First, SDMs can identify suitable habitat under current and future climates to reveal whether habitat suitability is likely to decline in regions currently occupied by the species (Fig. 2a), thereby supporting the decision of whether translocation is necessary (Hoegh-Guldberg *et al.* 2008; Thomas 2011). Second, if translocation is deemed necessary, SDMs can identify potential recipient sites, which may be climate refugia within the current range, or sites that are projected to become newly suitable (Chauvenet *et al.* 2012; McLane & Aitken 2012; Fig. 2b). Third, SDMs can be used to identify which local species may be at risk of impact from the introduction of a translocated species through predicted overlapping distributions, in the same way as they are used to identify conflict areas between native and invasive species (Vicente *et al.* 2011; Fig. 2c). An example of the identification of suitable translocation sites in present and/or future climates exist for the bighorn sheep (*Ovis canadensis sierrae*) in the Sierra Nevada (Johnson *et al.* 2007; NPS Seki 2011; Fig. 3d). An SDM was used to identify suitable sites for reintroductions and translocation by avoiding areas of overlap with existing grazing stock allotments and areas of high predator densities.

These four groups of examples show that SDMs can be used to guide different decision-making steps in different conservation contexts (Table 1, Figure 2). Yet, the bulk of SDMs currently remains primarily developed for scientific purposes. However, as we show below, the way SDMs are built may vary depending on the requirements of the decision-making context, which are primarily influenced by the conservation objectives and the decisions to be made (often – but not necessarily – defined independently of the SDMs; e.g. select reserves to minimise biodiversity loss below some arbitrary threshold).

TOWARD A DECISION-MAKERS PERSPECTIVE: HOW CAN THE DECISION-MAKING CONTEXT GUIDE SDM DEVELOPMENT?

Many methodological choices are made when building and using an SDM (Guisan & Thuiller 2005; Elith & Leathwick 2009; Franklin 2010; Peterson *et al.* 2011), often with very general, research-oriented objectives in mind, such as answering macro-ecological questions, predicting range shifts under climate change (Keith *et al.* 2008; Carvalho *et al.* 2011; Fordham *et al.* 2012) or assessing the potential spread of invasive species (Thuiller *et al.* 2005). The use of SDMs is conditional on the availability of suitable data, skilled staff, modelling tools, funds and time. Many methodological factors, such as error in locational or temporal accuracy, or biased data, also potentially affect SDMs and their predictions (Kadmon *et al.* 2003; Cayuela *et al.* 2009; Appendix S1). Using an inappropriate modelling method or disregarding influential methodological factors can have consequences for the intended use of an SDM. The utility of an SDM for decision makers is therefore highly context sensitive. Below, we present examples that show why choices of various options for building/using an SDM may require more careful attention in a decision-making context where modelling methods should be determined by the nature of the conservation problem at hand and the decision to be made (Table 1).

Decision context

The example from the northeast forests of New South Wales (Brown *et al.* 2000; Ferrier *et al.* 2002) provides a rare documented case where all necessary conditions for building SDMs in a conservation context were met. Foresight by planners in the state environmental agency and funding by both commonwealth and state governments, along with data availability and sufficient lead-time for skilled staff to develop SDMs appropriate for the conservation objectives, made the use of SDMs in the decision-making process possible. The Madagascar case is another example where careful evaluation of the decision needs led to appropriate decisions for building SDMs, in this case by: ensuring species-environment temporal matching, using models above some validation threshold only, correcting for biogeographical overprediction and adding expert validation. In some cases, however, an SDM could be constructed for a species in the context of a conservation action to be taken, but the desired outputs (e.g. spatial predictions, ecological response curves) may not meet the criteria (e.g. spatial accuracy, level of certainty) necessary for its contribution to a final decision. Hence, early awareness of decision criteria increases the chance of developing SDMs that are useful for decision makers. This requires a close association between decision makers and SDM-developers from the onset of SDM development (McAlpine *et al.* 2010). Collaboration between decision makers and SDM-developers also offers opportunities for evaluation of other sources of ecological knowledge and data as a substitute for or complement to SDMs.

Time

Many threatened species have restricted distributions and specific habitat requirements, so decisions to protect critical habitat may need to be made with some urgency to avoid extinction (Martin & Maron 2012). This urgency often leads to protection of minimum amounts of habitat based on occurrence data alone. For example, the endangered Banff Springs snail (*Physella johnsoni*) is found in only five thermal springs, all of which are designated as critical habitat for this species (Lepitzki & Pacas 2010). In such cases, allocating time to collect more data and build accurate SDMs or more complex spatially explicit population models may not necessarily improve predictions but may delay the action of protection. However, deciding to build a simple SDM, or to not build one at all, may overlook some potentially critical habitats for the species (Heinrichs *et al.* 2010). There is thus a trade-off between allocating conservation resources to model construction or to immediate action with uncertain consequences (McDonald-Madden *et al.* 2008). For situations where time is less critical, more sophisticated SDMs might suggest new sites where a threatened species could be found, or areas that could be recolonised (Fig. 2b), as demonstrated in the cases of the Sierra Nevada bighorn sheep (*Ovis canadensis sierra*; NPS Seki 2011; see above) and the whitebark pine (*Pinus albicaulis*) in western North America (McLane & Aitken 2012).

Population dynamics

Modelled probabilities of occurrence from SDMs may not always correlate with the population processes necessary for species' persistence (Fordham *et al.* 2012). In such cases, it may be necessary to combine process-models such as population viability analyses with

SDMs to better evaluate the effects of management actions on long-term species' persistence (Keith *et al.* 2008; Wintle *et al.* 2011; Fordham *et al.* 2012). Such an approach was recently used to assess critical habitats for Ord's kangaroo rat in Alberta, Canada (Heinrichs *et al.* 2010) and revealed that 39% of habitat predicted as suitable for this species is unlikely to contribute to population viability. These habitats are therefore unlikely to support long-term species persistence and should not be given high conservation priority. This study highlights the importance of using, e.g. hybrid SDM-population models and/or the use of proximal environmental variables (Austin 2007) directly relevant to the species' demography (Eckhart *et al.* 2011) when predictions of species' persistence are the primary modelling output.

Type of error

Species distribution model predictions are susceptible to two types of errors (Franklin 2010): suitable habitat predicted as unsuitable (false negatives) and unsuitable habitat predicted as suitable (false positives). Both errors can be costly when using SDMs to support conservation decisions. For example, for biological invaders, false negatives are considered more serious than false positives at the pre-border stage, as underestimating the extent of a species' potential distribution could lead to an incorrect decision to allow import (Pheloung *et al.* 1999), which might subsequently lead to high impact and mitigation costs (Yokomizo *et al.* 2009). However, for established invaders, both types of errors can matter. False negatives may result in invaders being incorrectly labelled as harmless in a given area, leading to a failure to establish appropriate surveillance or containment measures. Alternatively, false positives can lead to wasted surveillance effort, or concentration of management effort in inappropriate areas (Baxter & Possingham 2011). Deciding how to balance both types of error will thus vary from one decision-making context to another, depending on the consequences of the errors in relation to the conservation objective. Errors can emanate from several sources (e.g. data, algorithm, parameterisation options), but one factor that has a direct effect on error rates is the choice of a threshold to classify continuous predictions of environmental suitability as either 'unsuitable' or 'suitable' (Franklin 2010). Several criteria exist that depend on the type of species data. For SDMs built with presence-only data, predictions of environmental suitability are not probabilities of occupancy but rather relative surrogates of occupancy, as the baseline probability of occupancy (i.e. prevalence) is typically unknown and cannot be used as the criterion. For presence–absence SDMs, the decision to set a certain threshold can be formally considered by explicitly accounting for the respective consequences of each type of error (omissions, commissions) when choosing a threshold, or by using different thresholds for different decisions (e.g. when to monitor, when to eradicate, when to change categorisation of threat; Field *et al.* 2004; Royle & Link 2006). A promising alternative is to base decisions on the continuous environmental suitability predictions derived from SDMs and incorporate the uncertainty directly, rather than categorising 'suitable' and 'unsuitable' habitat using specific thresholds (Moilanen *et al.* 2005). The important point is that decision makers need to specify the intent of SDM predictions so that modellers can understand the implications of the different types of errors. Ideally, this would be an iterative process involving modellers and decision makers, whereby methodological decisions such as model complexity and choice of threshold are continuously updated until decision-makers are satisfied with the balance of both types of errors.

Uncertainty

Given the large variability in output resulting from using different SDM techniques, data or environmental change scenarios (Appendix S1), it is important to quantify uncertainty in environmental suitability predictions used to make decisions (Moilanen *et al.* 2006; Carvalho *et al.* 2011). However, it is critical that conservation scientists specify which components of uncertainty are estimated (Barry & Elith 2006) and which are not. For example, using an ensemble of global climate models (GCMs) to project future distributions will provide a suite of projections from which means and variances of suitability can be calculated. This measure of uncertainty, however, can only capture the uncertainty derived from different projections of future climate and does not include uncertainty that derives from different model constructions, errors in the species data used to fit the model, in the estimation of current climate, or in the goodness-of-fit of the SDM. In addition, this uncertainty estimate assumes that the ensemble model captures the spectrum of potential future climates: an attribute that the current suite of GCMs is not designed to have (Schwartz 2012). New structured approaches for dealing with uncertainty associated with SDM outputs (Barry & Elith 2006; Appendix S1) exist in conservation decision support tools such as Marxan (Carvalho *et al.* 2011) and Zonation (Moilanen *et al.* 2006). These generally involve some form of assessment of the robustness of decisions to large errors in key data, models or assumptions (Regan *et al.* 2005; Wintle *et al.* 2011). For instance, info-gap decision theory has been used to identify reserve networks that achieve conservation targets with the highest robustness to uncertainty (Moilanen *et al.* 2006). Because much uncertainty about the predictions of SDMs is irreducible (Regan *et al.* 2005; Barry & Elith 2006), methods for explicitly dealing with this uncertainty in decision making will be critical for successful application.

WHY HAVE SUCCESSFUL EXAMPLES OF SDM SUPPORTING DECISION MAKING BEEN SO POORLY REPORTED?

We have found evidence that SDMs can help guide decisions (e.g. Brown *et al.* 2000; Soberón *et al.* 2001; NTA 2007; US Fish & Wildlife Service 2007; CTFC 2008; Cayuela *et al.* 2009; NTA 2009; DMAH 2010; Lepitzki & Pacas 2010; Environment Canada 2011; NPS Seki 2011), but most examples are hidden in the grey literature and only rarely reported in the peer-reviewed literature. Our keyword search (Fig 1 and Appendix S3) suggested that applications to decision problems are rare compared to the breadth of published SDM-based conservation papers. This suggests that reporting, to the scientific community, of successful use of SDMs to support decision making is sparse, and leaves open the question as to how many of these successful applications actually exist but remain largely hidden? A useful perspective in this regard would be to assess comprehensively how frequently and how effectively SDMs have been used in practice to support conservation decisions in a large number of countries.

Greater clarity in these issues is incumbent upon both scientists, who need to better explain the potential value of their models to managers, and managers, who need to feed the results of existing model applications back to scientists. This viewpoint considers the whole conservation decision-making framework and process as one within which these two groups should have ideally been involved. A variety of decision-making systems exist. Here, we have outlined a decision process that entails defining a problem, defining objectives, identifying potential actions, describing consequences of those actions, assessing associated uncertainty and considering trade-offs among these consequences (Gregory *et al.* 2012; Schwartz *et al.* 2012; Addison *et al.* 2013; Fig. 2). Having a common, transparent framework that both decision makers and modellers can access is part of the solution to making better conservation decisions. However, considerable barriers remain which must be overcome. Broader inclusion of SDMs in decision-making processes seems limited by engagement impediments (see below). The published cases of SDMs developed for conservation purposes highlight the need for scientists to do a better job of engaging decision makers early in the development of SDMs but also conversely for decision makers to involve scientists early in the decision process. It is easy for scientists to become focused on developing and improving tools with relatively little attention to the information needs of decision makers. In turn, SDMs remain difficult for non-experts to use confidently, because there are many methodological options, high output variability and many nuances to consider for their targeted applications (Addison *et al.* 2013). Consequently, although scientists and decision makers often need similar information to solve their respective questions (e.g. spatially explicit distribution data), these communities can remain disconnected, with results from research left unread and unused by decision makers, and constraints faced by decision makers not known or not considered by researchers (Soberón 2004; Sutherland & Freckleton 2012).

There are also cultural differences between researchers and decision makers arising from differences in sources of funding, career aspirations, temporal contingencies to solve problems, or differences in the philosophy of the evaluation of the work done (i.e. economic vs. peer-reviewed; Laurance *et al.* 2012). This disparity results in researchers too rarely communicating with decision makers, and decision makers too often not inviting researchers (and especially modellers) to participate in the decision-making process (Cash *et al.* 2003; Soberón 2004; Addison *et al.* 2013). The lack of information exchange across the research/management boundary reflects a failure of researchers to answer real conservation management questions (Knight *et al.* 2008), and a failure of decision makers to capitalise on useful research outputs (Schmolke *et al.* 2010; Addison *et al.* 2013). This problem is exacerbated by the almost overwhelming peer-reviewed science literature, the bulk of which can be hard to access and/or not directly relevant to management needs (Haines *et al.* 2004; Sutherland *et al.* 2004; Pullin & Knight 2005; Knight *et al.* 2008), controversy surrounding terminology and modelling philosophy (Appendix S1) and by the often confidential communication streams that drive agency and organisational decisions (Cash *et al.* 2003; Schwartz *et al.* 2012). Finally, SDMs may be used, but their conservation application not reported, since practitioners often lack the time or incentive for publishing their findings in the scientific literature.

BRIDGING THE GAP BETWEEN MODELLERS AND DECISION MAKERS

Making SDMs more useful in decision making requires improved communication, appropriate translation of scientific and decision-context knowledge, mediation and timely collaboration between researchers and decision makers to ensure that SDMs are designed to meet the needs of, and constraints faced by decision makers (Cash *et al.* 2003; Addison *et al.* 2013). This could partly be achieved by making SDMs compliant with the *Open Standards for the Practice of Conservation* (Schwartz *et al.* 2012), an operationalised multi-criteria framework used to plan and prioritise conservation actions. In many instances, however, decision making does not proceed in a linear fashion (as in Fig. 2), or managers may object to the use of models (Addison *et al.* 2013), making it difficult for researchers to design the most appropriate SDMs. Therefore, the greater the transparency in the decision-making process (Gregory *et al.* 2012; Schwartz *et al.* 2012), the more likely researchers will be able to provide models and outputs that are actually useful in that process. In turn, the greater the transparency in the modelling tools, and their linkage to ecological theory (Appendix S1), the more likely managers will be able to use them (Schmolke *et al.* 2010). We have observed that SDM applications and their explicit conservation objectives, particularly in the grey literature, tend to be insufficiently documented and, therefore, are difficult to assess and reproduce, with some notable exceptions (e.g. the Madagascar case study in Appendix S5, NaturePrint in S7). Developing SDMs with a clear understanding of the decision problem at hand fosters the development of SDMs that deal appropriately with issues such as spatial scale, species considered, variables to include in the model, time frame for the study and the use of projections of environmental change (Schwartz 2012).

Developing more useful SDMs to assist conservation decisions is a necessary condition, but obviously not sufficient to have SDMs routinely used by decision makers. Communication, translation and mediation between scientists and decision makers are reported as necessary functions to better bridge the research/management gap in other fields (Cash *et al.* 2003), and reported as particularly critical in the case of SDMs (e.g. Schwartz *et al.* 2012; Addison *et al.* 2013). As suggested by Soberón (2004), these functions could be performed by intermediate institutions playing the role of 'translator' (or facilitators) between scientists and decision makers (Fig. 4), but the concept can also be expanded to individuals, groups or consortia (e.g. BI/FAO/IUCN/UNEP; see van Zonneveld *et al.* 2011; Appendix S6). These translators would synthesise, standardise and communicate the most recent scientific insights useful for solving identified problems to managers (Fig. 4), and mediate the different steps of a structured decision process (Fig. 2) to ensure that modellers and managers are jointly involved where needed. It is an important aim of our paper to promote this linkage. Such institutions already exist in some countries (see Table 1 in Soberón 2004; Appendix S6), but could be promoted in other countries and their role as translator institutions clarified and made more systematic. Such institutions could ensure that modellers are informed on precisely how SDMs are used in particular decision contexts so that their development can be adjusted and improved in future applications (Fig. 4). Such translators could also ensure that SDMs comply with the Open Standards for conservation discussed above (Schwartz *et al.* 2012). Institutions playing this translator role may stand alone as governmental or non-governmental bodies (e.g. CONABIO in Mexico or the Future Earth programme; Appendix S6), be nested within institutions with other primary functions (e.g. universities, government departments; e.g. Centre for Evidence-Based Conservation; Appendix S6), or be virtual web-based entities such as the recent Environmental Evidence initiative (Pullin & Knight 2005; Appendix S6). Individuals need to be trained, encouraged and

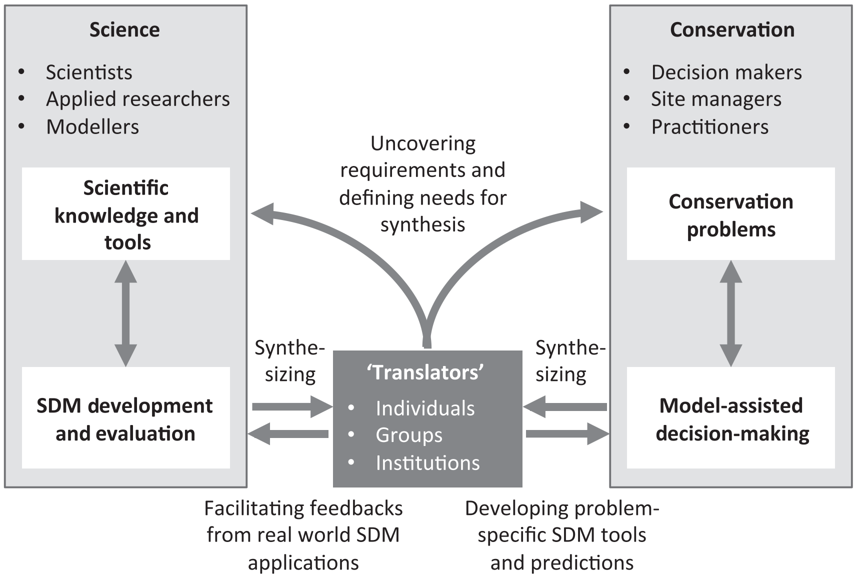

Figure 4 Proposed role of 'Translators' (being individuals, groups or institutions; Cash *et al.* 2003; Soberón 2004) as bridges between SDM development and conservation decision making. See Figure 2 for details of the steps of the structured decision-making process and where SDM can provide support.

rewarded for taking on 'translator' roles and engaging directly with modellers and decision makers.

Translators can provide a valuable service in promoting and supporting the development of appropriate tools for management. However, although an increasing number of online initiatives are making it easier for non-experts to directly access biodiversity data and build SDMs through user-friendly web interfaces (Graham *et al.* 2010; Jetz *et al.* 2012), these web tools only afford – in their current implementation – a limited ability to explore different data sets and model settings (Table 2; Appendix S7). They therefore currently cannot be considered sufficient alternatives to the direct involvement of professional modellers in a decision process, ideally mediated by translators. For example, key components of the model building process (e.g. use of a combination of techniques, evaluation of model fit and performance, uncertainty assessment, inspection of response curves) are currently not available in most of the popular applications (Table 2), although potentially crucial to support decision making. While we hope that options to refine biodiversity data sets and SDM settings become more widely available in the future (Jetz *et al.* 2012), we cannot advocate the use of overly simplified tools to support conservation decisions (e.g. the use of box-like envelopes may inflate areas identified as critical habitat requiring protection, and thus conservation cost). The increasing availability of these tools in the future will therefore make close collaboration between modellers and decision makers even more critical, as there is the potential for perverse conservation decisions to be made on the basis of poorly developed and understood models. What we need is not simpler implementations of SDMs, but a wider recognition that SDMs should be developed by experts with a clear conservation objective in mind and a clear knowledge of the decision process in which they take part. Translators, participatory or co-design principles (Appendix S6) may all be involved in achieving useful and appropriately used SDMs.

Better understanding of the decision process and its constraints would allow modellers to determine whether or not an SDM can be used, and if so, which type of SDM is best suited. It is usually not enough to read about a conservation problem, it is incumbent upon scientists to reach out to decision makers to understand their needs in making a decision, and it is incumbent upon decision makers to report to modellers how SDMs have been used to support decisions to enable iterative improvement of models. More visibility of partnerships between researchers and decision makers in the scientific literature will motivate the development of better-integrated SDM approaches that have a higher chance of being used to inform important conservation decisions. Finally, a better integration of SDM science and management would be beneficial to conservation decision making but would also advance our understanding of basic ecological processes.

THE OUTLOOK

This study was motivated by our observation that conserving biodiversity is important, that SDMs may contribute to this aim, but that more useful SDMs can be developed through practice-oriented case studies. Conservation science has made significant progress in developing an applied arm that helps managers make better decisions (Sutherland *et al.* 2004; Pullin & Knight 2005; Gregory *et al.* 2012; Schwartz *et al.* 2012; Sutherland & Freckleton 2012). At the same time, SDMs have benefitted from over two decades of development as a set of tools with many potential conservation applications (Guisan & Thuiller 2005; Rodriguez *et al.* 2007; Franklin 2010; Peterson *et al.* 2011), but have remained largely the purview of academic studies that inform other academic scientists. These tools are now sufficiently mature to take on a larger role in supporting conservation decisions. Yet, although successful SDM applications exist, they remain poorly reported in the scientific literature, suggesting the linkage between SDM science and practice is still weak. We identified three critical components likely to better bridge these two communities. First, SDM scientists need to better engage decision makers and understand the decision-making process, to better assess how and when SDMs could be used to guide conservation decisions. Second, SDMs must be designed to meet the spatial and tem-

Table 2 Examples of online SDM tools (web information acquired May 2013) for predicting the distributions of a large number of species. All examples allow users to upload occurrence data and fit models online, but with very little flexibility in model parameterisation and evaluation. See also Appendix S7.

Programme	Atlas of Living Australia (ALA)	LifeMapper (LM)	National Institute of Invasive Species Science (NIISS)	OpenModeller (OM) coupled with Global Biodiversity Information Facility (GBIF)
1. Name of supporting organisation(s)	Atlas of Living Australia, Canberra (Australian branch of GBIF)	Consortium of US Universities and University of Goias in Brasil	National Institute of Invasive Species Science (US consortium of govern. and non-govern. organisations)	Centro de Referência em Informação Ambiental (CRIA), Escola Politécnica da USP (Poli), and Instituto Nacional de Pesquisas Espaciais (INPE), Brasil
2. Can occurrence data be vetted for accuracy?	Yes	No	No	Yes
3. Predictors available	Climate, topography, land-use	Climate	Climate	Terrestrial – climate; Marine –climate, bathymetry and satellite data
4. Modelling techniques	MaxEnt, GDM	BIOCLIM, GARP*	Maxent, BRT	Envelope Score
5. Spatial coverage	Australia	Global	USA	Global
6. Temporal extent of predictor variables	Current	Current + Future (3 IPCC scenarios)	Current + Future (1 scenario/GCM)	Current
7. Uncertainty assessment?	No	No	Yes (SD across 3 runs)	No
8. Website link	http://www.ala.org.au/	http://lifemapper.org/	www.niiss.org	http://data.gbif.org/http://openmodeller.sourceforge.net/
9. Link to an official occurrence database	ALA	GBIF	NIISS	GBIF
10. Reference (if available)	–	Stockwell *et al.* 2006;	Graham *et al.* 2010;	Munoz *et al.* 2011

*ANN, Aquamaps, CSM, SVM and ED to be included in future versions.

poral needs of the conservation problems using transparent methods (e.g. Open Standards) that incorporate uncertainties and recognise model limitations, especially given potential legal consequences of decisions. Third, decision makers must in turn provide feedback to modellers about the success or failure of SDMs used to guide conservation decisions (i.e. practical limitations, key features of success). To achieve progress, we support the role of 'translators' (institutions, groups or individuals) to facilitate the link between modellers and decision makers. We strongly encourage species distribution modellers to get involved in real decision-making processes that will benefit from their technical input. This strategy has the potential to better bridge theory and practice, and to contribute to improve both scientific knowledge and conservation outcomes.

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AUTHORSHIP

AG organised the three workshops and study design, with support from YMB and HPP. All co-authors attended at least one of the workshops and/or interacted by videoconference with the group. All authors helped outlining the manuscript and contributed substantially to its writing. RT and YMB led the invasive literature search with help from SAS, OB, JE, LB and AG. AITT, PRS and HPP led the reserve selection literature search, with help from LB, CMP, JRR, SF, JE, LB, INL and AG. JBB and TJR led the translocation literature search, with help from EMM, CMP, TGM, MRK and AG. INL and TGM led the critical habitat literature search, with help from RM, AITT, LB and AG. MWS and BAW contributed substantially to the bridge with practitioners section. MWS and YMB drafted Table 1. AG and OB prepared all figures.

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How species distribution models can improve cat conservation - jaguars in Brazil

Modeling species distribution is a promising field of research for improving conservation efforts and setting priorities. The aim of this study was to produce an environmental suitability map for jaguar distribution in two biomes in Brazil – Caatinga and Atlantic Forest – , where the species is Critically Endangered as part of the Jaguar National Action Plan workshop (Atibaia, São Paulo state). Species occurrence (N = 57 for Caatinga and N = 118 for Atlantic Forest), provided by jaguar specialists, and ten environmental predictors (elevation, land cover, distance from water and bioclimatic variables) were used to generate species distribution models in Maxent. Both models presented high predictive success (AUC = 0.880 ± 0.027 for Caatinga and AUC = 0.944 ± 0.022 for Atlantic Forest) and were highly significant (p < 0.001), predicting only 18.64% of Caatinga and 10.32% of Atlantic Forest as suitable for jaguar occurrence. The species distribution models revealed the low environmental suitability of both biomes for jaguar occurrence, emphasizing the urgency of setting conservation priorities and strategies to improve jaguar conservation such as the implementation of new protected areas and corridors for species dispersal.

Predicting species distribution has made enormous progress during the past decade. A wide variety of modeling techniques (see Guisan & Thuiller 2005) have been intensively explored aiming to improve the comprehension of species-environment relationships (Peterson 2001). The species distribution modeling (SDM) relates species distribution data to information on the environmental and/or spatial characteristics of those locations. Combinations of environmental variables most closely associated to presence points can then be identified and projected onto landscapes to identify areas of predicted presence on the map (Soberón & Peterson 2005, Elith & Leathwick 2009). The geographic projection of these conditions (i.e., where both abiotic and biotic requirements are fulfilled) represents the potential distribution of the species. Finally, those areas where the potential distribution is accessible to the species are likely to approximate the actual distribution of it.

The jaguar, the largest felid in the Americas, has been heavily affected by retaliation killing for livestock predation, fear, skin trade, prey depletion, trophy hunting (e.g. Smith 1976, Conforti & Azevedo 2003) and habitat loss (Sanderson et al. 2002). As a consequence, it is now restricted to ca. 46% of its former range (Sanderson et al. 2002).

Table 1. Environmental predictor variables used in jaguar distribution model.

Variables	Description
Land cover	Land cover map from GlobCover Land Cover version V2.3, 2009
Elevation	Elevation map by NASA Shuttle Radar Topography Mission
Distance from water	Map of gradient distance from water obtained from vector map of rivers from IBGE
Bioclimatic variables	Maps of bioclimatic variables from Worldclim:
	Bio1 = Annual mean temperature
	Bio2 = Mean diurnal range (mean of monthly (max temp - min temp))
	Bio5 = Max temperature of warmest month
	Bio6 = Min temperature of coldest month
	Bio12 = Annual precipitation
	Bio13 = Precipitation of wettest month
	Bio14 = Precipitation of driest month

Environmental suitability models have been produced for jaguar distribution in Brazil during the Jaguar National Action Plan Workshop, facilitated by IUCN/SSC CBSG Brazil and organized and funded by CENAP/ICMBio, Pró Carnívoros and Panthera, in November 2009, Atibaia, São Paulo state, Brazil. During the workshop, jaguar specialists provided occurrence point data for species distribution modeling. A jaguar database was composed only by recent (less than five years) and confirmed records (e.g., signs, telemetry, camera-trapping, chance observations). All models and detailed information about the procedure and the results are included in the Jaguar National Action Plan. Background information on SDM and necessary considerations are summarized in the Supporting Online Material Appendix I (www.catsg.org/catnews). Here, to illustrate the potential of the use of the SDM for cat conservation, we presented the environmental suitability models for jaguar in two biomes (Caatinga and Atlantic Forest, Fig. 1), where the species is considered Critically Endangered in Brazil (de Paula et al. 2012, this issue; Beisiegel et al. 2012, this issue).

Methods

Jaguar distribution was modeled for each biome separately considering the differences between the environmental spaces (i.e., conceptual space defined by the environmental variables to which the species responds). The biome map used was obtained from a Land Cover Map of Brazil (1:5.000.000), 2004, by the Brazilian Institute of Geography and Statistics, IBGE (available for download at http://www.ibge.gov.br/).

Predictive distribution models were formulated considering the entire available jaguar dataset as the dependent variable (presence points) and the selected environmental variables as the predictors (Table 1). Jaguar data available for modeling (N = 57 for Caatinga; N = 118 for Atlantic Forest; Fig. 2) were plotted as lat/long coordinates on environmental maps with a grid cell size of 0.0083 decimal degree^2 (~1 km^2).

Models were obtained by Maxent 3.3.3e (Phillips & Dudík 2008) using 70% of the data for training (N = 40 for Caatinga and N = 66 for Atlantic Forest) and 30% for testing the models (N = 17 for Caatinga and N = 28 for Atlantic Forest; Pearson 2007). Data were sampled by bootstrapping with 10 random partitions with replacements. All runs were set with a convergence threshold of 1.0E–5 with 500 iterations, with 10,000 background points.

The logistic threshold output format was used resulting in continuous values for each grid cell in the map from 0 (unsuitable) to 1 (most suitable). These values can be interpreted as the probability of presence of suitable environmental condition for the target species (Veloz 2009). The logistic threshold used to "cut-off" the models converting the continuous probability model in a binary model was the one that assumed 10 percentile training presence provided by the Maxent outputs 0.300 for Caatinga; 0.100 for Atlantic forest. These thresholds were selected by the specialists as the best one to represent the suitable areas for recent jaguar distribution in both biomes.

Models were evaluated by the AUC value, the omission error and by the binomial probability (Pearson 2007).

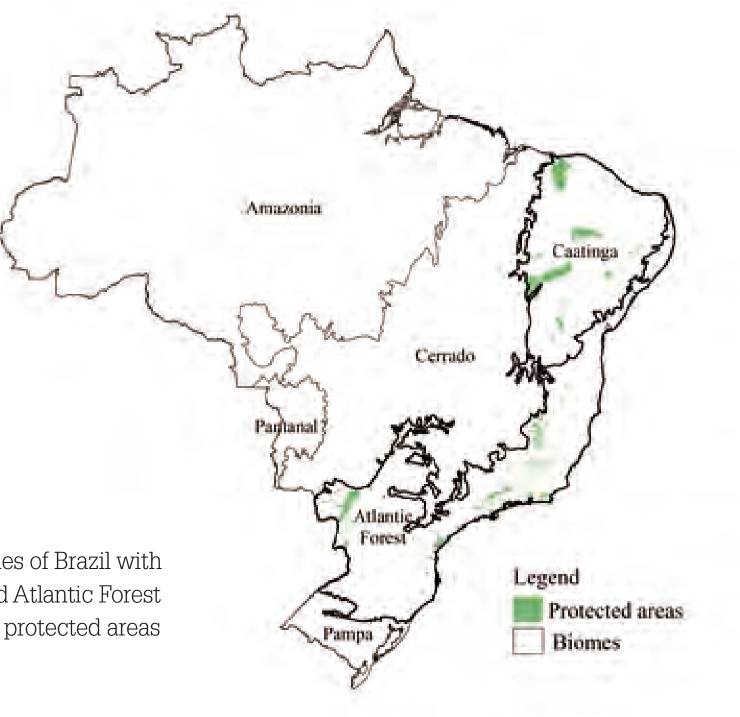

Fig. 1. Biomes of Brazil with Caatinga and Atlantic Forest biomes with protected areas (green).

Results and Discussion

The SDM for Caatinga and Atlantic Forest biomes presented high predictive success and were highly statistically significant (AUC = 0.880 ± 0.027, omission error = 0.206, $p < 0.001$; AUC = 0.944 ± 0.022, omission error = 0.129, $p < 0.001$, respectively; SOM Fig. 1, 2), predicting about 18.64% of the Caatinga (Fig. 3) and 10.32% of the Atlantic Forest (Fig. 4) as suitable for jaguar occurrence.

Much of the Caatinga biome (844,453 km^2) predicted as suitable (54.77%) for jaguar occurrence encompassed the closed to open (>15%) shrubland. Meanwhile, much of the unsuitable area (26.62%) for the species also encompassed this land cover. This discrepancy is due especially to human development or simply occupation that leads to medium to high level of disturbance in the environment. These habitat alterations are especially due to mining activities, agriculture, timber extraction, firewood production, and lowering of prey items due to excessive hunting activities. The closed to open shrubland covers about 40.67% of total biome area. The closed formations have 60% to 80% of plant cover, whereas the open formations have only 40 to 60% (Chaves et al. 2008). The vegetation type is deciduous, generally with thorny woody species > 4.5 m tall, interspersed with succulent plants, especially cacti. The trees are 7-15 m high, with thin trunks. Several have tiny leaves where others have spines or thorns (Andrade-Lima 1981).

The semi-arid Caatinga domain is one of the most threatened biomes in Brazil with less than 50% of its natural cover and greatly impacted and fragmented by human activities (Leal et al. 2005). Most of the protected areas found in this biome (Fig. 3) presented large areas as suitable for jaguar occurrence, such as Serra Branca Ecological Station (ES) and Serra da Capivara National Park (NP) with 100%, Morro do Chapéu State Park (SP) with 91.29% and Serra das Confusões NP with 71.51%. Nevertheless Serra das Confusões and Chapada Diamantina NPs (with 62.63%) are the only two protected areas that are located in transitional areas with the Cerrado biome, hence the lower suitability within the Caatinga. Serra das Confusões NP is indeed a very important area for jaguars as it is large (5,238 km^2), connected to Serra da Capivara NP/Serra Branca ES and also somehow bridges the Caatinga jaguar population with those of the Nascentes do Rio Parnaíba protected areas complex, likely the most important of the Cerrado domain. The bulk of prime areas for jaguars, located within the center of the Caatinga domain are being proposed as a new NP, created to protect one of the most important populations of the Critically Endangered Caatinga jaguar, Boqueirão da Onça NP (Fig. 3). The creation of this new protected area should be of utmost importance for jaguar conservation in the Caatinga. If the NP will be created according to the proposed limits, it will encompass 24.66% of the highly suitable area for jaguars.

Much of the Atlantic Forest biome (1,110,182 km^2) predicted as suitable (27.44%) for jaguar occurrence encompassed the closed to open (>15%) broadleaved evergreen or semi-deciduous forest (55.26%), while unsuitable areas encompassed mainly mosaic cropland (50-70%)/ vegetation (grassland/shrubland/ forest) (20-50%).

Most of the continuous forest remains indicated as suitable for the jaguars at the Atlantic Forest biome correspond to the Brazilian protected areas (Fig. 4) such as Morro do Diabo SP, Mico Leão Preto ES, Caiuá ES, Carlos Botelho SP, Intervales SP, Alto Ribeira Touristic SP and Xitué ES, Iguaçu NP, Serra da Bocaina NP, Tinguá Biological Reserve (BR) and Serra dos Órgãos NP, besides surroundings areas and some isolated forest remains (e.g., Rio Doce SP and Itatiaia NP). The marshlands in the Upper Paraná River, in the west portion of the Atlantic Forest biome, are as important as forest areas to jaguar conservation. The most suitable areas in the region includes continuous protected areas such the Ilha Grande NP, Várzeas do Rio Ivinhema SP and Ilhas e Várzeas do Rio Paraná Environmental Protection Area (EPA).

Some suitable areas indicated by the model such as Cantareira SP and its surrounding did not present any recent record of the species presence. The depauperate quality of forest cover of these areas with high human pressure probably explains the absence of the species there. This clearly illustrates the overprediction (i.e., commission error), frequently observed in SDM. In this particular situation, the degraded vegetation and human pressure are not contemplated in the environmental variables input in the modeling, decreasing

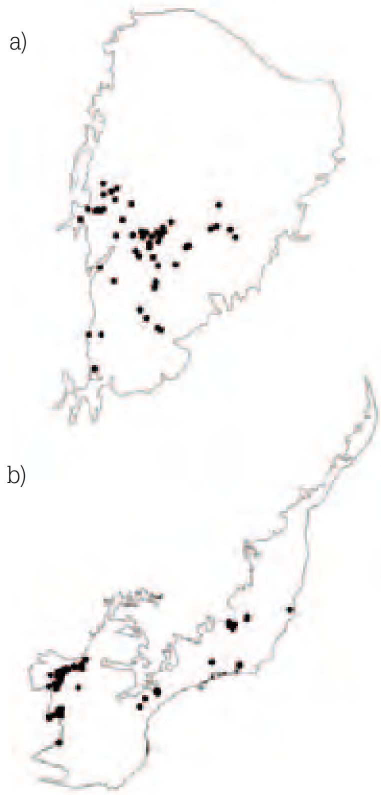

Fig. 2. Jaguar presence points for (a) Caatinga (N = 57) and (b) Atlantic Forest (N = 118) biomes in Brazil.

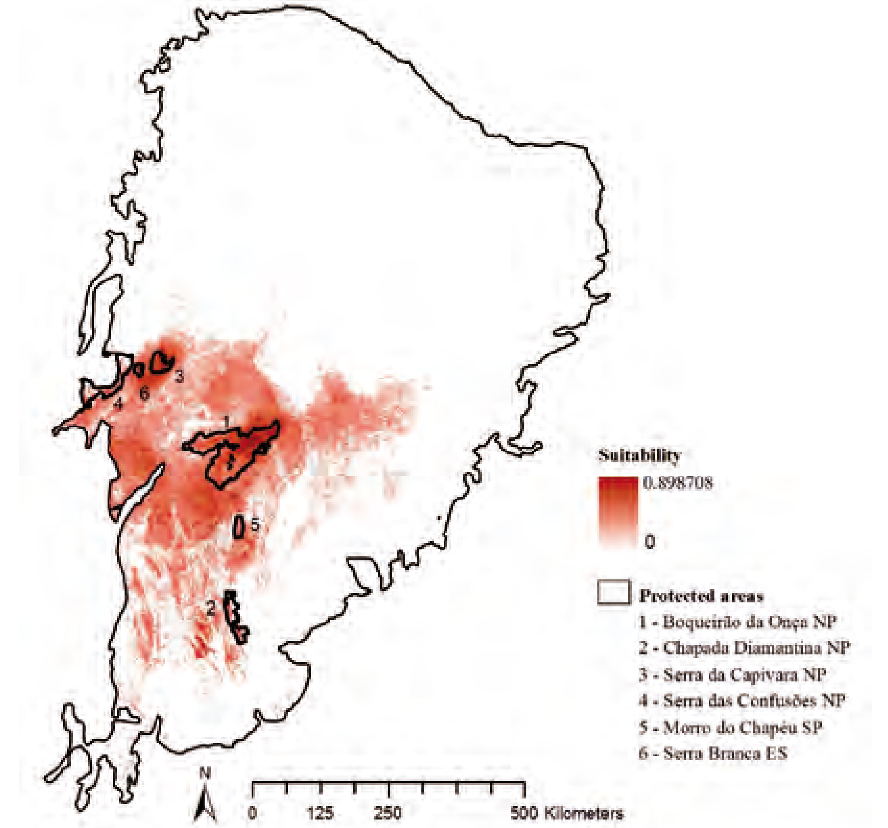

Fig. 3. Potential distribution model for jaguar in Caatinga biome with some protected areas highlighted.

its predictive power. On the other hand, some areas with recent records of the species (not included in the modeling) were not indicated as suitable by the model such as the Juréia-Itatins ES and Caraguatatuba area of Serra do Mar SP. The omission and commission errors are common and frequent in SDM (Fielding & Bell 1997, Pearson 2007), emphasizing the need of cautious interpretation as local characteristics could decrease the model predictive success.

Most of the cropland areas (rainfed croplands, mosaic croplands/vegetation, mosaic croplands/forest; 64.67%) were considered unsuitable for the species occurrence. Jaguars depend on large prey such as peccaries, which are very susceptible to environmental degradation and poaching (e.g. Cullen Jr. et al. 2000), which is intense throughout the Atlantic forest, with the exception of a few well preserved areas. Accordingly, Cullen Jr. et al. (2005) had already verified that jaguars display a strong selection for primary and secondary forests, a strong avoidance of pastures and a weak use of agricultural areas.

The probability of jaguar presence was associated differently to the environmental predictor variables. Elevation (19.03%), the precipitation of driest month (Bio14; 18.08%) and

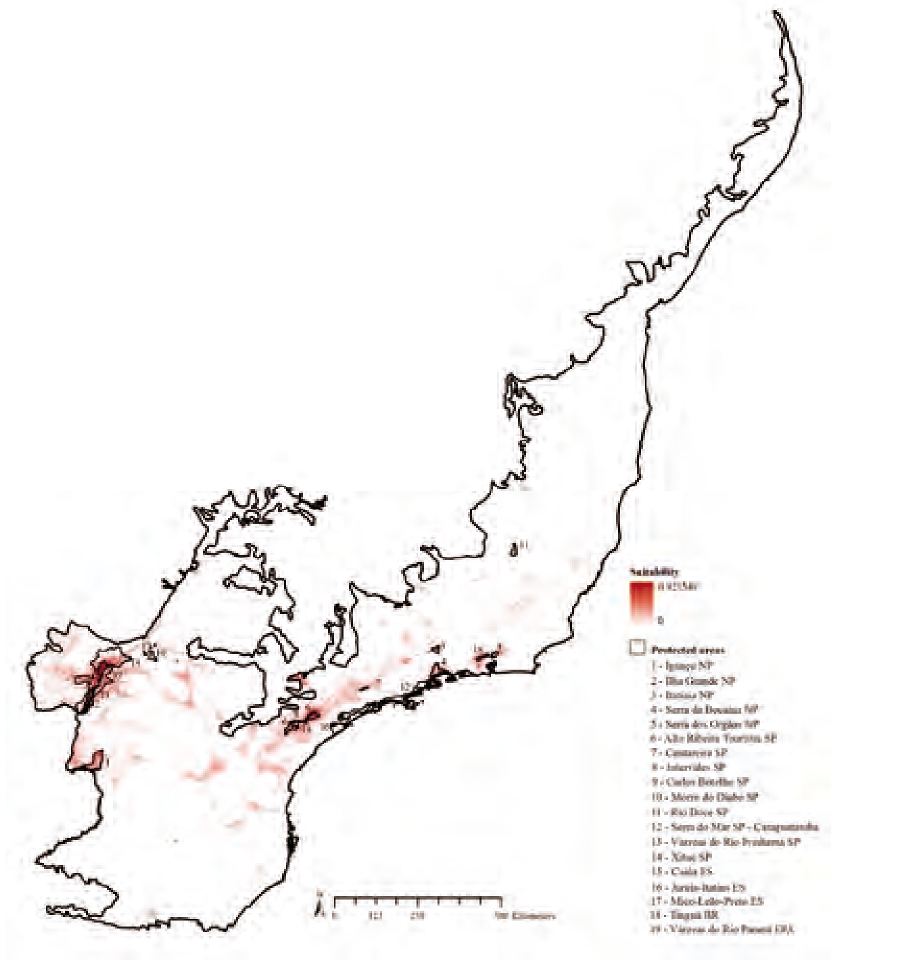

Fig. 4. Potential distribution model for jaguar in Atlantic Forest biome with some protected areas highlighted.

the mean diurnal range (Bio2; 17.25%) were the highest contributor variables for jaguar model at the Caatinga biome. The probability of jaguar presence increased as elevation and the mean diurnal range increased, but decreased as the precipitation of driest month increased (Fig. 5). The presence of jaguar in Caatinga is associated with higher areas probably because of the lower human pressure and more pristine vegetation (e.g., Boqueirão da Onça NP). Although variables Bio14 and Bio2 had important contributions to the model its relationships with jaguar presence were not so clear.

Land cover (41.29%) was the highest contributor variable for the jaguar model in the Atlantic Forest biome. The high probability of jaguar presence was related to the closed to open (>15%) grassland or woody vegetation regularly flooded (Fig. 6). Wetland areas and riparian vegetation (Fig. 7) are core areas and dispersal corridors for jaguars (Cullen Jr. et al. 2005). However, only 30% of the original area of the Paraná River is left because of the construction of hydroelectric power stations (Agostinho & Zalewski 1996).

Future for SDM as a tool for cat conservation

The field of SDM is promising for improving conservation efforts and priorities (e.g. Thorn et al. 2009, Costa et al. 2010, Marini et al. 2010). SDM is a useful tool for resolving practical questions in applied ecology and conservation biology, but also in fundamental sciences (e.g. biogeography and phylogeography) (Guisan & Thuiller 2005). It represents an empirical method to draw statistical inferences about the drivers of species' ranges under different conservation, ecological and evolutionary processes (Zimmermann et al. 2010).

The SDM approach can improve our knowledge about cat species worldwide by 1) highlighting areas where the species might occur but confirmed observation is missing, 2) identifying gaps in data collection and guiding the sampling efforts, 3) identifying key areas for conservation efforts and potential corridors linking protected areas and/or populations, 4) contributing for the assessment of IUCN red list categories, 5) helping to reduce conflicts (e.g., zoning), among others. Moreover, this modeling technique can provide a comprehensive understanding of the historical, current and future ranges of cat species, providing insights to conservation planning (e.g., Marini et al. 2010). Modeling should also be of paramount importance for predicting threatened species range in a world of climatic change. In fact, this kind of prediction could be vital for setting proper and effective action plans for critically endangered populations/species.

In practice, one of the most useful contributions from SDMs could be the prediction of suitable areas for species occurrence as well as helping to delineate potential corridors which link populations on a continental scale. The environmental suitability maps in a modeling framework could be used as a basis to improve the already existing extraordinary initiatives that seek to create such linkages (e.g. jaguar corridor initiative). This, in turn, has been considered one of the most effective conservation strategies to guarantee cat species conservation (Macdonald et al. 2010).

The assessment of conservation priorities for felids should consider the environmental suitability of landscape in a modeling framework. Suitability maps could be considered by stakeholders for defining priority areas for the establishment of new protected areas or corridors. However, conservation inferences should rely on robust models, avoiding omission and overprediction in species distribution range.

The modeling exercise defining priority areas for conservation efforts should be a useful first evaluation. In this workshop one of the most valuable contributions of this exercise was the participatory manner in which this model was constructed. Furthermore the resulting maps provided stakeholders with distribution information and clear results to discuss, and it stimulated debates and discussions which otherwise may not have occurred. However, for reliable conservation decisions suitability models must rely on well-delineated field inventories (Costa et al. 2010) and model results must be validated.

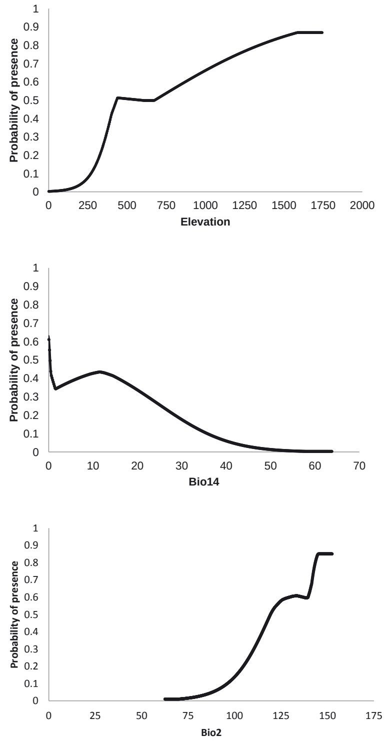

Fig. 5. Marginal response curves of the predicted probability of jaguar occurrence at the Caatinga biome for the environmental predictor variables that contributed substantially to the SDM.

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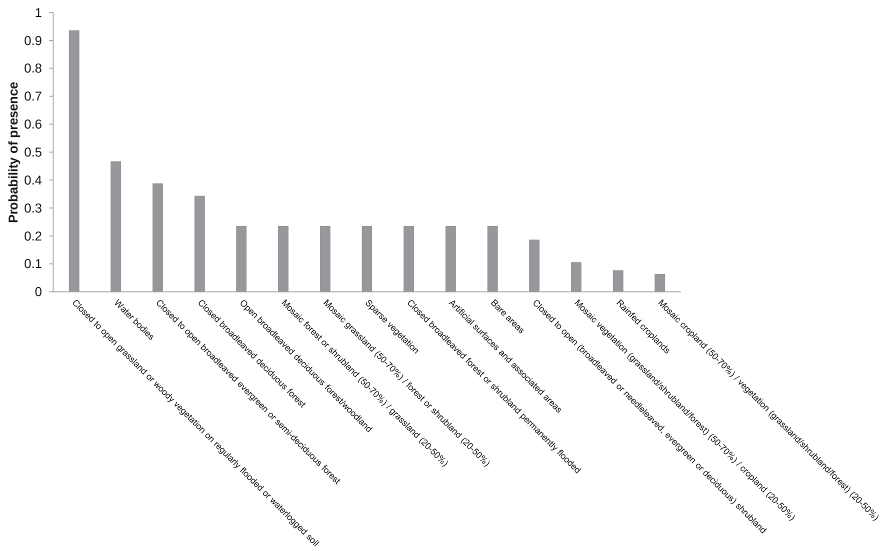

Fig. 6. . Marginal response curve of the predicted probability of jaguar occurrence at the Atlantic Forest biome for the environmental predictor variable that contributed substantially to the species distribution model.

Fig. 7. Riparian vegetation is an important part of jaguar core areas and corridors (Photo A. Gambarini),

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Supporting Online Material SOM available at www.catsg.org/catnews

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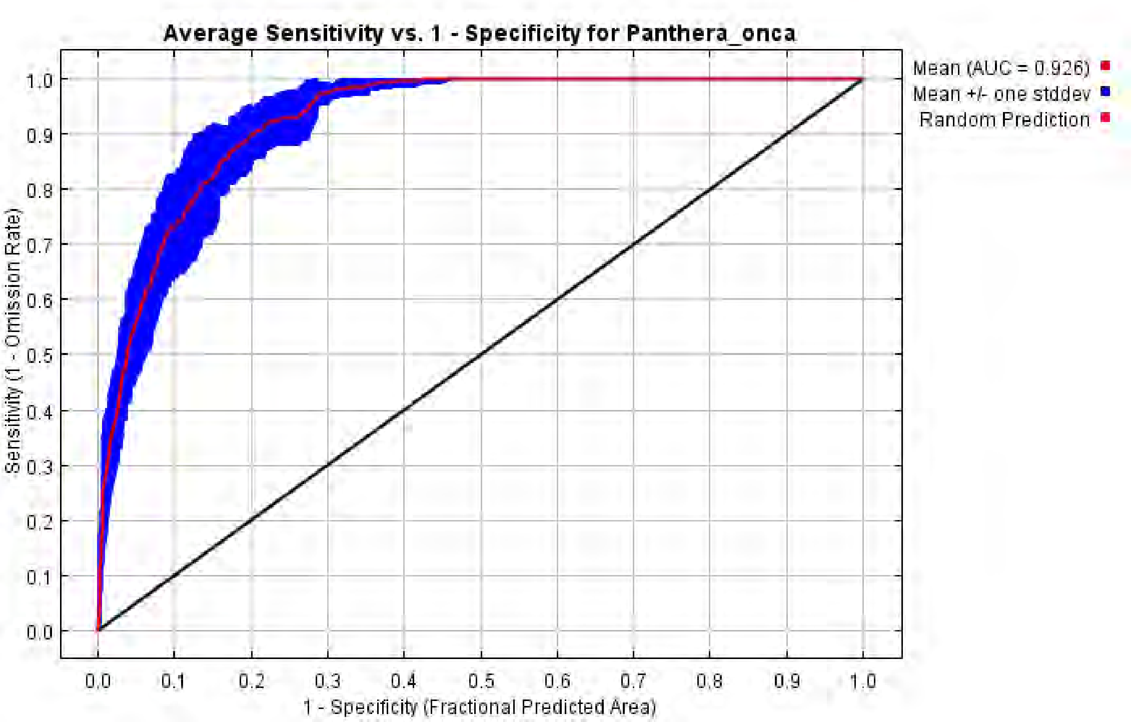
Supporting Online Material SOM Figures 1 and 2.

a)



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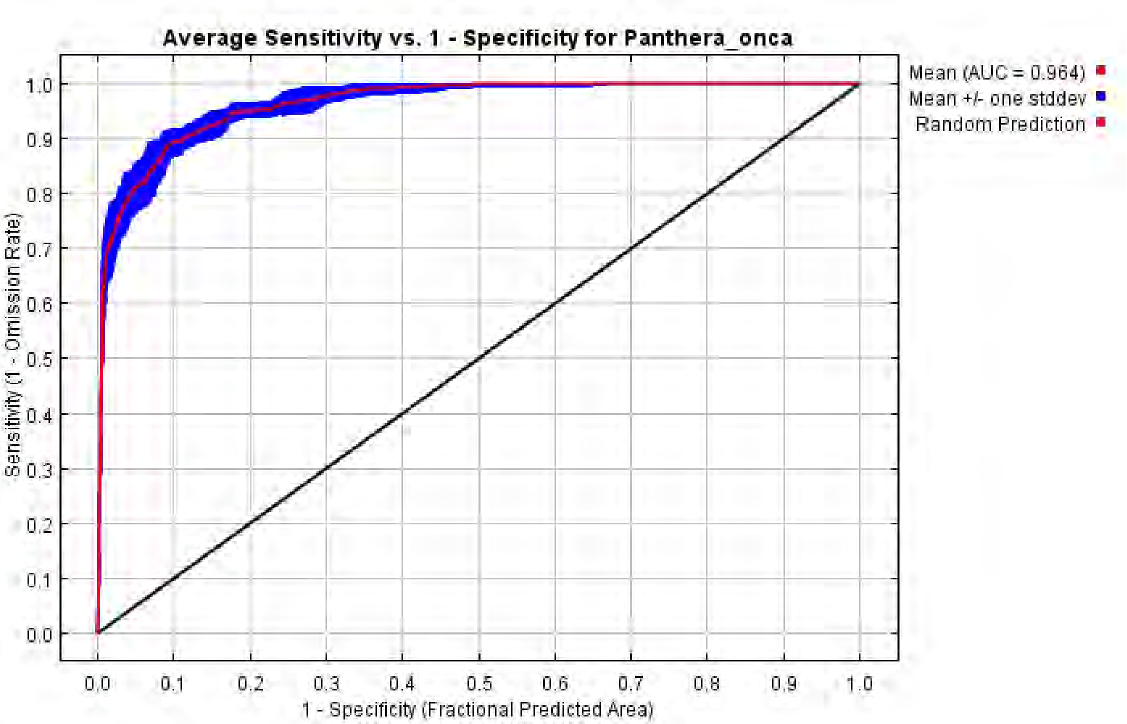

SOM Fig. 1. ROC plot curve for (a) Caatinga and (b) Atlantic Forest.

a)

b)

SOM Fig. 2. Jaguar distribution area at (a) Caatinga and (b) Atlantic Forest in Brazil.

Ferraz et al. 2012. How species distribution models can improve cat conservation - jaguars in Brazil. Cat News Special Issue 7, 38-42.

Supporting Online Material SOM Appendix I. Background information on Species Distribution Modeling SDM

Predicting species distribution has made enormous progress in the last decade. A wide variety of modeling techniques (see Guisan & Thuiller 2005) have been intensively explored aiming to improve the comprehension of species-environment relationships (Guisan & Zimmermann 2000, Peterson 2001, Hirzel & Lay 2008, Elith & Leathwick 2009, Franklin 2009). The species distribution modeling (SDM) relate species distribution data to information on the environmental and/or spatial characteristics of those locations. Combinations of environmental variables most closely associated to presence points can then be identified and projected onto landscapes to identify areas of predicted presence on the map (Soberón & Peterson 2005, Peterson 2006). The geographic projection of these conditions (i.e., where both abiotic and biotic requirements are fulfilled) represents the potential distribution of the species. Finally, those areas where the potential distribution is accessible to the species are likely to approximate the actual distribution of the species.

The SDMs have also been termed as ecological niche models (ENMs) or habitat models (sometimes with different emphases and meanings; Elith & Leathwick 2009, Soberón & Nakamura 2009). According to Elith & Leathwick (2009) the use of neutral terminology to describe species distribution models (SDM rather than ENM) seems preferable. Despite its extensive use, there is an enormous debate about terminology and concepts in predictive modeling and a consensus about what we are modeling – habitat, niche, environment, species distribution – does not exists until now (Soberón & Peterson 2005, Kearney 2006, Peterson 2006, Austin 2007, Soberón 2007, Hirzel & Lay 2008, Jiménez-Valverde et al. 2008, Soberón & Nakamura 2009).

The use of predictive models of species potential distribution has been increasingly used in many areas related to species ecology and conservation, such as to predict areas that could potentially be re-colonised by an expanding species, to choose the best location for reintroduction/restocking or even to indicate potential areas to be prioritized for conservation purposes, including conservation planning, management and restoration (Guisan & Zimmermann 2000, Ferrier et al. 2002a,b, Soberón & Peterson 2004, Peterson 2006, Franklin 2009, Wilson et al. 2010, Rodríguez-Soto et al. 2011). Published examples indicate that SDMs can perform well in characterizing the natural distributions of species (within their current range), particularly when well-designed survey data and functionally relevant predictors are analyzed with an appropriately specified model (Elith & Leathwick 2009). Despite the widespread use of these models, some authors (Pulliam 2000, Soberón & Peterson 2005, Araujo & Guisan 2006, Peterson 2006, Soberón 2007, Jiménez-Valverde et al. 2008) have pointed out important conceptual ambiguities as well as biotic and algorithm uncertainties that need to be investigated in order to increase confidence in model results, such as 1) clarification of model aims; 2) clarification of niche concept, including the distinction between potential and realized distribution; 3) improved design for sampling data for building model; 4) improved model parameterization; 5) improved model selection and predictor contribution; and 6) improved model evaluation.

Modeling the species distribution

Biological data as good-quality source data

Occurrence data for species distribution models can only include presence or presence-absence data. The type of data available for modeling will determine the algorithm and model procedure selection. Species distribution data can be obtained from museum or scientific collections or by field surveys. Many scientific datasets are available for download such as Global Biodiversity Information Facility (GBIF, http://www.gbif.org/) and SpeciesLink (http://splink.cria.org.br/). There are many problems associated to these data sets mainly related to the species identification, sampling effort bias and precision of records (Soberón & Peterson 2004). Field survey data, generally obtained by species observation, trapping or track surveys, from sampling procedure ensuring a broad environmental coverage of gradients in the species distribution range (Vaughan & Ormerod 2003), avoiding bias and pitfalls, are supposed to be good quality data for species distribution modeling. Occurrence data obtained by interviews are generally not recommended to be used in modeling as they are usually not accurate in regards to the species occurrence site.

Many problems have been faced by modelers due mainly to clustered datasets and biased sampling not covering the full range of environmental conditions (e.g., environmental heterogeneity) within the landscape, especially for wide ranging species. Clustered data, especially when provided by telemetry data, could lead to a potential bias in the final model. An option to solve this apparent problem is to subsample the dataset in order to dilute the oversampling in some parts of the species distribution range (Veloz 2009).

Environmental variables as good predictors

Environmental data sets matter in species distribution modeling (Peterson & Nakazawa 2008). The role of a distribution model may be primarily predictive or, alternatively, may emphasize the relationship between an organism and its habitat (Vaughan & Ormerod 2003). So the environmental predictors should therefore have a biological relationship with the organism. The spatial scale should be carefully defined as it can influence the results and/or not resolve the motivated question of the study (Vaughan & Ormerod 2003). The selection of resolution and extent is a critical step in SDM building, and an inappropriate selection can yield misleading results (Guisan & Thuiller 2005). Ideally, models should examine a series of spatial scales, increasing the understanding of organism-environmental relationship (Vaughan & Ormerod 2003).

Many environmental variables, used as predictors, are available for download by many International Agencies. Some examples of frequently used environmental databases are global climate layers from Worldclim (http://www.worldclim.org/), elevation from the NASA Shuttle Radar Topography Mission (SRTM, http://www2.jpl.nasa.gov/srtm/), climate data from past, present and future from Intergovernmental Panel on Climate Change (IPCC, http://www.ipcc-data.org/), Hidro1K elevation derivative database from Earth Resources Observation and Science (EROS, http://eros.usgs.gov/), global land cover from ESA GlobCover 2009 Project (http://ionia1.esrin.esa.int/), and satellite images from MODIS (https://wist.echo.nasa.gov/api/).

Procedure of species distribution modeling

Some models are presence-only models such as DOMAIN (Carpenter et al. 1993) and BIOCLIM (Busby 1986, Nix 1986), while others demand presence and absence data, such as the GLM (Generalized Linear Model) and GAM (Additive Linear Model; Guisan & Zimmermann 2000). Others demand presence and background points such as Biomapper (Hirzel et al. 2002) and Maxent (Phillips et al. 2004, 2006) or presence and pseudoabsence such as GARP (Stockwell & Peter 1999). The latter was generated by locating sites randomly across the total geographical area, or 'domain', of interest (Ferrier et al. 2002a).

Maxent, one of the most recently used algorithm, estimates a target probability distribution by finding the probability distribution of maximum entropy (i.e., that is most spread out, or closest to uniform), subject to a set of constraints that represent our incomplete information about the target distribution (Phillips et al. 2004, 2006). When Maxent is applied to presence-only species distribution modeling, the pixels of the study area make up the space on which the Maxent probability distribution is defined, pixels with known species occurrence records constitute the sample points, and the features are climatic variables, elevation, soil category, vegetation type or other environmental variables, and functions thereof (Phillips et al. 2006). Maxent offers many advantages performing extremely well in predicting occurrences in relation to other approaches (e.g., Elith et al. 2006, Phillips et al. 2006, Elith & Graham 2009) such as the better discrimination of suitable versus unsuitable areas for the species (Phillips et al. 2006), a good performance on small samples (Phillips & Dudik 2008), and theoretical properties that are analogous to the unbiased case when modeling presence-only data (Phillips et al. 2009), this is why it has been frequently used.

Model evaluation can be done by different approaches. One of the most common ones for model evaluation is the calculation of the Receiver Operating Curve (ROC) (DeLong et al. 1988). ROC plot is obtained by plotting all sensitivity values (true positive fraction) on the y axis against their equivalent (1 – sensitivity) values (false positive fraction) for all available thresholds on the *x* axis. The area under the ROC curve (AUC) provides a threshold-independent measure of overall model accuracy. AUC values should be between 0.5 (random) and 1.0 (perfect discrimination). Values lower than 0.5 indicates that prediction is worse than random (Fielding & Bell 1997).

Another option for model evaluation is measuring the model predictive success, which is the percentage of occurrence data correctly classified as positive, so measuring the omission error rate. This evaluation requires a specific threshold to convert continuous model predictions to a dichotomous classification of presence/absence (Hernandez et al. 2006). Optimal thresholds are presented and discussed on a comparative study by Liu et al. (2005). Also, Lobo et al. (2008) recommends that sensitivity and specificity should be also reported, so that the relative importance of commission and omission errors can be considered to assess the method performance.

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Identification of Priority Conservation Areas and Potential Corridors for Jaguars in the Caatinga Biome, Brazil

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Abstract

The jaguar, *Panthera onca*, is a top predator with the extant population found within the Brazilian Caatinga biome now known to be on the brink of extinction. Designing new conservation units and potential corridors are therefore crucial for the long-term survival of the species within the Caatinga biome. Thus, our aims were: 1) to recognize suitable areas for jaguar occurrence, 2) to delineate areas for jaguar conservation (PJCUs), 3) to design corridors among priority areas, and 4) to prioritize PJCUs. A total of 62 points records of jaguar occurrence and 10 potential predictors were analyzed in a GIS environment. A predictive distributional map was obtained using Species Distribution Modeling (SDM) as performed by the Maximum Entropy (Maxent) algorithm. Areas equal to or higher than the median suitability value of 0.595 were selected as of high suitability for jaguar occurrence and named as Priority Jaguar Conservation Units (PJCU). Ten PJCUs with sizes varying from 23.6 km^2 to 4,311.0 km^2 were identified. Afterwards, we combined the response curve, as generated by SDM, and expert opinions to create a permeability matrix and to identify least cost corridors and buffer zones between each PJCU pair. Connectivity corridors and buffer zone for jaguar movement included an area of 8.884,26 km^2 and the total corridor length is about 160.94 km. Prioritizing criteria indicated the PJCU representing c.a. 68.61% of the total PJCU area (PJCU # 1) as of high priority for conservation and connectivity with others PJCUs (PJCUs # 4, 5 and 7) desirable for the long term survival of the species. In conclusion, by using the jaguar as a focal species and combining SDM and expert opinion we were able to create a valid framework for practical conservation actions at the Caatinga biome. The same approach could be used for the conservation of other carnivores.

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Introduction

Habitat fragmentation has been recognized as a major threat to the conservation of a variety of species [1] [2] mainly because it can isolate previously connected populations and, consequently, disrupt original patterns of gene flow likely to lead to drift-induced differentiation among local population units [3]. For this reason, corridors are considered a valuable conservation tool [4] to promote the ability of individuals to move among habitat patches [5] and provide, in this way, an opportunity to mitigate the negative effects of demographic and environmental stochasticity [6] [7] and to sustain the population's genetic diversity and maintain the evolutionary processes associated [8].

Connectivity is a key factor supporting the long-term survival of a variety of species in fragmented areas. However, designing corridors has been a challenge due to the lack of methodological examples found in the literature, no widely accepted protocols, and few available practical examples of field assessment of wildlife corridors [9].

Different approaches have been used for designing corridors, with most of them based on target species and taking into account the behavioural response of these organisms to the landscape structure. Patterns of animal movement may be used as the baseline for corridor design; however, it depends on time-consuming methods, such as the use long-term field data, dispersal movements, and demographics [10]. In this way, using models that rely solely on presence data to evaluate a species potential distribution and identify high suitable areas for a focal species could be a very useful tool for building ''potential corridors'' [11] [12]. In general this information can be applied for identifying core populations or habitat [11], which could be connected. In addition, these models could estimate the probability of a species occurrence related to different environmental variables [12]. Considering that some population models frequently used to evaluate connectivity, such as the least-cost path analyses models, depend on an understanding of how animals move through a landscape [13] such information can indicate environmental factors facilitating or impeaching animal movement or survival.

Large carnivores are often proposed as focal species when evaluating landscape connectivity [10] due to their large area requirements [14] and because their dispersal through a landscape is frequently limited or blocked by areas of high human development or access [15].

The jaguar (*Panthera onca*), the largest cat of the Americas, has a broad distribution throughout Central and South America [16]. It is considered a focal species since its survival requirements encompass multiple factors that are essential for maintaining an ecologically healthy environment [17]. Recent research indicates that the reduction of a focal species population size, such as the jaguar, can lead to the extinction of another species in the community [18]. In this way, a range-wide model of landscape connectivity has been proposed using the jaguar as a focal species [19]. Besides the importance of this framework, we state the need of continuing studies at regional or local level. Also, it is important to mention that jaguars can occupy different habitat types and the use and selection of this space can be influenced by a variety of factors across its distribution range. In this way, connectivity models, using the jaguar as a focal species, should consider factors affecting its behaviour at more refined scales.

We focused this study in the Caatinga biome, considered a priority area for jaguar conservation since its population is listed as critically endangered [20]. Considering the entire jaguar distribution the Caatinga biome represents one of the few Xeric type regions where jaguars still persist. In addition, this kind of habitat is atypical for the jaguar where the species remains poorly studied [21]. The Caatinga biome encompass an area of 844,453 km^2 and represents 9.9% of the Brazilian territory [22], however only 7.3% of this biome falls within the boundaries of protected areas and only 1% is within any strictly protected Conservation Unit [23], making urgent the establishment of strategies for biodiversity conservation in this region. Until recently, jaguar occurrence was supposed to be restricted to 0.1% of the Caatinga biome, within the Serra da Capivara National Park (1,000 km^2) representing the unique jaguar core population in the biome which probability of long-term survival was considered low [24]. However, recently we reported jaguar presence [25] on areas where it had been thought to be long extirpated. By taking the jaguar as our focal species in the Caatinga biome, the objectives of this study were: 1) to recognize suitable areas for jaguar occurrence; 2) to delineate areas for jaguar conservation (hereafter PJCUs); 3) to design corridors among priority areas; 4) to prioritize PJCUs. Although the expected results focus on jaguar in the Caatinga biome, the methodology and conclusions drawn present a model for conservation planning that could be applied to other areas of jaguar distribution and also to other widely ranging species.

Methods

Study area

This study was carried out in the Caatinga biome (844,453 km^2), arid and semi-arid regions extending across eight states of Brazil: Bahia, Sergipe, Alagoas, Pernambuco, Paraíba, Rio Grande do Norte, Ceará, Piauí, and extreme north of Minas Gerais [26] (Figure 1). Xerophytic vegetation type dominated the Caatinga, characterized by spiny deciduous shrubs and trees in association with succulent plants, cacti and bromeliads [27]. In agreement with Andrade-Lima [28], there are twelve Caatinga types distributed in seven physiognomies and six physical units. Annual rainfall may vary from close to zero to as much as ten times the long-term annual average and deviation from the normal rainfall may be higher than 55%. Usually, 20% of the annual rainfall occurs on a single day and 60% in a single month [28] [29]. Most rain falls between September and March. Average annual rainfall is 644 mm, with a 50-year maximum of 1,131 mm and minimum of 250 mm [30]. Mean annual temperature is 27.6°C.

Species Distribution Modeling

The Species Distribution Modeling (hereafter SDM) for jaguar occurrence in Caatinga biome was generated by the maximum entropy algorithm, as implemented in Maxent software 3.3.3e [31] [32]. Maxent is a recently introduced modeling technique, achieving high predictive accuracy and enjoying several additional attractive properties [32]. The idea of Maxent is to estimate a target probability distribution by finding the probability distribution of maximum entropy (i.e., that is most spread out, or closest to uniform), subject to a set of constraints that represent our incomplete information about the target distribution. When Maxent is applied to presence-only species distribution modeling, the pixels of the study area make up the space on which the Maxent probability distribution is defined [31]. Different studies have demonstrated the utility of species distribution modeling to identify areas of high conservation value, as performed by Maxent [12] or ensemble models [11], with Maxent showing, in general, best performance [11] [33] [34] [35] [36] [37].

Models were generated using presence-only data (N = 62) (Table S1; Figure 1) and environmental variables (Table 1) at a spatial resolution of 0.0083 decimal degree (~1 km^2). We selected functionally relevant variables for the species [38], avoiding the autocorrelation. We considered climatic and topographic factors assumed to be important to determine the jaguar distribution, as previously reported [11] [40]. We add two factors that have been reported to be important to determine jaguar presence in the Caatinga biome: distance from water [41] and precipitation of driest month as reported by local people. All presence records were obtained from National Predator Center (CENAP-ICMBio) database and literature [42] [43]. All runs were set with a convergence threshold of 1.0^{E-5} with 500 iteractions and with 10,000 background points, auto features, and analysis of variable importance measured by Jackknife, response curves and random seed.

The SDM was generated by bootstrapping methods with 10 random partitions with replacements using 70% of the dataset for training and 30% for testing models [44]. The average model was cut off by the 10 percentile training presence logistic threshold (0.2613) as it provided the best accurate model for the species occurrence in the biome. We tested the SDM's predictive ability for jaguar occurrence in the Caatinga biome by plotting a new independent dataset not used for modeling (N = 38; Table S2) from recent species occurrence points.

The SDM was evaluated by AUC value, binomial probability and omission error [44] [45].

High Priority Areas for Conservation

We used a different approach from that proposed by Sanderson et al. [24] to identify jaguar conservation units. From the SDM, we selected areas equal to or higher than the median suitability value of 0.595, which represents areas of high suitability for jaguar occurrence [11]. Then, we used the percent volume contour (i.e., raster layer representing a probability density distribution) from Kernel tools in Hawth's analysis tools for ArcGis [46] to delimit these areas, which we named as Priority Jaguar Conservation

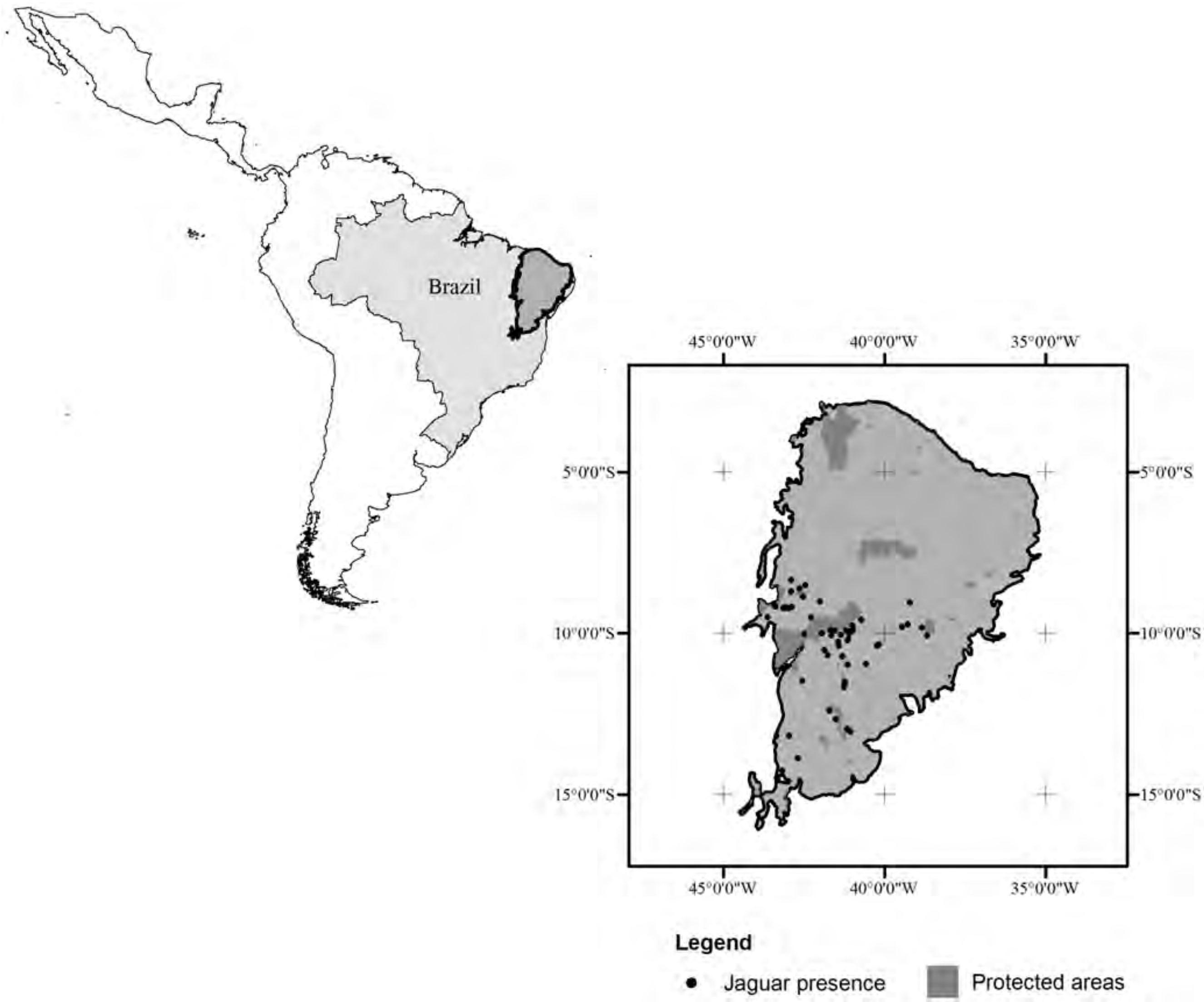

Figure 1. Location of Caatinga biome in Brazil, protected areas in the Caatinga biome and the presence data used for modeling.
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Table 1. Environmental variables used for Species Distribution Modeling (SDM) for jaguar at Caatinga biome, Brazil.

Variables	Dataset name	Spatial Resolution	Year	Source
Land cover	GlobCover Land Cover version v2.3	300 meters	2009	ESA GlobCover 2009 Project
Elevation	Global elevation data	30 arc-second	2004	NASA Shuttle Radar Topography Mission
Distance from water	Gradient distance from vetor map from water	1:5,000,000	2004	Brazilian Institute of Geography and Statistics (IBGE)
Bioclimatic variables	Bio1 = Annual mean temperature	30 arc second	2005	Data layers from Worldclim global climate variables
	Bio2 = Mean diurnal range*			
	Bio5 = Max temperature of warmest month			
	Bio6 = Min temperature of coldest month			
	Bio12 = Annual precipitation			
	Bio13 = Precipitation of wettest month			
	Bio14 = Precipitation of driest month			

*mean of monthly (max temp - min temp).
doi:10.1371/journal.pone.0092950.t001

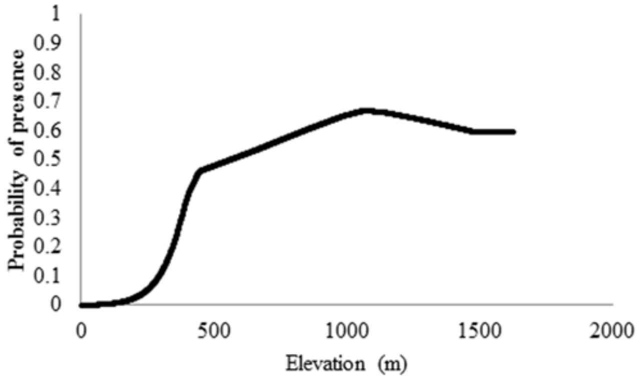

Figure 2. Marginal response curve of altitude, the variable that contributed most to the SDM of jaguar occurrence at the Caatinga biome.
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Units (PJCUs) (i.e., continuous areas of high suitability for jaguar occurrence).

Corridors Modeling

Connectivity modeling was performed among PJCUs as proposed by Rabinowitz and Zeller [19]. We defined five predictors (Table 2) for creating the cost surface or permeability matrix (Table 3) and attributed cost values (ranging from 0 – no cost for jaguar movement – to 10 – high cost for jaguar movement) for each according to Rabinowitz and Zeller [19]. Cost values for elevation, the variable that contributed substantially to the SDM, were attributed based on the marginal response curve provided by the SDM (Figure 2). Following the procedures proposed by Rabinowitz and Zeller [19], we used the Cost-Distance function (Spatial Analyst, ArcGis 9.3) to delineate movement cost grids for each PJCU. After, we used the cost-distance grids as inputs for the Corridor function in Spatial Analyst for all proximate pairs of PJCUs, resulting in least-cost corridors among each pair. Then, we used the minimum mosaic method, combining all overlapping corridors to generate the final least-cost corridor model. Finally, differently from Rabinowitz and Zeller [19], we used the cost path function with cost-distance grids and PJCUs as inputs to calculate the least-cost path from a source to a destination. Crossing the least-cost paths to least-cost corridor model we then selected the best routes, hereafter named corridors, for jaguar dispersal through surfaces with no or low cost for movement. In addition, we identified "buffer zones" around PJCUs and corridors.

PJCUs categorization

For categorizing PJCUs we considered the follow aspects, in order of importance: 1) PJCU size; 2) connectivity, and; 3) jaguar population status [24]. For PJCU size we estimate the smallest continuous area necessary to preserve a viable population of 50 individuals [24] as suggested by Rodriguez-Soto et al. [11]. In brief, we assumed (1) a sex ratio of at least one male every two females [47] [48] and thus counting on 15 males and 35 females, (2) an average home range of 130 km^2 for males and 41 km^2 for females [41] and (3) a complete overlap of the home range of one male with two females [49]. In this way the smallest continuous area necessary to preserve a viable jaguar population corresponds roughly to 1,700 km^2 of high suitability habitats. In this way, PJCUs$\geq$1,700 km^2 received three points. Areas smaller than 1,700 km^2 but with adequate habitat where jaguar populations can increase if threats were alleviated received two points. Finally, areas that cannot hold a jaguar population but still can function as stepping stone areas received one point. For connectivity, each PJCU received one point for each possible connection. Considering the jaguar population status, we combined the PJCU size previously calculated, with density estimate (1.57 ± 0.43) previously reported by Sollmann et al. [21] (Table 4). Despite other available densities, Sollmann et al. [21] presented a spatially explicit capture-recapture model resulting in more precise estimates [50] than previously published non-spatial estimates [51] [52]. PJCUs containing at least 50 individuals, considering it to be genetically stable for 100 years [24], received three points, PJCUs containing fewer than 50 individuals but still can increase if threats can be reduced [24] received two points. PJCUs where the smaller estimated population is less than 1.0 but still can function as stepping stone areas received one point. Arbitrarily, we defined PJCUs with 8–9 points as high priority, PJCUs between 5–7 points as medium priority and PJCUs with 3–4 points as low priority.

Results

The SDM for jaguar at Caatinga biome (Figure 3) was highly significant ($AUC = 0.882 \pm 0.028$, omission error = 0.283, $p < 0.001$). The model also was highly accurate: 97% of the new independent data set was correctly predicted by the model and 52.94% of the presence points were predicted in highly suitable areas ($\geq$70%). Elevation (27.34%) was the variable that most influenced jaguar presence in the Caatinga biome (Figure 2). The suitable area for jaguar occurrence in the Caatinga biome encompasses a total of 155,544 km^2 (18.46% of the total biome). This area is composed mostly by closed to open shrubland (50.87%; 79,130 km^2).

Table 2. Geographical databases used for connectivity modeling.

Variable	Dataset name	Spatial resolution or scale	Year of data	Source
Land cover	GlobCover Land Cover version v2.3	300 meters	2009	ESA GlobCover 2009 Project
Elevation	Global elevation data	30 arc-second	2004	NASA Shuttle Radar Topography Mission
Human Population density	Gridded population of the world v3	2.5 min	2010	Center for International Earth Science Information Network (CIESIN)
Distance from settlements	Gradient distance from vetor map from settlements	1:5,000,000 scale	2004	Brazilian Institute of Geography and Statistics (IBGE)
Roads	Gradient distance from vector map from roads	1:5,000,000 scale	2004	Brazilian Institute of Geography and Statistics (IBGE)

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Table 3. Classes of landscape layers and cost values for jaguar movement.

Landscape cover			Elevation (m)		Human Population Density (inhabitants/km^2)		Distance from roads (km)		Distance from settlements (km)	
ID	**Classes**	**Cost values**	**Classes**	**Cost values**	**Classes**	**Cost values**	**Classes**	**Cost values**	**Classes**	**Cost values**
14	Rainfed croplands	2	0–250	7	0–20	1	0–2	7	0–2	8
20	Mosaic cropland (50–70%)/vegetation (grassland/shrubland/forest) (20–50%)	4	250–500	6	20–40	5	2–4	4	2–4	5
30	Mosaic vegetation (grassland/shrubland/ forest) (50–70%)/cropland (20–50%)	6	500–750	4	40–80	7	4–8	2	4–8	4
40	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5 m)	2	750–1000	2	80–160	9	8–16	1	8–16	1
50	Closed (>40%) broadleaved deciduous forest (>5 m)	2	1000–1700	0	160–320	10	>16	0	>16	0
60	Open (15–40%) broadleaved deciduous forest/woodland (>5 m)	0			>320	BA				
110	Mosaic forest or shrubland (50–70%)/ grassland (20–50%)	4								
120	Mosaic grassland (50–70%)/forest or shrubland (20–50%)	4								
130	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5 m)	0								
140	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/ mosses)	4								
150	Sparse (<15%) vegetation	4								
160	Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water	4								
170	Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water	4								
180	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water	4								
190	Artificial surfaces and associated areas (Urban areas >50%)	4								
200	Bare areas	4								
210	Water bodies	4								

Costs values ranged from 0 (no cost for jaguar movement) to 10 (high cost for jaguar movement). BA means barrier for jaguar movement.
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Table 4. Priority Jaguar Conservation Units (PJCUs) identified in the Caatinga Biome.

PJCUs	Area (km^2)	Mean estimated population size (minimum-maximum)	Number of possible connections	Priority values (points)	Priority Status
1	4311.0	67.7 (49.1–86.2)	3	9	High
2	1053.7	16.5 (12.0–21.0)	1	5	Medium
3	386.3	6.1 (4.4–7.7)	1	5	Medium
4	264.0	4.1 (3.0–5.2)	3	7	Medium
5	82.7	NA	2	4	Low
6	46.5	NA	2	4	Low
7	45.5	NA	2	4	Low
8	29.4	NA	1	3	Low
9	40.5	NA	1	3	Low
10	23.6	NA	1	3	Low
Total	**6,283.2**	**94.4 (68.52–120.1)**			

Total area, estimated population size and connectivity were used to prioritize the PJCUs.
NA = smaller estimated population is less than 1.0.
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We identified ten PJCUs (6,283.2 km^2) that represented areas of high environmental suitability for jaguar occurrence at the Caatinga (Figure 3). PJCU #1 represented approximately 68.61% of the total PJCUs area and could sustain a population of 67.7 (49.1–86.2) individuals (Table 4). Five PJCUs (#1, 3, 5, 8, 10) predominantly encompassed the closed to open shrubland, which is the main land cover type in both the Caatinga biome (31.81%) and the potential distribution area for jaguar occurrence (50.87%).

Connectivity modeling revealed high permeability or low cost surface around most PJCUs (Figure 4 and 5). The least-cost corridor analysis indicated three groups of well-connected PJCUs. The first and the biggest group (PJCUs #1, 5, 4 and 7) contained approximately 74.80% of the total area of all PJCUs. The second (PJCUs #9 and 6) and third (PJCUs #8 and 10) groups contained about 19% of the total area. All the three groups are isolated from each other. Modeling also revealed two PJCUs (#2 and 3) with no connections to any other PJCU.

Connectivity corridors and buffer zone for jaguar movement (Figure 5) included an area of 8,884.26 km^2, encompassing 50.89% (~4,524.3 km^2) of closed to open shrubland. The area also included 13.22% (~1,175 km^2) of a mosaic with predominance of cropland, and less than 50% of grassland, shrubland or forest, and 11.61% (~1,032.5 km^2) of an open (15–40%) broadleaved deciduous forest. The corridors for jaguar dispersal (Figure 5) totalize about 160.94 km.

Discussion

We identified high priority or core areas for jaguar conservation in the Caatinga biome by using the SDM. In addition we were able to identify feasible corridors by connectivity modelling. Our model increased the total suitable area for jaguar to almost seven times than previously reported by Sanderson et al. [24]; similar results were reported in Mexico after applying species distribution model techniques [11]. In addition to a core area previously described by Sanderson et al. [24] and Zeller [53], our model identified nine new highly suitable areas where the size varies from 23.6 km^2 to 4,311.0 km^2. Different from those authors, we used SDM to identify "core areas" with 62 point locations distributed in the biome, compared with five restricted to Serra da Capivara National Park previously described by Sanderson et al. [24]. Since this first report, further scientific studies in the field [25] [42] [43] and literature reviews [54] [55] have been performed, resulting in a higher number of jaguar point locations and better knowledge of the Caatinga's fauna [56].

Except for PJCUs # 8 and 10, jaguars have been reported in or near all the PJCUs. It is clear that most PJCUs cannot sustain a long-term viable population (see Table 4), considering 50 individuals living in a suitable habitat [24]. However, for conservation purposes, we also need to consider the potential connectivity between the PJCUs to manage it as a unique population. In this way, even small patches can function as stepping stone islands, where jaguars can feed or rest, facilitating the migration of dispersal individuals [57] that, sometimes, can travel over 1,607 km [19]. In addition, we need to reinforce the fact that the Caatinga biome has only 1% of strictly protected areas [23] and any additional unit can be important for the conservation of other species.

Despite the suitability of the 18.46% biome to jaguar occupancy, less than 1% is considered of high probability of occurrence (the PJCUs) as indicated by our model. We consider that the status of jaguar populations and their occupancy in the biome reflects the situation of the environment itself. The Caatinga is under severe threats due to an unsustainable land use such as unplanned expansion of croplands and cattle ranching activities, mining and eolic energy matrix [58] [59]. Jaguar is a sensitive species to human activities being subject to an inappropriate land use [39].

Jaguars in the Caatinga biome seem to be isolated from other populations. There is no recent report of jaguar presence in the northern part of the Caatinga suggesting that contact with the Amazon population is disrupted. Connectivity with the Atlantic Rain Forest seems to be unfeasible at this moment, since important anthropogenic factors, such as human density, can impeach jaguar movement in these areas. In fact, Rabinowitz and Zeller [19] described these areas as corridors of concern indicating that more investigation is required to verify jaguar movement between the Caatinga and the Atlantic Rain Forest. Moreover our recent survey in the east part of the Caatinga did not report jaguar presence (data not shown), which corroborates the indication of an ongoing local extinction in the last 10 years [60]. The only possible

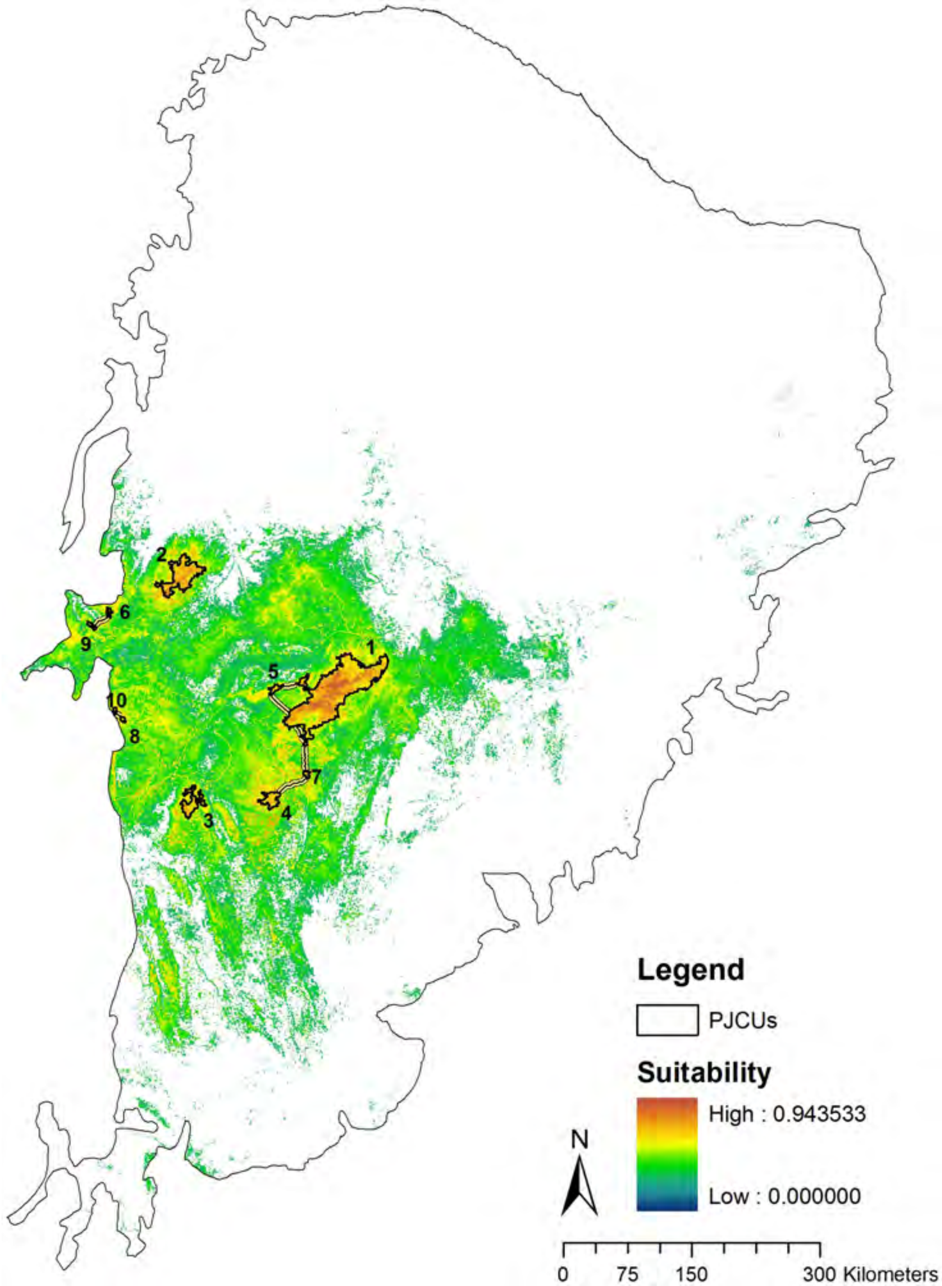

Figure 3. Jaguar distribution model and the Priority Jaguar Conservation Units (PJCUs) with high suitability areas (equal to or higher than the median suitability value of 0.595) (in detail).
doi:10.1371/journal.pone.0092950.g003

connection of Caatinga's jaguar populations would be with the Cerrado biome through the western PJCU's (# 6, 8, 9 and 10). The PJCU group composed by # 8 and 10 is somewhat far from viable jaguar populations from the Cerrado due to the expansion of crop fields in the savannas [61]. Feasible possibilities of connections with the Cerrado's populations are limited to the PJCU group composed by # 6 and 9 that might contact other populations due to a large mosaic of remaining natural areas. In other hand, this group is still isolated from the others Caatinga's PJCUs. Nevertheless, further investigation on the western area is necessary to verify the status and movements of jaguars in this region. Furthermore, we expected that the PJCU # 2 would play an essential role in the Caatinga's jaguar conservation, as previously reported by Sanderson et al. [24]. However, our model indicated that this PJCU is completely isolated corroborating a recent study that showed signs of reduced gene flow between jaguars from Serra da Capivara National Park (PJCU #2) and other regions [62].

Considering the jaguar critical status in the Caatinga biome [20] the population isolation can perform a final stage to the species extinction in the biome. In this way, the implementation of our corridor proposal represents a crucial alternative to long-term preservation of the Caatinga's jaguar population. However, strategies to ameliorate the negative effects of this isolation, such as habitat restoration [63] population supplementation and reintroductions [64] should be considered.

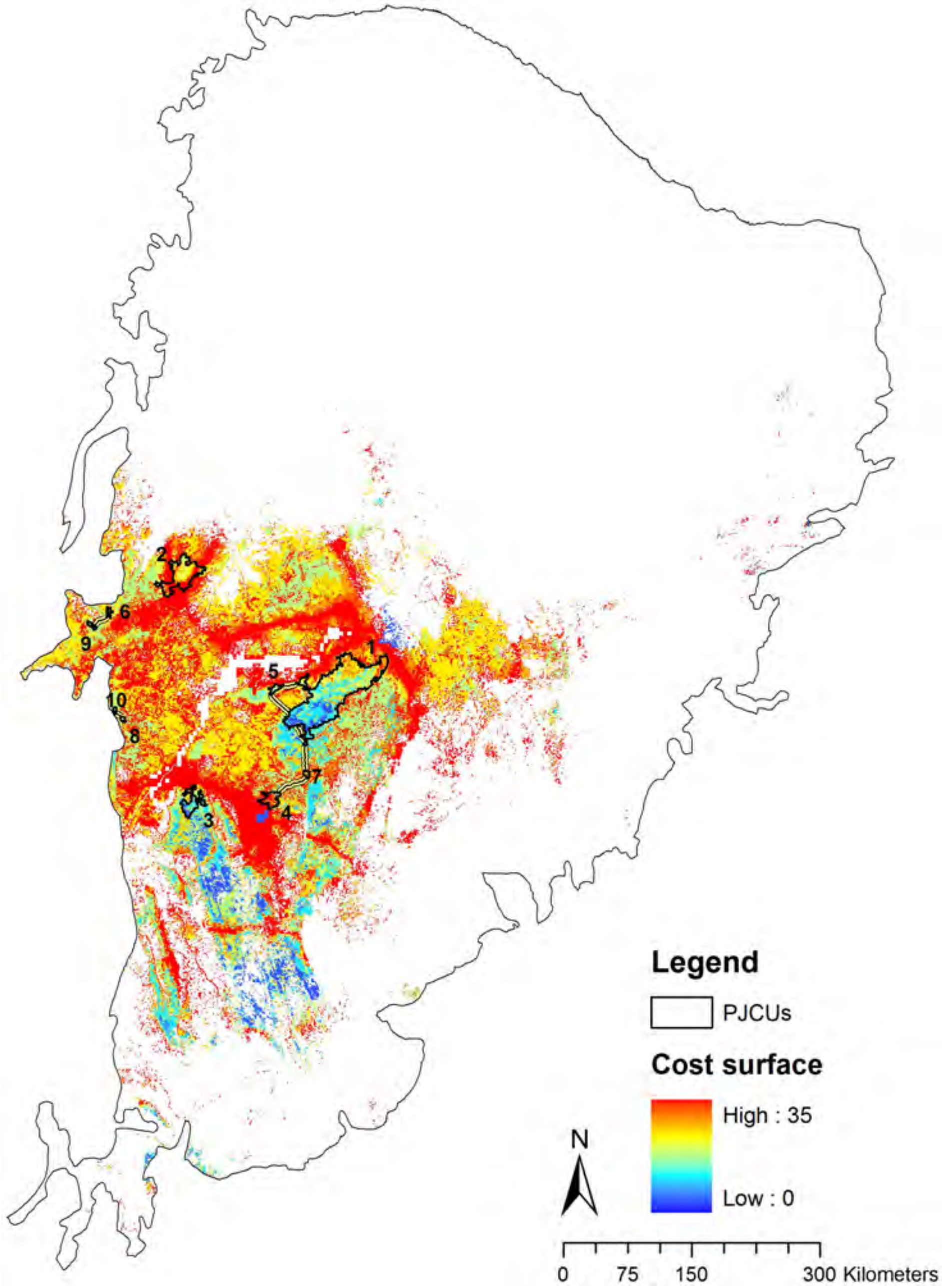

Figure 4. Cost surface for jaguar movement in the Caatinga biome with the Priority Jaguar Conservation Units (PCJUs). The higher the value of the cost surface, the less permeable is the pixel for jaguar movement.
doi:10.1371/journal.pone.0092950.g004

For our purposes, Maxent has the advantage of generating response curves of the predicted probability of occurrence for the jaguar facing different variables, where final results were used to construct the permeability matrix for connectivity modelling. In this way, our elevation cost values differed from those reported by Rabinowitz and Zeller [19]. In this study, higher elevation (1000 to 1700 m) is favoring jaguar presence in the Caatinga biome (see Figure 2). On the contrary, the jaguar detection probability is higher in lower elevation areas of the Nicaragua forests [9]. Two factors can explain our findings: 1) high elevation areas have low human density and also very restricted access to people, as consequence low human activity. Besides we did not use the human density and activities as layers in our model, overlapping human settlements maps from Instituto Brasileiro de Geografia e Estatística [61] with our final model corroborate our hypothesis. Jaguars, in general, avoid disturbed areas [39] [65] [66] [67] [68] and anthropogenic land uses can negatively affect jaguar presence [69]; 2) most of the high elevation areas are covered by the main vegetation types favoring jaguar presence. Precipitation in the driest month seems to play an important role for jaguar presence in this arid and semi-arid region. During the dry season natural holes can store water for large periods, however not for the entire season. In this way, we can speculate that occasional rains will "refill" this water sources avoiding animals moving long distances searching for it. It is in accord with Astete [41] findings since the

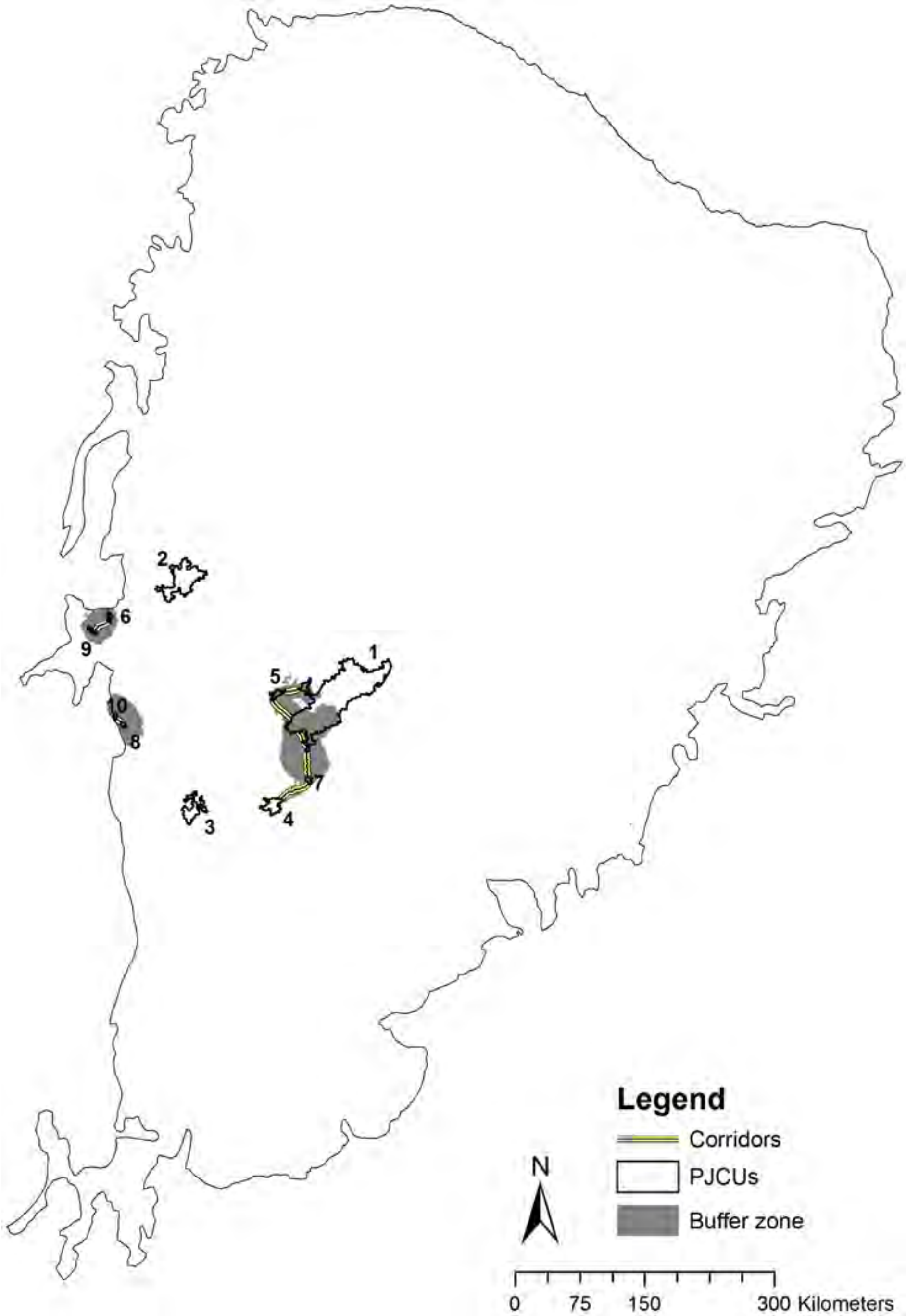

Figure 5. Connectivity corridors and buffer zones for jaguar movement and dispersal among the Priority Jaguar Conservation Units (PJCUs) in the Caatinga biome.
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author reports the positive influence of waterholes in the jaguar presence at Serra da Capivara National Park.

Our final model is primarily based on a focal species, presence-only data and posteriori least-cost patch analysis. The construction of the permeability matrix followed the model proposed by Rabinowitz and Zeller [19] with two differences: 1) elevation classes and values were built based on the response curves of the predicted probability of jaguar occurrence, and; 2) land cover values were based on experts' opinions working in the biome, resulting in different values used in Rabinowitz and Zeller [19] model. Closed to open broadleaved evergreen or semi-deciduous forest and open (15–40%) broadleaved deciduous forests were the main land cover types facilitating jaguar movement and/or dispersal, according to expert opinions. It differs from Rabinowitz and Zeller [19] and Rodriguez-Soto et al. [11] that reported lower probability of jaguar occurrence in these types of land cover.

Costs for creating national parks or any other type of protected area can be extremely high and prioritizing this action can help decision makers. Based on the prioritization criteria we applied, the PJCU # 1 has high priority while PJCUs #2, 3, 4, are of medium priority and PJCUs # 5, 6, 7, 8, 9 and 10 of low priority for jaguar conservation in the biome. Unfortunately, PJCU #1 area is not strictly protected and also is not included in any protected area category according to the Brazilian protected areas system [70], instead this area has been claimed as a potential area for installing an Eolic energy matrix and mine exploitation [59]. PJCUs # 2 (Serra da Capivara National Park), 6 and 9 (Serra das Confusões National Park) are strictly protected by law. A potential corridor between the PJCUs # 2 and 6 (not identified by the model) has already been implemented by the Brazilian government. The lack of connectivity between the PJCU # 2 and the rest is of major concern since this has been considered as a stronghold of jaguars in the Biome, as previously reported [24]. According to this, either a better management of the existing corridor or new bridges to the other PJCUs must be of priority for implementation in short-term. In this way, continuous assessment of wildlife can be helpful for evaluating the viability of such areas including the legal corridor. Based on our criteria PJCUs # 8 and 10 were classified as low priority for jaguar conservation. Yet we stress the need of accumulating information in this area since local people have reported jaguar presence.

The integration of spatially explicit models with expert opinions can assist in the identification and prioritization of sites such as core areas and potential corridors [71]. In this study, species distribution modeling technique were crucial for selecting core areas as to identify main environmental factors driving jaguar presence in the Caatinga biome. Expert opinions contribute with the construction of the permeability matrix and final designed corridors can be considered feasible. Besides carnivores have been used as focal species for connectivity modeling, we should be careful when modeling connectivity in a broad range, using the jaguar as focal species, since many factors can influence its presence and movement pattern across its distribution range. Previous study has designed jaguar corridors on a global scale using a slightly different approach [19]. Our study is zooming in a particular area of the distribution range of the jaguar and presents a comprehensive conservation plan for the species in the Caatinga biome, complementing and strengthening previous findings.

Although the creation of protected areas are more urgent and significant initiative to biodiversity conservation, this strategy will only be able to partially mitigate the problem. In this context, corridors can complement the role of protected areas, increasing the ecological function by means of bridging viable areas to biodiversity conservation. With the creation of corridors, government is able to regulate the land use within its areas favoring jaguar movements and resulting on the increase of the species population viability in the biome.

In conclusion, we emphasize the urgency of establishing a protected unit at the PJCU #1 and corridors with PJCUs # 4, 5 and 7, otherwise, we expect the most important jaguar population currently found in the biome to be extirpated and, consequently, disrupt predator-prey interactions affecting the entire ecosystem functioning [72].

Supporting Information

Table S1 Occurrence data of jaguars used to species distribution modeling, by site and/or city (Datum SAD69).
(DOCX)

Table S2 Occurrence data of jaguars used to validation*, by site and/or city (Datum SAD69).
(DOCX)

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Author Contributions

Conceived and designed the experiments: RGM RCP CBC KMPMBF. Analyzed the data: KMPMBF RGM RCP CBC. Wrote the paper: RGM KMPMBF RCP CBC. Acquired the data: CBC RCP RGM.

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Predicting the current distribution of the Chacoan peccary (*Catagonus wagneri*) in the Gran Chaco

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Abstract

The Chacoan peccary (*Catagonus wagneri*), or Tagua, an endemic species living in the Chaco eco-region, is endangered by highly increasing deforestation rates across the region, particularly in the last decade. This situation highlights the need to better understand the current distribution of the species, as well as how environmental conditions affect habitat suitability. This study predicts the distribution of the Chacoan peccary and evaluates the current environmental conditions in the Chaco for this species. Using six environmental variables and 177 confirmed

occurrence records (from 2000 to 2015) provided by researchers, we developed a Species Distribution Model (SDM) applying the Maxent algorithm. The final model was highly accurate and significant ($p < 0.001$; AUC 0.860 ± 0.0268; omission error 1.82%; post-hoc validation of omission error using independent presence-only records 1.33%), predicting that 46.24% of the Chaco is suitable habitat for the Chacoan peccary, with the most important areas concentrated in the middle of Paraguay and northern Argentina. Land cover, isothermality and elevation were the variables that better explained the habitat suitability for the Chacoan peccary. Despite some portions of suitable areas occurring inside protected areas, the borders and the central portions of suitable areas have recently suffered from intensive deforestation and development, and most of the highly suitable areas for the species are not under protection. The results provide fundamental insights for the establishment of priority Chacoan peccary conservation areas within its range.

Introduction

The Chacoan peccary (*Catagonus wagneri*) is an endemic species living in the Chaco eco-region (Mayer and Wetzel, 1986; Redford and Eisenberg, 1992; Taber, 1993). Evolutionary speaking, the species represents a very distinctive and unique pattern (Gasparini et al., 2011). Due to a serious decline in numbers and range size of Chacoan peccary, it is considered "Endangered" by the IUCN Red List (Altrichter et al., 2015). The species' geographical range has been reduced in the three countries it occupies: Argentina, Bolivia and Paraguay (Altrichter, 2006; Neris et al., 2002). Due to their behavior and their low reproductive rate, Chacoan peccaries are vulnerable to human disturbance (Taber et al., 1993; Altrichter and Boaglio, 2004). The presence of the species is associated to native forests (Taber et al., 1993; Altrichter and Boaglio, 2004; Saldivar-Ballesai, 2015; Camino, 2016) and therefore Chacoan peccaries may be seriously threatened by the increasing deforestation rates in the Gran Chaco (Cardozo et al., 2014; Vallejos et al., 2014). This threatening situation attracted the attention of conservation scientists in an attempt to protect the Gran Chaco, and develop a current strategy to prevent the peccary's extinction. One of our most urgent goals was to re-assess the current distribution of the species, as well as understand how habitat conditions and characteristics (e.g. land cover, climate and topographic variables) affect the suitability of the habitat for implementing proper conservation measures.

Species Distribution Models (SDMs) are an important tool often used to assess the relationship between a species, its distribution, and the environmental conditions. They integrate species occurrence records and environmental variables to develop environmental suitability maps for a species in space and time (Peterson, 2006; Pearson, 2007; Elith and Leathwick, 2009). SDMs have been used not only to describe the environmental requirements of a species, but also to be applied for: identifying sites for translocation and reintroduction of species (Peterson, 2006; Jiménez-Valverde et al., 2008), identifying priority areas for conservation (Morato *et al*., 2014), managing invasive species (Ficetola et al., 2007), assessing species distribution in human-modified landscapes (Ferraz *et al*., 2010; Angelieri et al., 2016) and finally predicting biodiversity response to both climate change (Adams-Hosking et al., 2012; Freeman et al., 2013; Lemes and Loyola, 2013) and land use change (Ficetola, 2010; Angelieri et al., 2016). In summary, SDMs also provide important elements for future conservation planning and management (Araújo and New, 2006).

With the goal of determining priority conservation areas and generating information for appropriate conservation strategies, we used a SDM with occurrence records provided by researchers, and then corroborated by the attendants to the Chacoan peccary conservation planning workshop held in Asuncion, Paraguay. The objectives of this study were: (1) to predict the Chacoan peccary distribution, and (2) to evaluate the current environmental conditions of the

Chaco for the species occurrence. The SDM developed was evaluated for accuracy by the specialists considering the current known distribution of the species.

Materials and Methods

Study area

Predictive models for the Chacoan peccary were generated for the full extent of the Gran Chaco region (1,076,035 km^2 in the central South American, Fig 1). The Chaco ecoregion (Olson, 2000) includes territories of western and central Paraguay, southeastern Bolivia, northwestern Argentina, and a small part of Brazil. The predominant habitats in the Gran Chaco include a seasonal, open to semi-open palm savanna and grassland (Wet or Humid Chaco), and a low, closed-canopy seasonal or semi-arid deciduous thorn forests (Dry Chaco); many areas incorporate a gradient between this two environments. The Dry Chaco is dominated by thorny bushes, shrubs, and cacti, with dense, closed canopy trees up to 13 m high called "Quebracho woodland" (Short, 1975). Some of this impenetrable primary thorn forest still remains in the region, and its isolation led to the discovery of new species of endemic vertebrates, including the Chacoan peccary, as recently as the 1970's (Wetzel et al., 1975). Since then however, this region has become more developed and deforestation has increased rapidly in the last few years; total deforestation in the Chaco account for 265.169 ha in 2010, 336.445 ha in 2011, 539.233 ha in 2012, and 502.308 ha in 2013 (Cardozo et al., 2014).

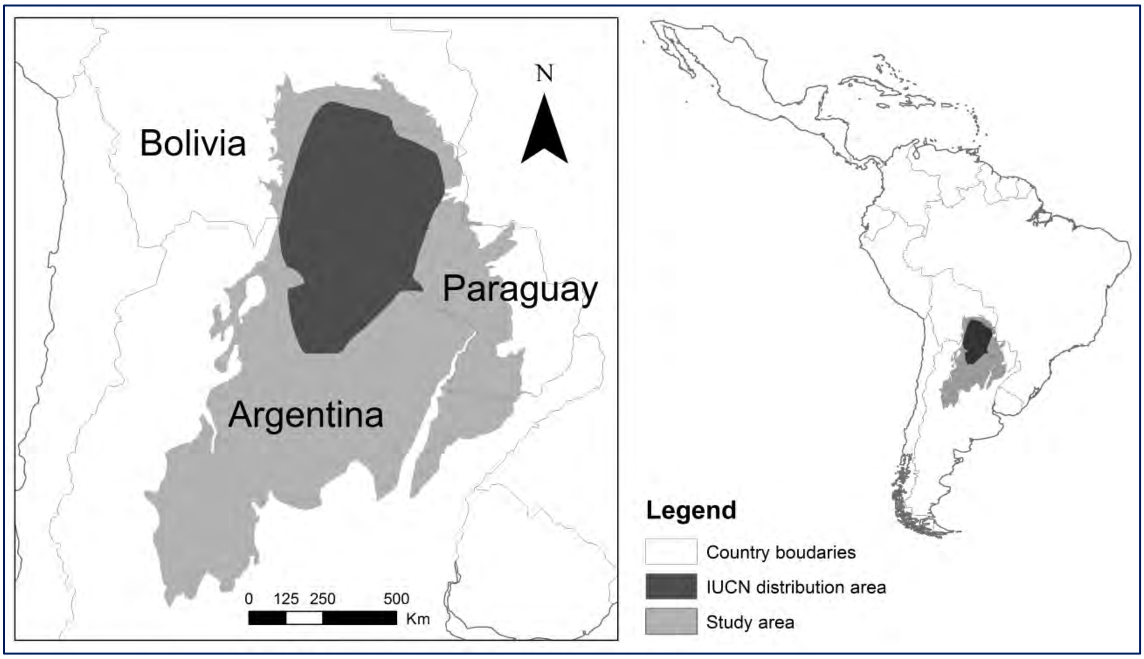

Fig 1. Map of the study area for the Chacoan peccary distribution model.

Data collection

Through expert consultation we gathered 177 Chacoan peccary presence records (e.g. sightings, camera trapping, capture, feces, tracks, interviews, etc.) occurring between 2000 and 2015 (Fig 2a). All presence points used for modeling and validation represented accurate records with exact locations. In order to reduce spatial autocorrelation and to compensate biases in data that usually occur when some areas in a landscape are sampled more intensively than others (Elith et al., 2011), we used the spatially rarefied occurrence data to produce SDMs via the SDM

Toolbox v1.1b (Brown, 2014), which resulted in 87 spatially independent presence points used for the modeling process (Fig 2a). The predictive ability of the average SDM was tested by plotting a new, independent dataset (not used for modeling, N = 990), against species presence records sampled after 2000 (Fig 2b).

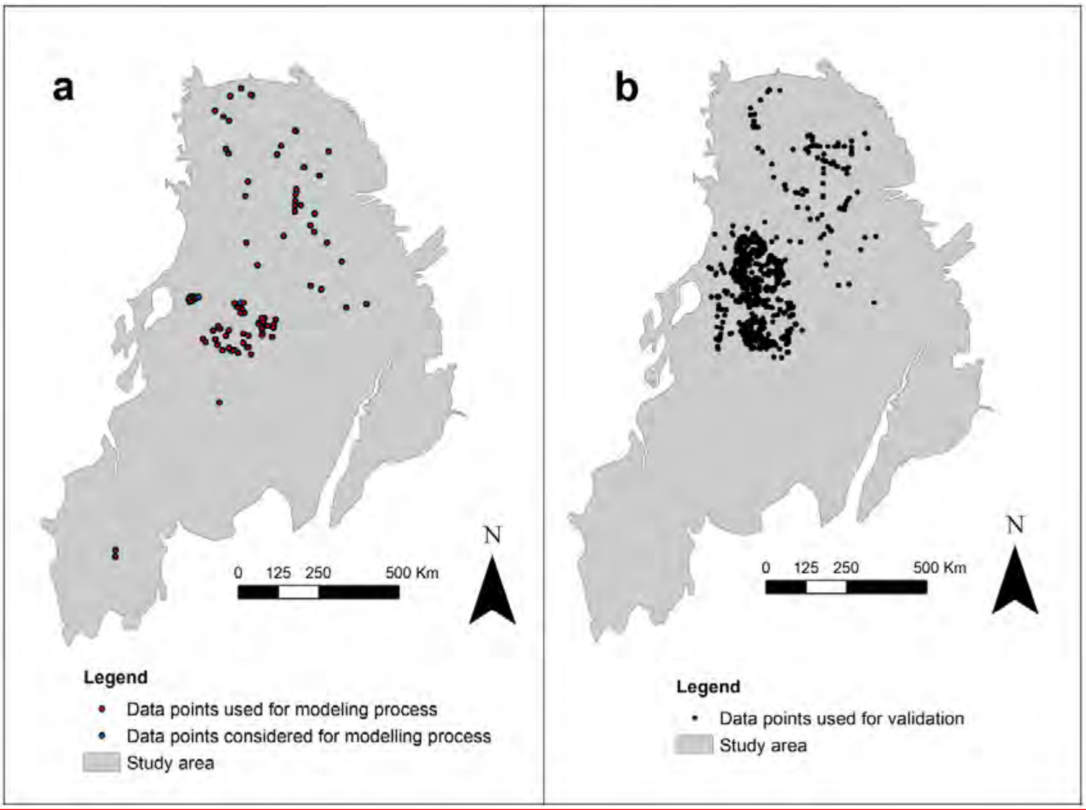

Fig 2. Chacoan peccary presence records considered (N=177) and used (N=87) for modeling (a) and presence points used for model validation (N=990) (b).

Environmental variables

We initially selected 21 environmental variables (i.e., 19 bioclimatic variables plus elevation and land cover) to examine for inclusion in our SDM's. After analyzing autocorrelation among variables, 15 were discarded (correlations > 0.7), leaving only six environmental variables to be used as model predictors (Table 1; Figure 3) at a spatial resolution of 0.0083 decimal degrees (~1 Km^2).

Table 1. Environmental variables used for predictive models.

Variable	Description	Year	Source
Elevation	Map of elevation	2004	NASA Shuttle Radar Topography Mission
Globcover with deforestation	Map of land cover classes, with deforestation included	2009	Globcover map from ESA GlobCover 2009 Project Deforestation map from Guyra Paraguay
Bioclimatic variables	Bio 1 = Annual mean temperature Bio 2 = Mean diurnal range Bio 3 = Isothermality* Bio 12 = Annual precipitation		Data layers from Worldclim global climate variables

Isothermality = Mean diurnal range (Mean of monthly (max temp - min temp))/Temperature annual range) (100)

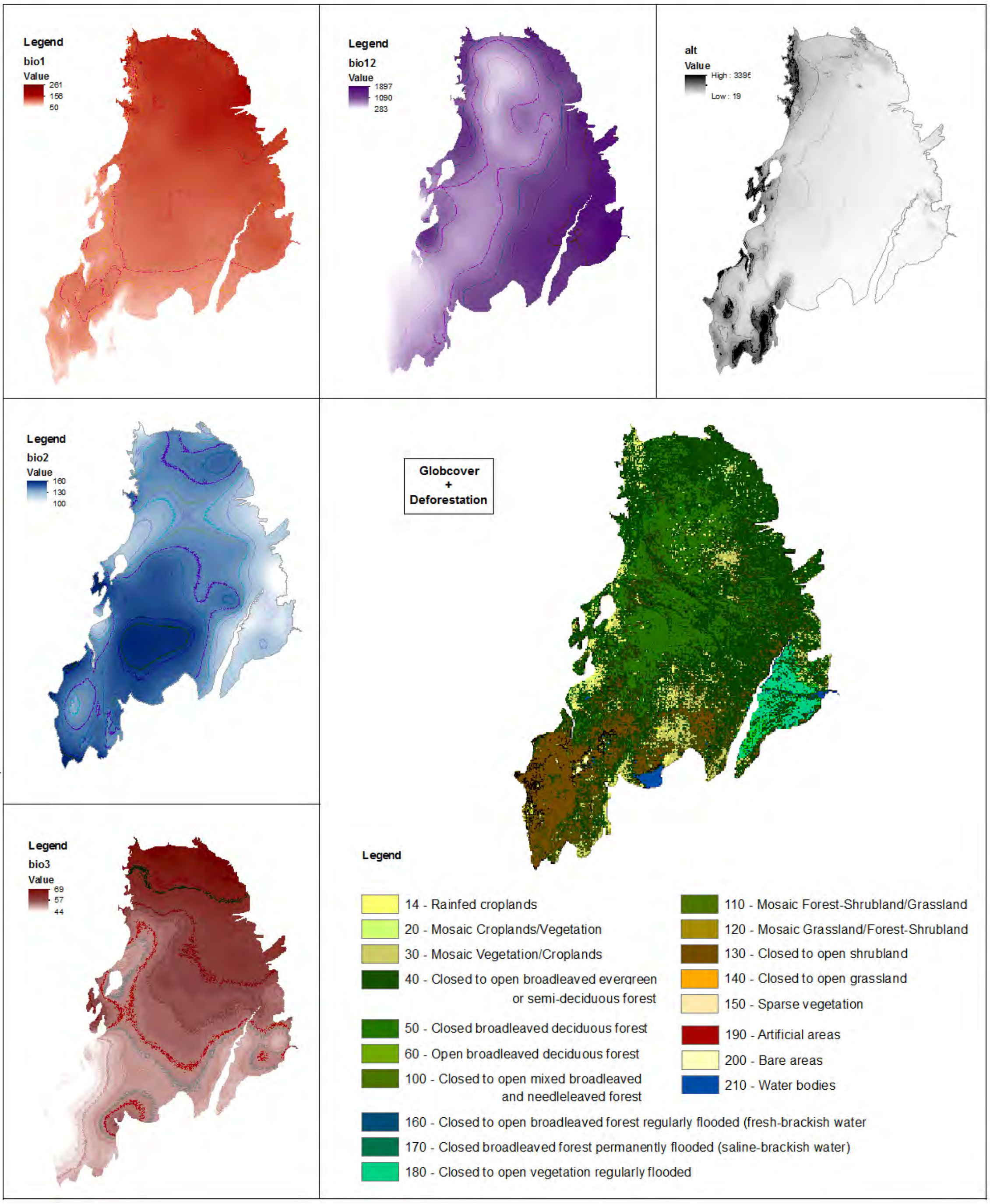

Fig 3. Environmental variables used in the Chacoan peccary model.

Modeling procedures

Species Distribution Models (SDMs) were generated using a maximum entropy algorithm via the program Maxent, version 3.3.3.k (Phillips et al., 2006; Phillips and Dudik, 2008). Maximum entropy is a widely accepted and used algorithm for modeling species distribution, generally performing better than alternative approaches (Elith et al., 2006; Elith and Graham, 2009). In particular, Maxent proposes a target probability distribution for a species by estimating the distribution of maximum entropy (i.e., the distribution that is closest to uniform, or most "spread out") as it is constrained by missing information about that target distribution (Phillips *et al.*, 2006).

SDMs were generated using bootstrapping methods with 10 random partitions with replacement using 70% of the full dataset for training models and 30% for testing (Pearson, 2007). Parameters set for all runs were based on a convergence threshold of 10^{-5} with 500 iterations, and with 10,000 background points. The average model was cut off by the minimum training presence logistic threshold (0.0975), which resulted in a binary map (0 = unsuitable, 1 = suitable). When multiplied by the average model, this binary map yielded the final model describing the probability of the species occurrence in the biome. The final model was evaluated by AUC value, binomial probability and omission error (Pearson, 2007).

Maxent's average distribution model was also categorized into three habitat suitability classes: low suitability (values from $0.0975 \leq 0.25$), medium suitability ($0.25 \leq$ values ≤ 0.50) and high suitability ($0.50 \leq$ values ≤ 1) with the manual classification method using the reclassify tool in ArcGIS 10.1 Spatial Analyst. A shapefile of areas of varying protection levels was provided by the IUCN PSG [Peccary Specialist Group], 2016, which and converted into a raster dataset to create the current protected areas file. ArcGIS 10.1 Spatial Analyst Zonal tool was then applied to cross-tabulated areas between the suitability area classes and the protected areas zone.

Results and Discussion

Predictive distribution model for the Chacoan peccary (0.860 ± 0.0268) was highly significant ($p < 0.001$) with low omission error (1.82%) (Fig 4a). The post-hoc validation using the independent presence-only records confirmed that the model was highly accurate, with only 1.33% of omission error. The model predicted that 46.24% (~497,577.34 Km^2) of the Gran Chaco is suitable for the Chacoan peccary (Fig 4b). Suitable areas are concentrated in the Paraguayan department of Presidente Hayes, Boqueron and Alto Paraguay, and in northern Argentina, especially near the borders of Formosa, Chaco, Salta and Santiago del Estero Provinces, as well as in the north-central portions of the Bolivian Chaco. The limits of the current distribution area have suffered intensive habitat loss due to recent land cover conversion, especially in Paraguay (Caldas et al., 2013; Cardozo et al., 2014), suggesting that the Chacoan peccary distribution range is probably retracting rapidly.

Deforestation rates in Chaco were among the highest of the world between 2000 and 2010 (Aide *et al.*, 2013; Hansen *et al.*, 2013) and potentially affecting the distribution of Chacoan peccaries. In Bolivia, deforestation remains low, however, in both Argentina and Paraguay deforestation is associated to intensive agriculture and cattle production (Caldas *et al.*, 2013; Piquer-Rodriguez *et al.*, 2015). Moreover, there is an expanding urban area (i.g. the city of Filadelfia) in the center of the high suitability area in Central Paraguay and the species is one of the most hunted animals in the Dry Paraguayan Chaco (Neris *et al.*, 2010).

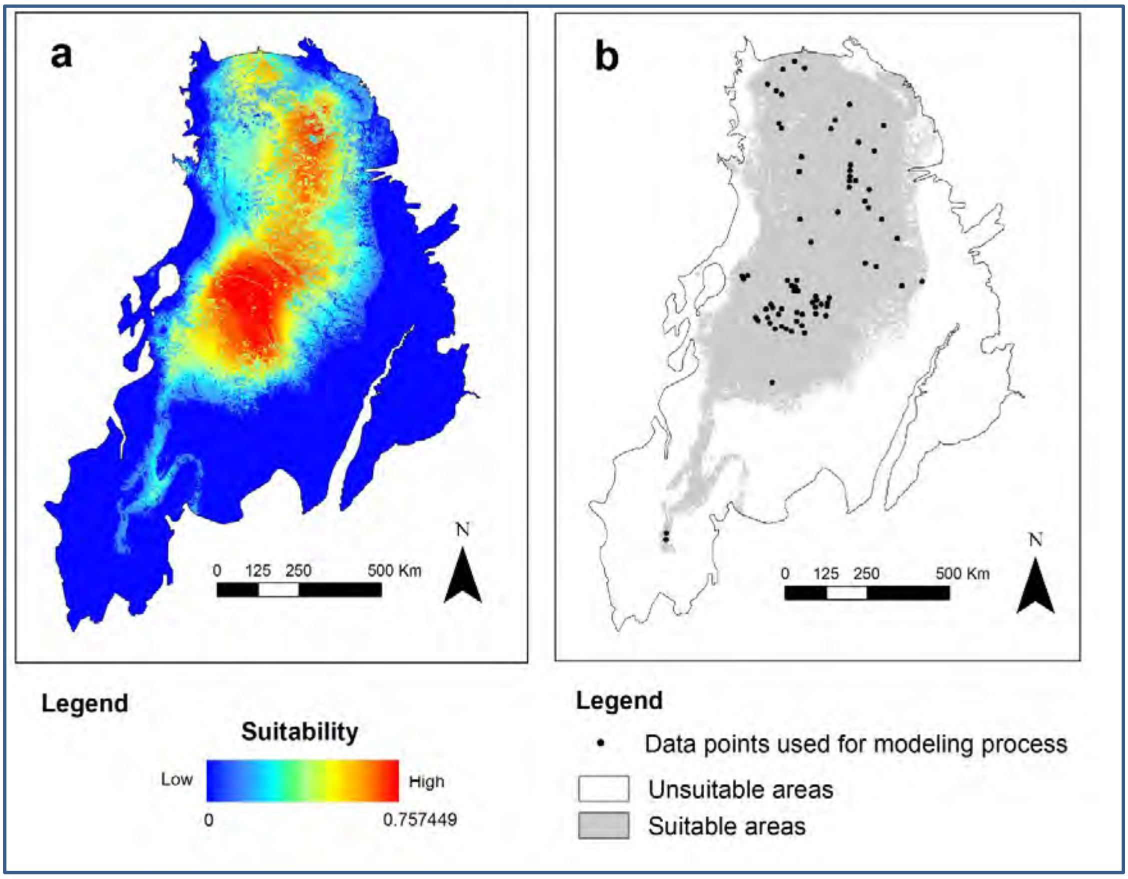

Fig 4. Predictive distribution model of Chacoan peccary. (a) Maxent average model shows the continuous suitability of the Chaco for the species. (b) Categorical suitable and unsuitable areas.

The three variables that better explained the predictive distribution model were land cover (31.57%) (Fig 5a), isothermality (22.52%) (Fig 5b) and elevation (21.60%) (Fig 5c). Suitable areas for Chacoan peccary were characterized by closed broadleaf deciduous forest so called Chaco-Quebracho (Paraguay) and Chiquitano (Bolivia) woodlands (57.93%), closed to open broadleaf forest/shrubland (21.86%) and by mosaic vegetation/cropland (13.67%). The association between suitable habitat and forest cover is probably positive, as found in previous studies (Taber et al., 1993; Altrichter and Boaglio, 2004; Camino, 2016). However, this is the first published study that shows that the species' habitat is composed of closed and semi-deciduous forests, and forests with shrublands. As far as we know, no other study differentiated the type of forests used by this species.

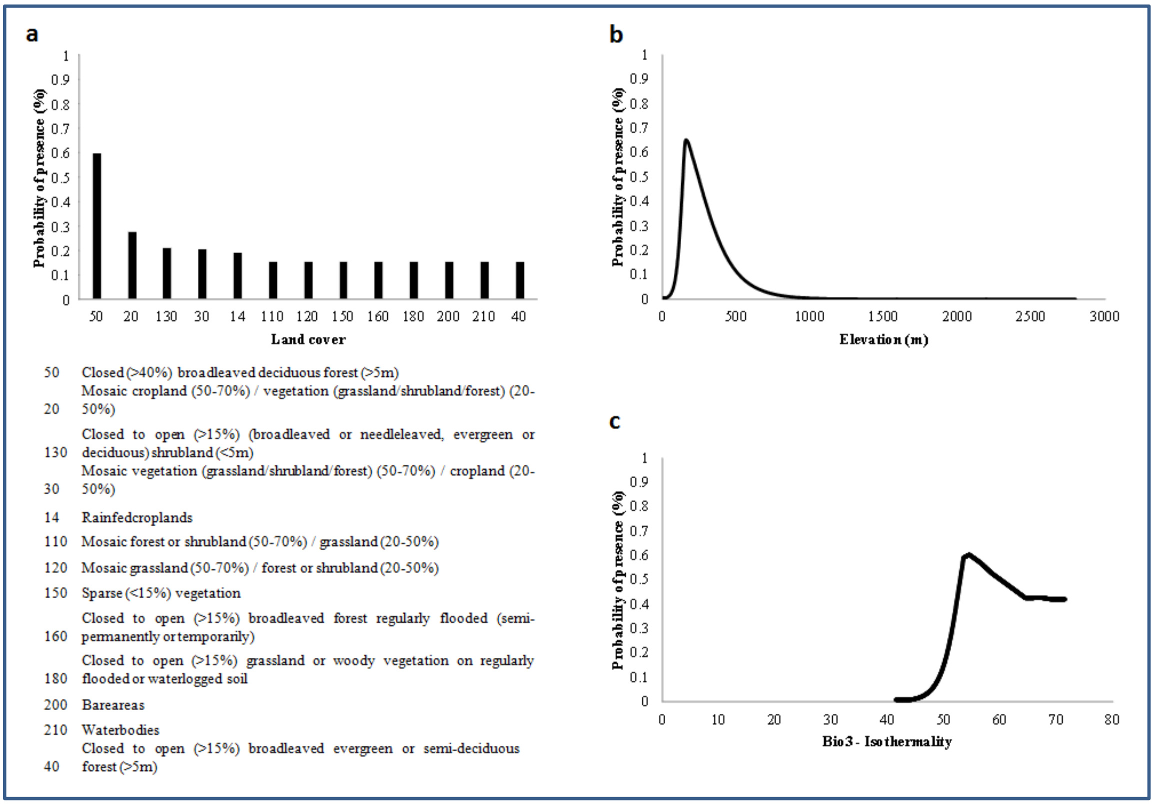

Fig 5. Response curves of probability of presence (%) according to Land Cover (a), Elevation (b) and Bio 3 – Isothermality (c).

Despite that some portions of suitable areas are legally protected, most parts of highly suitable areas for the species are not included in an official protection system. Less than 17% of the areas under some type of protection occur in areas suitable for the Chacoan peccary (Figure 6b), and only 12% of high suitability areas for Chacoan peccary are protected in the Chaco (Table 2). Furthermore, when analyzing suitable areas by country, only 7% of the high suitability areas in Argentina, and 13% in Paraguay, are currently under some kind of protection. Therefore, the existent protected areas are not effective at protecting suitable areas for the Chacoan peccary. In Bolivia, almost 79% of the high suitability areas for the species are already under protection in the Kaa-Iya del Gran Chaco National Park; however, we believe that the suitability inside this inaccessible area may be underestimated due to a lack of presence records.

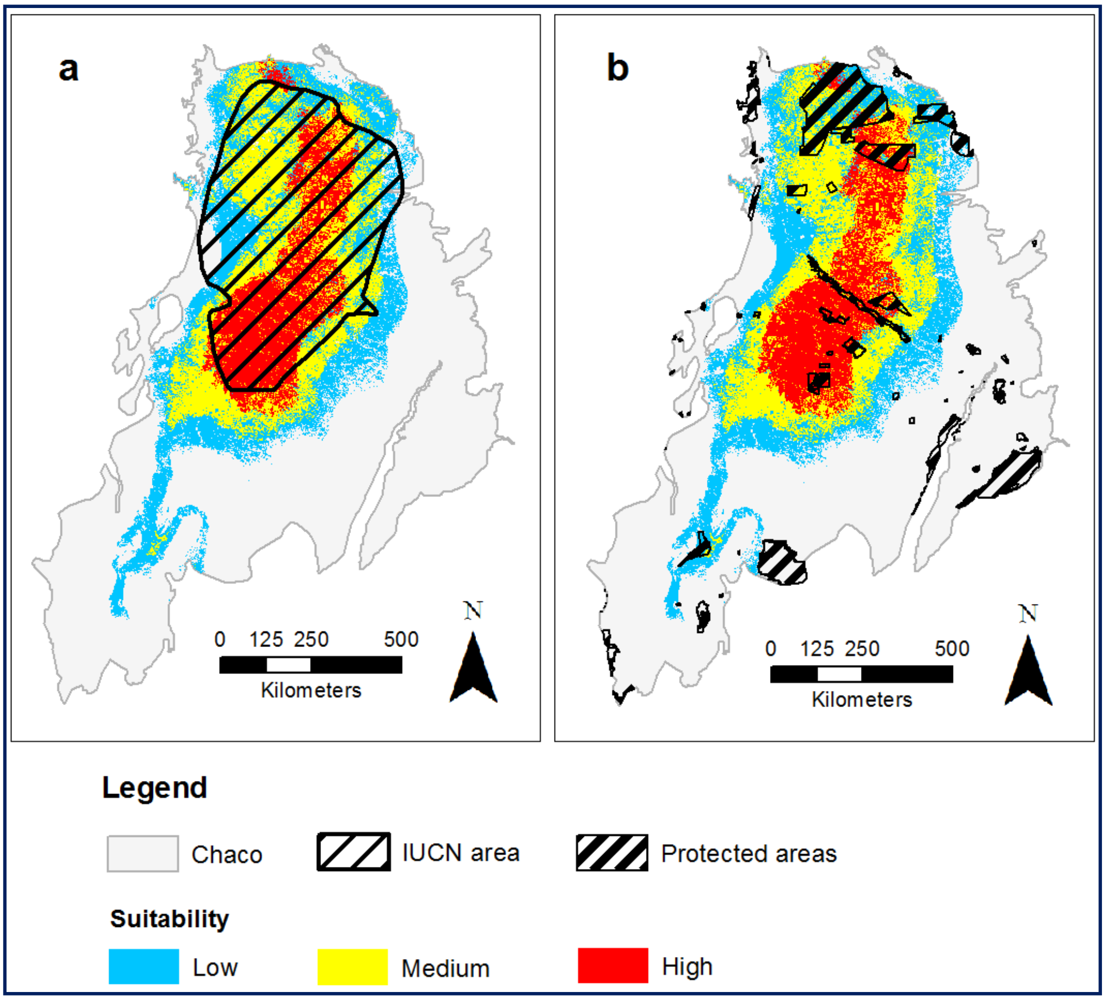

Fig 6. Suitable areas for the Chacoan peccary showing low suitability in blue (probability of presence from 0.0975 to 0.25), medium suitability in yellow (probability of presence from 0.25 to 0.50) and high suitability in red (probability of presence from 0.50 to 0.76), overlain with IUCN distribution area (a) and protected areas (b).

Table 2. Suitable areas for Chacoan peccary (i.e. low, medium and high suitability) protected by country and in total across all countries.

	Argentina			**Bolivia**		
Suitability	Total area (km^2)	Protected (km^2)	%	Total area (km^2)	Protected (km^2)	%
Low	93,637.81	2,462.29	2.63	49,192.99	17,674.56	35.93
Medium	66,336.67	2,779.66	4.19	37,218.70	16,638.37	44.70
High	68,124.66	5,021.85	7.37	4,137.34	3,265.19	78.92
	Paraguay			**All countries**		
Suitability	Total area (km^2)	Protected (km^2)	%	Total area (km^2)	Protected (km^2)	%
Low	50,978.50	2,128.43	4.18	193,809.30	22,265.28	11.49
Medium	80,849.08	4,620.40	5.71	184,404.46	24,038.42	13.04
High	46,940.08	6,163.55	13.13	119,202.07	14,450.58	12.12

Finally, high suitability areas for the Chacoan peccary showed here must be considered as key localities for conservation efforts aiming to protect the species and its habitat, and to avoid human conflicts (e.g., hunting pressure), particularly if these areas are not protected by law. Such areas might also guide the establishment of new protected areas and their connectivity should be considered in land-use planning. A key factor for the successful conservation of the species will be to involve the indigenous people and the local pheasants, that historically occupied some of these areas (Camino et al., 2016). Regardless of which combination of approaches are employed, urgent measures are needed to stop deforestation across the Gran Chaco, one of the most threatened ecological regions in South America today.

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Integrating human dimensions into conservation

Working Group
2016 CBSG Annual Meeting
Puebla, Mexico

Integrating human dimensions into conservation planning

Sarah Long

Aim

The aim of this Working Group session is to explore how we can more systematically gather and integrate information about human dimensions into the conservation process.

Background

Conserving species requires basic biological and ecological data relevant to the threats to a species and its biological potential for overcoming these threats. While conservation planning often factors in non-biological information, including economic costs and the potential impact on multiple stakeholders, the influence of the human dimension on conservation is often underestimated. With the growth and expansion of human populations and increasing urbanization, the conservation of species will more than likely need to occur in a human-dominated landscape. However, there is still an expectation among both scientists and citizens that species can be conserved behind fences away from people (e.g., on government land), rather than coexisting alongside people (e.g., on a patchwork of private and public lands). To achieve success in this new model, conservation planning will increasingly benefit from the integration of data from social scientists regarding perceived costs and benefits, values, and attitudes of a wide range of potential stakeholders. Beyond the input of social science, conservation planning could also benefit greatly from strategically planned education initiatives and public relations efforts.

Process

The working group will begin by discussing concepts and examples of how to integrate human dimensions into the traditionally biologically driven conservation planning process. An example focal species conservation effort for this discussion could be the endangered red wolf in the southeastern United States. At the time of this writing, the recovery program for this species in North Carolina is currently under review, but there may be new recovery efforts needed for this species. The reintroductions of different wolf species in the United States, or of any predator species coexisting near people, provide a good opportunity to discuss the historical successes and challenges relating to this topic.

Outcomes

The group will produce a set of recommendations that describe various ways in which CBSG and other conservation planners can better integrate social sciences, human behavioral data, and the skills of non-scientists into the conservation planning process for more successful conservation outcomes.

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Review

Contribution of social science to large scale biodiversity conservation: A review of research about the Natura 2000 network

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ABSTRACT

Successful conservation needs to be informed by social science because it is closely linked to socio-economic processes and human behaviour. Limited knowledge about ecosystems' interactions with these processes currently undermines conservation efforts. This review provides a comprehensive synthesis of social science concerning the world's largest multinationally-coordinated conservation infrastructure: the European Ecological Network - 'Natura 2000'. Based on a review of 149 publications, we analyse and discuss the main findings and outline key social-science research gaps with regard to the Natura 2000 network. The review shows that human dimension of the Natura 2000 network is complex and varies among EU Member States. In general, low level and quality of public participation in implementation of the Natura 2000 network and its management, negative public perceptions of the network, lack of flexibility of responsible authorities and insufficient consideration of the local context pose the greatest challenges to the network's functioning. Important but hitherto little studied research topics include: evaluation of participation; effects of education on potential to raise public awareness; effects of potential financing mechanisms for compensating private land-owners; economic studies on cost-effectiveness; and benefits from conservation and ecosystem services. These knowledge gaps will need to be filled for the Natura 2000 network to reach its goals.

Contents

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1. Introduction

Conservation science is characterised by a “tight coupling of social and natural systems” (Kareiva and Marvier, 2012). Successful conservation is not solely contingent on ecological knowledge, but should also incorporate human behaviour and the resulting social processes which eventually influence the status of biodiversity (Ban et al., 2013; Fox et al., 2006). It is vital for conservation professionals to understand the factors shaping human-environment interactions, particularly human choices concerning the use or conservation of natural resources (Mascia et al., 2003). For example, the human-induced global water crisis endangers not only human societies, but also affects freshwater biodiversity (Vörösmarty et al., 2010). Anthropogenic global climate change is not only posing challenges to humans, but is also perceived as one of the most serious threats to the planet's biodiversity (Malcolm et al., 2006). Moreover, it has become obvious that conservation measures cannot be fully successful if poverty issues are not tackled (Adams et al., 2004). Therefore successful conservation requires recognition and understanding of the value of social science research, i.e. research that uses conceptual and theoretical underpinnings of social sciences, such as sociology, human geography, social policy, social psychology, political sciences, economy, public communication and management to investigate human behaviour and associated social processes (Bryman and Teevan, 2005).

However, there is an increasingly recognised gap in understanding and tradition of co-operation between natural and social scientists, and particularly a lack of appreciation of social science knowledge in practical operation of conservation policy (Liu et al., 2007). This problem needs to be addressed if we want to produce knowledge that truly contributes to solving today's conservation challenges (Fox et al., 2006; Nyhus et al., 2002). Comprehensive syntheses of social science research concerning major conservation initiatives may contribute to building that knowledge.

One key conservation action worldwide is the development of large-scale networks of protected areas (Rodrigues et al., 2004). In spite of the fact that over 200,000 protected areas cover ~14% of the world's land area (Deguignet et al., 2014), there are very few coordinated networks of protected areas aiming at continental-scale conservation. Examples of such networks stretching across national borders include the Yellowstone-to-Yukon Conservation Initiative in North America and the European Ecological Network – ‘Natura 2000’. The latter is the world's largest multinationally coordinated conservation infrastructure.

As the centrepiece of the European Union's (EU) biodiversity conservation policy, the Natura 2000 network was created based on the Article 3 of the EU's Habitats Directive (CEC, 1992). It aims at protecting habitats and species of EU interest, listed both in the Habitats Directive and Birds Directive (CEC, 1979, 1992). The Natura 2000 network plays a key role in protection of biodiversity in the EU territory by “assuring the long-term survival of Europe's most valuable and threatened species and habitats” (EC, 2015a). The network consists of Special Protection Areas – SPA (for protecting species included in Birds Directive), Special Areas of Conservation – SAC (species and habitats included in Habitats Directive), and also includes marine environments (EC, 2015a). Natura 2000 has been implemented gradually, starting in 1992 in the 12 EU countries, followed by other countries joining the European Union afterwards. This initiative is considered critical for the implementation of international conservation policies such as the Convention on Biological Diversity (UN, 1992) and the European Strategy for Biological Diversity (EC, 2011). The Natura 2000 network considerably differs from previous conservation systems in Europe as it goes beyond a direct ban on damaging plants or killing animals and focuses on socially sustainable conservation harmonising the maintenance of species and habitats with economic, social and cultural human needs (Grodzińska-Jurczak, 2008). Because of that the meaningful involvement of affected stakeholders is seen as necessary for the network's success (EC, 2000).

The entire implementation process, starting from the selection of the protected sites till development of management plans, met opposition from various stakeholder groups in almost all EU Member States (Alphandéry and Fortier, 2001; Hiedanpää, 2002; Krott et al., 2000; Pietrzyk-Kaszyńska et al., 2012; Visser et al., 2007). The problems in implementation called for a proper assessment and monitoring of the network, and eventually led to the development of more effective implementation recommendations (Bouwma et al., 2008; Kati et al., 2015). In 2015, the European Commission initiated a process of fitness check on the implementation of the Birds and Habitats Directives. The fitness check aims at scrutinising the effectiveness, efficiency, relevance and coherence (EC, 2015b) of all stages of the network implementation, from the designation through inventory and monitoring to the development of management plans for particular sites.

Considering its importance for European nature conservation Natura 2000 has also been the subject of an increasing research interest, particularly from conservation scientists (Popescu et al., 2014). To achieve a good functionality of the network, there is a need for knowledge not only on the ecological conservation and management issues relevant to the Natura 2000 (e.g. status of species and habitats, ways of managing the sites), but also on key social, economic, political and managerial realities potentially influencing its effectiveness. In a recent review of published research on Natura 2000, Popescu et al. (2014) concluded that ecological research prevails, while social, economic and policy research on the network is underrepresented. Still, there is a non-negligible body of research focusing on the social aspects of the Natura 2000. However, perhaps as a consequence of its broad scope, there have been so far no attempts to comprehensively review this research. In this paper, we present a review of the published scientific literature focusing on the social aspects of the Natura 2000 network, expanding Popescu's et al. (2014) work by analysing in depth the findings of the existing social science studies. The aims are to (1) synthesise the existing social scientific knowledge on Natura 2000 and identify future research needs, and (2) inform conservation professionals and other relevant actors about the broad spectrum of challenges and solutions relevant to the implementation and functioning of the Natura 2000 network.

2. Methods

We performed an in-depth review and analyses of published English-language scientific papers applying a social science perspective in conservation research focused on Natura 2000. We are aware of the fact that some social aspects of Natura 2000 may be addressed in the “grey literature” or local manuscripts or reports. However, here we focused on the peer-reviewed literature only because (1) we wanted to concentrate on scientific knowledge, with a reliable level of scientific rigour, (2) it would have been logistically impossible to directly cover the diversity of “grey literature” characterised by a multiplicity of languages, and (3) the peer-reviewed literature builds to a large extent on analyses of various types of non-scientific texts (reports, legal texts, articles, etc.) published in different languages, and hence our approach does indirectly capture substantial parts of the information contained in these publications.

We collected the data through desk research. The main unit of our analysis was an individual article. We applied a mixed-mode social science research methodology (qualitative and quantitative) that allowed for a broader perspective of gathering and analysing of the data. We used the Web of Science™ Core Collection database for searching the literature. We searched for the phrase "Natura 2000" in the "topic" field of the database for the period 1998–2014. From the initial set of publications, we only retained studies that were either primary original research or reviews; thus, we removed publications categorised as correspondences, letters, responses, commentaries, policy perspectives, etc. Conference proceedings were only included if published in a peer-reviewed journal. We also removed publications in other languages than English, even if they had an English abstract. After this selection we ended up with 664 publications (as of January 1st, 2015).

We performed an initial scanning of selected publications to retain only articles that addressed social science or included a social analysis component (e.g. inter, multi or transdisciplinary studies combining social sciences with other disciplines). After that preliminarily scanning, 248 publications were classified as belonging to the social sciences or as having a social-science component. A review of the ecological literature about Natura 2000 will be published elsewhere (Orlikowska et al. unpublished results). Out of the 248 publications retained for the present review, we further removed 46 after in-depth examination, either because they were not research/review papers or because they did not address Natura 2000. For example, if a paper had "Natura 2000" merely in the abstract but did not focus at all on any aspect of Natura 2000, we removed it from the analysis. We removed another 39 publications because in-depth examination revealed that they did not include any social-science analysis. Finally, we removed 14 publications due to unavailability of the full-text versions. Thus, 149 publications were left for in-depth analysis, 112 classified as social science and 37 including some social-science analysis. The Results section below is based exclusively on these publications. However, in the Discussion section we also refer to some relevant studies not identified by our search, e.g. studies published after the closing date of our literature search. Note that 91 of the 149 publications retained for the present study were included in the recent review by Popescu et al. (2014). Our review includes 58 papers not analysed by these authors, while 29 of the papers they included were not retained for the present study. These differences are most likely due to the different inclusion criteria used in the two studies.

The first step of the analysis consisted in distinguishing eleven core categories of papers (Table 1) based on their main focus, identified through reading the title and abstract of each publication. We then used a qualitative content analysis method (Bryman and Teevan, 2005) for analysing all the papers. We utilised an open coding approach without pre-defined codes. Thus, the codes emerged in the course of analysis and involved identification of the most important issues and the key findings of the papers. We analysed each of the eleven categories of papers separately using specific codes for each particular category of papers. Because some of the initial categories were of a relatively broad scope, the analysis led to the identification of a set of sub-categories within five of the main categories of papers (see Table 1 for explanation). In the next step of the analysis, we used memos (Glaser and Strauss, 2008) for summing up information on the identified issues and key findings. Using the memos and building on the issues identified in them, we created summaries of the results by categories and discussed their determinants in the context of the main socio-economic findings for each category (see Results section). At the same time, we created a short summary of each paper (see online Appendix). We also recorded the country (or countries) investigated by each of the papers. Finally, we scrutinised the scope of all papers (based on their categories and sub-categories) to identify the most commonly addressed topics and the main research gaps.

Table 1
Categories and sub-categories used to structure the review process.

Category	Contents of the papers	Sub-categories
Conservation conflicts	Includes studies that analyse conservation conflicts, e.g. actual or potential conflicts between N2000 site protection and resource use, human well-being or tourism, potential problems in industrial/infrastructure development within or in the vicinity of N2000 sites, threats to N2000.	–Conservation vs. use –Conservation vs. development –Threats to N2000 sites –Combining tourism and conservation –Policy [a]
Implementation challenges and solutions	Includes studies that address different challenges faced during at least one stage of the N2000 policy implementation (including site designation, development of management plans, monitoring, etc.), and/or presents potential solutions to these challenges.	
Management	Includes assessment of the human dimension of management practices, adaptive measures or need for appropriate management plans to maintain species in favourable status, methodological studies on the development of management plans for N2000 sites or planning conservation action, studies proposing tools, approaches and frameworks for development of management plans and conservation strategies, etc.	–Tools, methods, approaches –Management and CC –Management evaluation –N2000 impact on management –Restoration management –Need for management
Perceptions, attitudes and values	Includes studies that investigates attitudes towards and perceptions of various aspects of the N2000 network, attitudes towards particular N2000 sites or their management, people's awareness of the N2000, etc.	–Local attitudes –Perceptions of management –Recreation and tourism –Other (see Online Appendix)
Valuation and economics	Includes studies that investigate costs or benefits of the N2000 establishment, management measures or restrictions, effectiveness of N2000 conservation funding, valuation (both use and non-use values) of the N2000 site, incentive mechanisms, etc.	–Preferences and WTP –Benefits from N2000 –Cost-effectiveness –Costs of N2000 –Incentives
Legal issues	Includes studies on legal aspects of N2000, e.g. analysis of legal acts and their consequences, or of some specific topic related to N2000 in relation to legal requirements.	–National level enforcement –Legislation effectiveness –CC in N2000 legislation –ES in N2000 legislation
Governance	Includes studies on different aspects of governance related to N2000, e.g. governance shifts due to implementation of the N2000, changes in possibilities of different actors to influence governance.	n/a
Policy integration	Includes studies that analyse N2000 policies that have been formulated and used during the designation and management processes, and potential problems connected with their relation to policies belonging to other sectors, e.g. potential overlaps, possibilities or barriers for integration of different policies.	n/a
Conservation priority setting	Includes studies that focus on determining conservation priorities or utilise systematic conservation planning with regard to N2000 which include socio-economic indices or criteria.	n/a
Participation evaluation	Includes studies that focus on evaluation of participatory processes in	n/a

(continued on next page)

Table 1 (*continued*)

Category	Contents of the papers	Sub-categories
	relation to N2000 implementation and operation, e.g. participatory aspects of the designation processes of particular sites or the whole network, or related to the N2000 network.	
Other	Studies that do not fit in any of the categories above.	See Online Appendix

Note: CC = climate change; ES = ecosystem services; N2000 = Natura 2000; WTP = willingness to pay.

n/a – not applicable; small category including few papers, no need to have sub-categories.

[a] The category "Implementation challenges and solutions" is a broad category including studies that analyse challenges and solutions from very different perspectives and at different stages of Natura 2000 implementation. Because of that inherent diversity at the level of individual papers, it was not possible to define distinct sub-categories that would include meaningful numbers of papers.

We are aware that the division into particular categories and sub-categories is to some extent subjective and arbitrary, as many papers address more than one issue and thus one paper could theoretically be included into two or more categories simultaneously. However, to allow a structured analysis we needed a clear division into categories. Thus, in cases where a particular paper fitted more than one category, we assigned the paper to the category which represented the main focus of the paper.

Even though some of the papers had a wider scope than Natura 2000, in the present review we only consider the information concerning this network. Thus, if a paper was about different kinds of protected areas including Natura 2000 sites, we only considered the contents which specifically concerned Natura 2000.

3. Results

3.1. Focus of the publications

Most of the publications belonged to the category of 'Conservation conflicts' (23 publications), 'Implementation challenges and solutions' (21), 'Management' (20), 'Perceptions, attitudes and values' (17), 'Valuation and economics' (16), 'Legal issues' (11), 'Governance' (8), 'Policy integration' (5), 'Conservation priority setting' (4), and 'Participation evaluation' (4). The remaining 20 publications were classified as 'Others' (Fig. 1).

The 'Conservation conflicts' category focused mainly on local land use or infrastructure development in potential conflict with conservation in particular locations (Fig. 2). Many papers focused on particular challenges faced by Natura 2000 and possible solutions (papers from 'Implementation challenges and solutions' category) or tools and methods for practical work with Natura 2000 (11 out of 20 papers in the 'Management' category) – both groups studying the factors influencing the practical implementation of the network. Within the category 'Perceptions, attitudes and values', the largest topic was the attitudes of local communities (10 out of 17 studies) (Fig. 2). Valuation/economic studies in most cases investigated preferences and willingness to pay for Natura 2000 conservation or management (5 out of 16 studies) or cost-effectiveness of conservation (5 out of 16 studies).

Twenty-five publications presented studies encompassing the entire EU. In terms of particular countries, Greece had the highest level of representation in the publications, followed by the Netherlands, UK, Germany, Poland, Romania and Italy (Fig. 3). In general, the EU-15 countries (i.e. countries that had joined the EU prior to 1st May 2004) had more (altogether 117, mean 11 per country) publications than the countries that joined the EU in and after 2004 (altogether 40, mean 4). Important exceptions were Belgium and Sweden, two EU-15 countries with only one publication each, as well as Poland and Romania, two late-accession countries with relatively large numbers of publications (Fig. 3). At the level of the whole EU, most of the publications concerned either legal issues (4 papers), followed by valuation, governance and implementation challenges and solution studies (3 papers in each of these categories). Most publications about management were conducted in Italy (5 papers), followed by Greece and the Netherlands (4 papers each), while Romanian studies focused on conservation conflicts (6 papers) (Fig. 4).

3.2. Synthesis of the main findings

In this section, we synthesise the findings of the reviewed articles for the different main categories (Table 1). We do not include the category 'Other' because it represents studies that lack common findings. A short summary of all the reviewed publications (including those in category 'Others') is included in the online Appendix.

3.2.1. Conservation conflicts and implementation challenges/solutions

'Conservation conflicts' and 'Implementation challenges and solutions' categories are related and therefore we address them together.

The potential conflicts in implementation and functioning of the network were those between conservation under Natura 2000 and different kinds of land and water use, such as forestry (Hiedanpää, 2002; Pecurul-Botines et al., 2014), farming (Gonzales et al., 2009; Oana, 2006; Visser et al., 2007), fishing (Pedersen et al., 2009; Zaharia et al., 2014; Zaharia et al., 2012), ship navigation (Freitag et al., 2008), as well as industry and infrastructure development (Andrulewicz et al., 2010; Bielecka and Różyński, 2014; Wszołek et al., 2014). Some studies

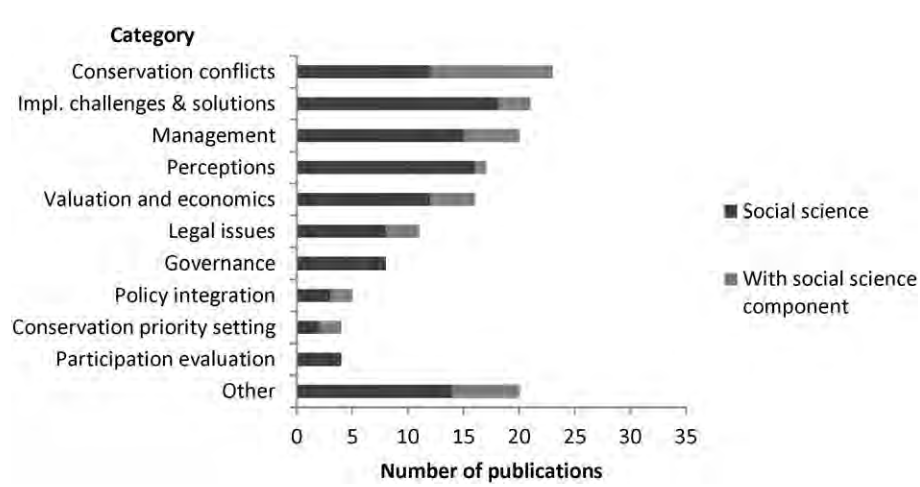

Fig. 1. Number of publications belonging to the main categories.

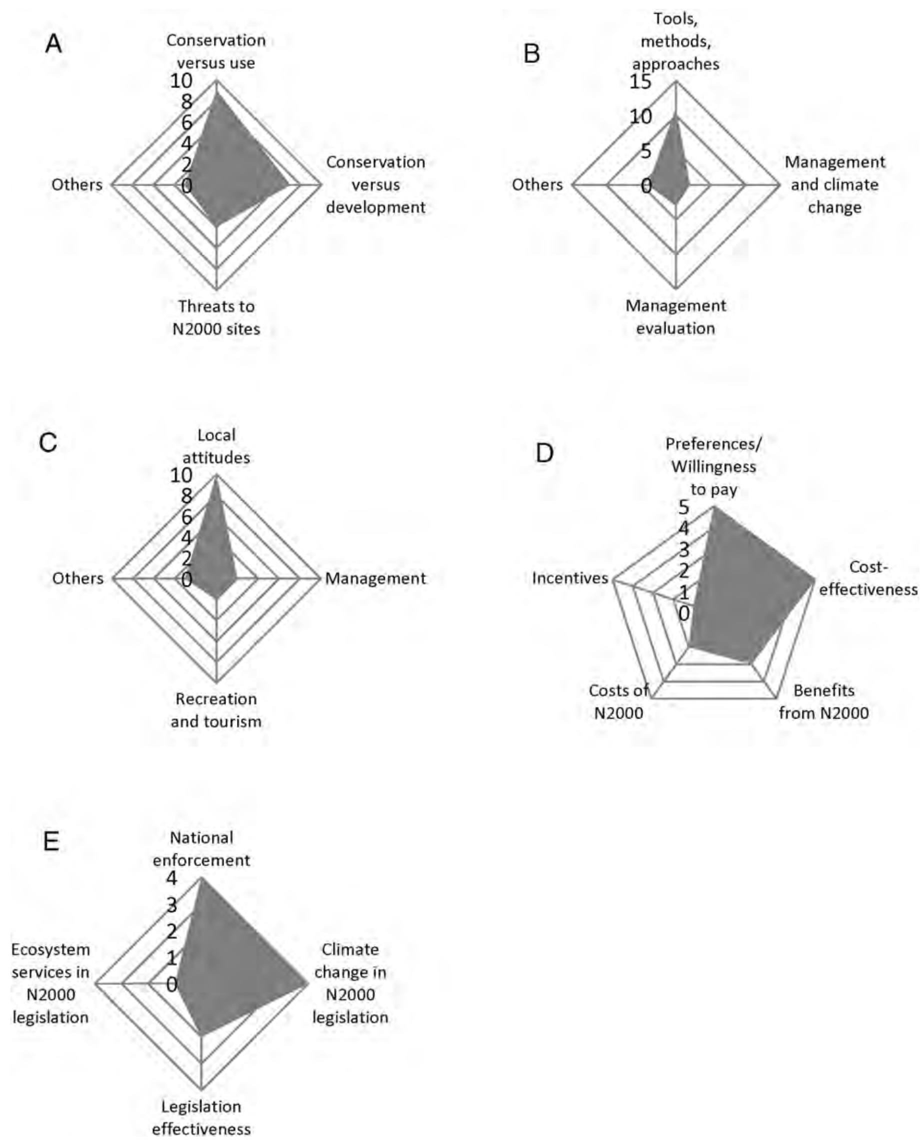

Fig. 2. Number of articles belonging to the different sub-categories within main categories. Only five categories are included, as other categories were not divided into sub-categories (for explanation see Table 1). A: conservation conflicts; B: management; C: perceptions attitudes and values; D: valuation and economics; E: legal issues.

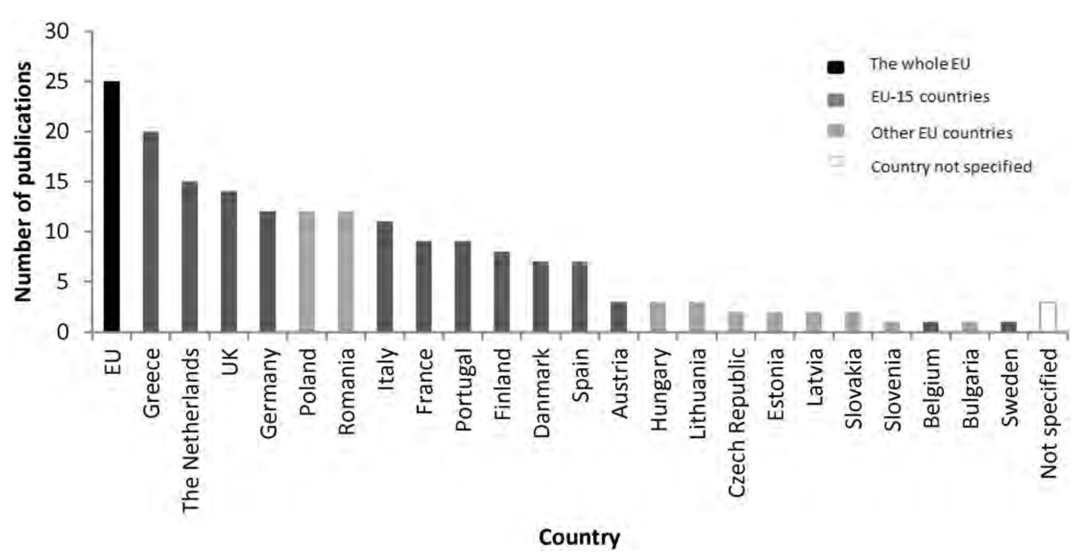

Fig. 3. Number of articles presenting research pertaining to individual EU countries. Note that in some articles more than one country was included, and thus one article could be listed under more than one country. Both social-science articles and articles with a social-science component are included.

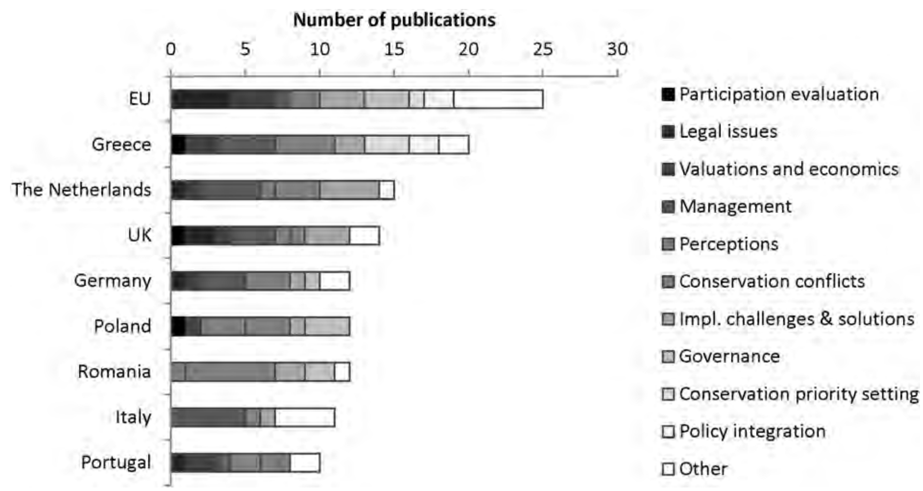

Fig. 4. Number of publications in each category for individual countries with ≥10 papers. Both social-science articles and articles with a social-science component are included.

in the 'Conservation conflicts' category investigated the impacts of different anthropogenic activities on Natura 2000 areas (Muntean et al., 2013; Pîrvu and Petrovici, 2013), with a particular focus on agro-tourism (Ciapala et al., 2014; de Noronha Vaz et al., 2012). According to Hiedanpää (2002), "the administrative environmental actions disturb localities in intended good ways, but also in many unintended and surprising ways" which can be perceived by local people as harmful and immoral. However, whether the conflict will arise depends on the local institutional context (Pecurul-Botines et al., 2014).

As key approaches for addressing existing conflicts, mitigating threats, and improving implementation and functioning of the network, different authors suggested cooperation and improved communication with the resource users, as well as development of management plans for each site using participatory approaches (Pedersen et al., 2009; Pîrvu and Petrovici, 2013; Visser et al., 2007; Zaharia et al., 2014). Indeed, increased social support of formal rules was considered a key to successful implementation (Beunen et al., 2013). Such cooperation can elicit valuable local knowledge helpful to conservation (Pedersen et al., 2009), but requires meaningful involvement of a wide spectrum of stakeholders (Ferranti et al., 2010). Hiedanpää (2005) described such involvement in terms of a "transactive approach", i.e. a "participatory, discursive, engagingly organised, sensitively operated, and decisively powerful approach". Participatory approaches should operate within and be sensitive to the local and regional economic context (Hiedanpää, 2002), address conflicting issues across different sectors (Andrulewicz et al., 2010) and enable land users to understand the benefits from particular Natura 2000 sites (Oana, 2006). This is particularly important with regard to farming: to avoid the ongoing in the EU land abandonment, there is a need to win "the minds and hearts of future farmers" (Visser et al., 2007). The latter need to be convinced about the benefits of conservation (Kamal and Grodzinska-Jurczak, 2014; Prazan et al., 2005) as they may fear potential limitations imposed by Natura 2000, including compromises linked to their place identity (Welch-Devine, 2012). This can only be accomplished when both sides (conservation and food production) acknowledge the importance of each other's priorities (Visser et al., 2007). Also, as conservation may imply significant costs for the landowners, there may be a need for financial instruments such as public funding or tax reductions (Rojas-Briales, 2000). The need for sufficient funding was underlined in several studies (Ferranti et al., 2010; Hochkirch et al., 2013; Iojă et al., 2010), for example as regards financial compensation schemes for landowners (Stancioiu et al., 2010) and activities that would increase general conservation awareness (Hochkirch et al., 2013). Similarly, Ciapala et al. (2014) suggested that tourism and recreation are "inherent element of human influence on biodiverse areas", and that such activities need to be considered when planning for and managing Natura 2000 sites. To address that, Parolo et al. (2009) proposed an optimisation model for allocating tourism infrastructure.

Regarding the key challenges of the Natura 2000 implementation, the studies identified problems pertaining to legitimacy of the implementation process (Alphandéry and Fortier, 2001), low capacity of the state in implementation (Apostolopoulou and Pantis, 2009) or weaknesses in the scientific work (Alphandéry and Fortier, 2001). A lack of proper participatory approaches implemented at the local level (Alphandéry and Fortier, 2001; Apostolopoulou and Pantis, 2009; Iojă et al., 2010) was also frequently mentioned. Even in cases where participation took place, emphasis on legal procedures could reduce the quality of deliberation (Beunen et al., 2013). On the other hand, some studies underlined that EU accession and associated implementation of EU policies provided new opportunities for participation of local actors and better cooperation among governmental institutions rarely used so far, especially in post communistic countries (Prazan et al., 2005).

Lack of clear implementation goals and discrepancy between stated and actual goals can also compromise the national-level implementation of the Habitats Directive (Apostolopoulou and Pantis, 2009). In addition, superimposing the Natura 2000 sites onto existing (e.g. national) systems of protected areas may lead to duplication of administration and legislation, as well as overly complex protection systems (Papageorgiou and Vogiatzakis, 2006). For example, in Romania the Natura 2000 network overlapped at ~96% with existing protected areas, with some sites having up to three different protection forms (Iojă et al., 2010).

Alphandery and Fortier (2010) emphasised that the implementation of the Habitats Directive is a non-linear, at times chaotic process that occurs at different scales from the local to the European level. In relation to this complex process, some authors highlighted the crucial role of local actors (Borrass, 2014). Ferranti et al. (2010) suggested education and training of local authorities to improve the practical implementation and Louette et al. (2011) proposed the development of regional conservation objectives as a means to bridge the gap between local and national interests. Several authors underlined the need for better cooperation among national-level authorities (Prazan et al., 2005) and the importance of inter-sectoral cooperation (Papageorgiou and Vogiatzakis, 2006; Sarvasova et al., 2013). Alphandery and Fortier (2010) argued that proliferation of procedures and provisionality in implementation are natural elements of the Natura 2000 implementation, and that they do not necessarily imply inefficiency of the government. Beunen et al. (2013) underlined the need to take into account the particular context and interests in the implementation process. Beunen and van Assche (2013) cautioned against the "blindness of legalism" and suggested flexible local planning as the best means of enabling space for deliberation of different interests when implementing Natura 2000. “Once we recognize that formal rules can never be sustained without public support and we understand that public narrative determines their success, we can no longer ignore this dimension of nature conservation in research and practice” (Beunen et al., 2013), as “the battle for biodiversity will be won or lost at local levels” (Bryan, 2012).

3.2.2. Management

A large proportion of the papers in this category (11 out of 20) proposed or examined different methods to facilitate the planning of management activities in Natura 2000 sites and support the development of management plans for these sites. These studies most commonly proposed participatory approaches to knowledge production, scenario development and planning of management activities (Bots et al., 2011; Gil et al., 2011; Graziano et al., 2008; Oikonomou et al., 2011). For example, Ernoul et al. (2011) and Teofili and Battisti (2011) proposed the use of ‘Open Standards for the Practice of Conservation’, adapted to the local specifics of each site, that promote participatory processes for adaptive management. Other approaches took into account the human dimension by using indices of human activities in management planning (Cortina and Boggia, 2014) or adopting an ecosystem services perspective (Scolozzi et al., 2014). The remaining studies were of a very diverse character. They focused, for example, on evaluating the management (Ganatsas et al., 2013; Morris et al., 2014; Winter et al., 2014) or implications of particular policies for the Natura 2000 network (Fock, 2011).

A number of recommendations have been made for the design of participatory process in management planning. For example, Bots et al. (2011) proposed that the process should be set up to favour openness, protection of the actors' core values, use of relevant knowledge and possibility to acknowledge uncertainties; Oikonomou et al. (2011) emphasised the necessity of considering the social value judgements of different actors; and Gil et al. (2011) underlined the need for participation and co-responsibility of all relevant stakeholders. Also, Malatinszky et al. (2014) emphasised the necessity to set a priority order of conservation aims at an early stage of management planning, based both on science and the needs and interests of relevant stakeholders. The issues identified in this set of papers included the lack of time, resources and qualified facilitators that could serve the participatory process (Ernoul et al., 2011) and lack of flexibility of authorities due to strict regulations (Malatinszky et al., 2014). According to Malatinszky et al. (2014), “management planning should be based on current, exact, relevant ecological and social circumstances, and historical land uses. Therefore, this process cannot be simplified into following a planning scheme”. It was also underlined that, to improve effectiveness of management schemes, legal provisions concerning management need to be matched with local capacity (Morris et al., 2014).

According to Cortina and Boggia (2014), a multi-criteria approach that incorporates both the ecological and the human dimension is particularly useful for Natura 2000 management planning, as it enables addressing a multidimensional decision process and the complex nature of biodiversity itself. Also Soane et al. (2012) underlined the multidimensional and dynamic nature of many Natura 2000 sites. These authors applied resilience theory to describe the complex socio-ecological systems of managed alpine grasslands. They proposed that this theory can support adaptive management of Natura 2000 sites, as it “offers useful insights into resource management and in particular for nature conservation interest sites, by focusing more on dynamics than on an optimal state of species assemblages”.

3.2.3. Perceptions, attitudes and values

Most of the publications in this category (10 out of 17) aimed at investigating the attitudes of various (predominantly local) stakeholders towards Natura 2000. They revealed both positive and negative attitudes towards the network. It was generally considered as a good tool for conservation (Dimitrakopoulos et al., 2010; Grodzinska-Jurczak and Cent, 2011; Mouro and Castro, 2009; Pietrzyk-Kaszyńska et al., 2012; Sumares and Fidelis, 2009), but also as an impediment to economic sustainability, whereby it was often perceived as being associated with a ban on development at practically all levels (from local to regional) (Grodzinska-Jurczak and Cent, 2011; Sumares and Fidelis, 2009). Moreover, in some cases, the perceived “dictatorship-style”, top-down implementation contributed to a low level of trust towards the network and associated authorities (Sumares and Fidelis, 2009). For example, many landowners in Poland viewed top-down management of private land as questioning their capability and rights to manage the land. As a consequence, these landowners tended to distrust the authorities (Kamal and Grodzinska-Jurczak, 2014). A study from Greece (Andrea et al., 2013) showed low satisfaction of the local people with the work of local authorities implementing the network. This case pointed to staff deficiencies and irregular funding as main obstacles for effective management. On the contrary, a study from another Greek region (Dimitrakopoulos et al., 2010) showed greater acceptance towards local implementing actors, but high distrust towards higher-level governmental actors, indicating that the local perceptions may be context dependent. In a study from Latvia (Pavasars, 2013) the problem of mistrust towards authorities was described in terms of existence of “parallel realities”, i.e. that of “official environmentalism” and that of the everyday life of people in the countryside.

Insufficient communication (Grodzinska-Jurczak and Cent, 2011; Tonder and Jurvelius, 2004) and weak, if any, traditions of participation (Grodzinska-Jurczak and Cent, 2011; Sumares and Fidelis, 2009) were underlined as factors contributing to low trust. Well organised and more meaningful participation, stronger collaboration with local stakeholders (Dimitrakopoulos et al., 2010; Kamal and Grodzinska-Jurczak, 2014) and better cooperation between administrative bodies (Andrea et al., 2013) were proposed as means to improve acceptance towards Natura 2000. The need to increase awareness towards N2000 through proper information campaigns was also underlined (Kafyri et al., 2012; Marmureanu and Geamana, 2012).

Numerous individual-level factors were found to influence attitudes towards conservation in general and Natura 2000 in particular. These were, for example, education, the fact of moving to the area affected by Natura 2000 designation in adulthood, ownership of a business (Pietrzyk-Kaszyńska et al., 2012), vested interests, institutional trust, place identification (Mouro and Castro, 2009), socio-economic position, culture and social backgrounds (Tonder and Jurvelius, 2004), as well as the degree of satisfaction with the recreational experience (Torbidoni, 2011).

3.2.4. Valuation and economics

Most publications in this category encompassed studies about people's preferences and their willingness to pay (WTP) for particular protection measures or management plans in Natura 2000 sites (Grammatikopoulou and Olsen, 2013; Hoyos et al., 2012; Jones et al., 2011; Li et al., 2004; Rekola et al., 2000; Strange et al., 2007). Moreover, some studies investigated the costs of particular measures and activities in the sites (Jacobsen et al., 2013; Lee, 2001), services and benefits from Natura 2000 (Cruz et al., 2011) and cost-effectiveness or efficiency of Natura 2000 (Jantke et al., 2010; Wätzold et al., 2010; Wätzold and Schwerdtner, 2005), particularly with regard to conservation funding (Lung et al., 2014; Santana et al., 2014).

Even though people often had positive attitudes towards proposed conservation measures (Grammatikopoulou and Olsen, 2013; Pouta et al., 2000), their WTP depended on different factors, such as the ability of the conservation programme to take into account the rights of landowners, the respondents' opinion about the importance of preserving species and biotopes (Pouta et al., 2000), their level of knowledge about species to be protected (Strange et al., 2007), and the level of trust towards particular options (Jones et al., 2011). Also socio-demographics were important predictors of the WTP, as young, high-income and urban populations show stronger support for conservation (Pouta et al., 2000). Moreover, respondents with lexicographic preferences for nature rights were willing to pay much more for conservation than those with preferences for property rights (Rekola et al., 2000).

Relatively few studies (3 out of 16) focused on the benefits from Natura 2000. Cruz et al. (2011) outlined ecosystem services provided by a Special Protected Area in the Azores Islands, such as those related to water provision, quality and regulation, and also underlined the role of Natura 2000 in job provision. Other studies showed that the non-use values of the protected areas can exceed the use values (Hoyos et al., 2012; Strange et al., 2007).

Studies that focused on cost-effectiveness of Natura 2000's implementation and functioning were scarce (Wätzold and Schwerdtner, 2005). Wätzold et al. (2010) pointed to lack of long-term funding, wrong allocation of funds between different tasks when designing and implementing management plans, and costly EU requirements on monitoring as key problems. Lung et al. (2014) concluded that the distribution of EU biodiversity funding was generally well aligned with the existing Natura 2000 network, but not with the future needs linked to climate change. Jantke et al. (2010) showed that the current Natura 2000 network does not cover well all endangered wetland vertebrate species. They estimated that additional 3 million ha of protected areas would be required to achieve coverage of all important species, at an estimated cost of 107 million Euros per year.

We identified only one study on economic incentives supporting Natura 2000 implementation (Anthon et al., 2010). The paper presented theoretical justification for using contracts when implementing the network in forest areas and discussed different mechanism of payment used in Natura 2000 contracts.

3.2.5. Legal issues

Publications about legal issues mostly investigated national-level enforcement of Natura 2000 legislation, particularly with regard to Environmental Impact Assessment (EIA). The general view was that Natura 2000 legislation was still not fully incorporated into national legislations (Vaiškūnaitė et al., 2012) although clear improvements could be observed (Christensen, 2006). It was proposed that specific socio-legal conditions must be fulfilled for a better implementation and functioning of the Natura 2000 legislation, such as e.g. capacity of the public interest groups and their access to national courts or the way in which European provisions are interpreted by national courts (Slepcevic, 2009). A study by Marandi et al. (2014) suggested that protection should be actually commenced as soon as a specific area is proposed for inclusion in the Natura 2000 network.

Other studies investigated the effectiveness of the Natura 2000 legislation. For example, Leone and Lovreglio (2004) described it as one of the most important building blocks contributing to conservation, and Mallard and François (2013) concluded that the Natura 2000 network is the most effective instrument for conservation in relation to road planning in France. However, they criticised the fact that the road construction permits can be issued for "imperative reason of major public interest", which limits the power of the Natura 2000 legal requirements in practice. Weaknesses of the national Natura 2000 legislation could be also observed in Lithuanian road planning, where EIA procedures and principles did not comply with EU requirements regarding the biodiversity impact assessment of roads (Vaiškūnaitė et al., 2012). Two studies considered legal issues related to marine conservation within Natura 2000. While Metcalfe et al. (2013) highlighted criticisms against the Habitats Directive as being ill-suited for marine conservation, Rees et al. (2013) claimed that "site integrity" and "favourable conservation status" are powerful legal terms that can facilitate effective marine conservation if fully transposed into the legislation of the EU Member States.

The remaining studies investigated the extent to which legal requirements regarding Natura 2000 incorporate considerations for some particular issues, such as climate change (Cliquet, 2014; Jackson, 2011) or the provision of ecosystem services (Kistenkas, 2014). According to Cliquet (2014), although the Natura 2000 legislation does not explicitly mention climate change, it "contain[s] sufficient tools to deal with the effects of climate change". Still, Cliquet (2014) argued that these tools have been insufficiently implemented so far and provided recommendations for improvement (see Table in online Appendix). On the contrary, Jackson (2011) suggested that legislation linked to Natura 2000 may potentially undermine climate change mitigation efforts by challenging many renewable energy projects. The author proposed to broaden the range of acceptable alternatives, and saw much potential in combining lower-impact renewable energy projects with Natura 2000 protection. Kistenkas (2014) advocated incorporation of the ecosystem services concept into EU's nature conservation law, emphasising that the present legislation is too rigid to enable proper assessment of these services.

3.2.6. Governance

The main focus of the papers in this category was on the effects of the implementation of Natura 2000 and, particularly, on the accompanying governance shifts. They described the general shift towards increased inclusion of more relevant stakeholders (Ferranti et al., 2014), the emergence of multilevel governance and an associated increase in implementation legitimacy (Niedziałkowski et al., 2012; Rauschmayer, 2009) with important input from environmental non-governmental organisations (NGOs) (Börzel and Buzogány, 2010; Cent et al., 2013; Weber and Christophersen, 2002). For example, both in Poland and Hungary, NGOs contributed strongly to the selection of Natura 2000 sites (Cent et al., 2013). In the course of action, the agendas and actions may change, which can contribute to increase in professionalization and institutionalisation of civil society groups (Börzel and Buzogány, 2010). However, this does not always result in sustainable cooperative state-society relations, particularly when both state actors and civil society are weak (Börzel and Buzogány, 2010). For example, Central Eastern European countries (CEE) are still characterised by top-down policy making. Here, conflict is still the main driver of the implementation of participatory processes (Rauschmayer, 2009), although there has been a recent shift to more multilevel governance in decision making (Niedziałkowski et al., 2012) and growing importance of NGOs in biodiversity conservation (Cent et al., 2013).

In Romania, Stringer and Paavola (2013) observed a lack of NGO involvement in the implementation of Natura 2000 and generally limited experience in public participation. They suggested that this is due to historical legacies of low participation and government reluctance towards more inclusive governance. Even in cases where governance shifts can be observed, there can be a gap between the rhetoric and practice of inclusive governance (Rauschmayer, 2009). Nevertheless, Börzel and Buzogány (2010) argued that an effective implementation of EU policies requires departure from top-down centralised steering, and that it demands meaningful inclusion of non-state stakeholders. Such shift can also address the existing problem of low acceptance of EU conservation policies, particularly among landowners (Weber and Christophersen, 2002).

3.2.7. Policy integration

This relatively small category included five papers that looked into integration of nature conservation policies concerning Natura 2000 with policies from other sectors. It was shown that policies and debates on issues other than conservation, e.g. agricultural land use (Koutseris, 2006), climate change (de Koning et al., 2014; Roggema, 2009), or noise protection (Votsi et al., 2014b) can affect conservation and management under Natura 2000 network. Thus better integration of different policies and Natura 2000 was advocated (Roggema, 2009; Votsi et al., 2014b).

3.2.8. Conservation priority setting

Several (4) papers discussed Natura 2000 implementation from the perspective of prioritization or systematic conservation planning. It was argued that implementation of the network should make better use of systematic conservation planning (Gaston et al., 2008) incorporating socio-economic indices or human related criteria (Giakoumi et al., 2011; Tsianou et al., 2013) to facilitate the achievement of conservation goals. This may lead to very different outcomes on the ground compared to less systematic approaches. For example, by using spatial prioritization software including innovative socio-economic cost indices in the eastern Mediterranean Sea, Giakoumi et al. (2011) showed that only a few of the sites selected through the systematic approach overlapped with those previously identified in an unsystematic way.

3.2.9. Participation evaluation

Four studies directly evaluated the participation processes related to Natura 2000 – either during the designation of the network (Apostolopoulou et al., 2012; Cent et al., 2014), or development and implementation of management plans (Enengel et al., 2014; Young et al., 2013). The general picture was one of relatively low prevalence of participatory practices in Natura 2000. These were commonly rather superficial, operating mostly on paper (Apostolopoulou et al., 2012), and did not enable all relevant stakeholders to exert meaningful participation (Cent et al., 2014). The process of participation was usually steered in a top-down manner, with highly asymmetric power distribution among the involved actors. The governmental actors were the ones deciding who may participate and in what form (Apostolopoulou et al., 2012; Cent et al., 2014), aiming at fulfilling legal requirements or the needs of the organisers rather than empowering the participants (Cent et al., 2014). Even when the participation process was in principle open to everyone, a need for broader involvement of local people was expressed (Enengel et al., 2014). In addition, in some cases there was a lack of formal governance structures that would require procedures of participation in decision making (Apostolopoulou et al., 2012). Overlapping responsibilities of management agencies, governance fragmentation and heavy bureaucracy led to many parallel co-decision procedures for a specific site, causing problems in terms of accountability and legitimacy of the process (Apostolopoulou et al., 2012). Moreover, lack of precise information and trust was identified as a barrier to a more effective participation process (Enengel et al., 2014; Young et al., 2013).

Notwithstanding the above mentioned shortcomings, in three of the four studies in this category the participation process was deemed positive at least to some extent by the relevant stakeholders, as it increased their knowledge about and overall satisfaction with the Natura 2000 network (Cent et al., 2014), contributing to attitude changes towards the network (Young et al., 2013), and allowed the participants to contribute with their own knowledge and experiences (Enengel et al., 2014).

4. Discussion

4.1. Main findings and their implications

The reviewed literature showed a very wide scope of topics, indicating that the social dimension of Natura 2000 is complex and multidimensional, and varies among EU countries. The introduction of Natura 2000 met the opposition of various stakeholder groups in almost all Member States. Thus, an implementation of Natura 2000 policy may require a definite shift towards recognition of a wide range of social aspects relevant to the particular contexts of individual countries. One of the most conspicuous aspects identified by our review was the question of public participation or, broadly, stakeholder involvement. There were relatively few papers that focused mostly on public participation and its role (included in 'Participation evaluation' category). Still, in several categories of papers such as e.g. 'Conservation conflicts', 'Management' or 'Perceptions', this issue was mentioned. The reviewed papers indicated a general trend towards more inclusive approaches in implementation and management of Natura 2000, practically at all stages. However, stakeholder involvement, especially at the local level, was reported to be still of relatively small magnitude and low quality, and numerous challenges were identified. Even if new modes of governance emerged during the implementation and more power was given to non-state stakeholders such as NGOs or private landowners (Cent et al., 2013; Niedziałkowski et al., 2012) the effect was not always enduring. Sotirov et al. (2015) called such effect "symbolic transformation", where informal institution and practical behaviour did not change in line with formal domestic policy and institutions. This was particularly evident for the CEE countries that still bear some legacies of their communist past, characterised by top-down governance and practically no tradition of a broad stakeholder inclusion, especially those from non-public sector (Cherp, 2001; Kluvánková-Oravská et al., 2009). Yet, many studies underlined that meaningful participation is a key to successful Natura 2000 implementation and functioning and a necessary ingredient for efficient management of the sites. This is particularly important in the case of private land (e.g. farmland), as private landowners seem to be the most reluctant group in regard to the implementation of Natura 2000 requirements, due to potential limitations on land use (Geitzenauer et al., 2016). On the other hand, local governments seem to be a crucial group in the network's implementation and functioning, because Natura 2000 is in practice governed at the municipality level.

Our review revealed that although Natura 2000 was generally perceived as a useful conservation approach, there were also many negative perceptions of the network. The network was seen by many as an impediment to economic development. However, recent research from Poland (including all municipalities with at least one site of Natura 2000) did not support the assertion that the network was a significant negative barrier to economic development (Gutowska et al., unpublished). Indeed, a majority of municipalities were able to overcome the potential economic barriers, in most cases thanks to an operative local government. Our analysis showed, however, that the overall low representativeness and quality of stakeholder involvement could have greatly contributed to negative perceptions of Natura 2000, resulting in challenges in the network's implementation and functioning.

Another important obstacle reported in several studies was the low flexibility of the Natura 2000 regulations and their implementing authorities. It was emphasised that the local context matters, and hence that decisions based solely on strict rules and templates may not always be appropriate. This is particularly important with regard to the development of management plans for particular sites. Again, a participatory approach to management planning, with meaningful involvement of all relevant stakeholders, was suggested as a key component. A wide range of socio-cultural, institutional and discursive factors may influence the probability of success or failure of policy implementation, and thus taking them into considerations is essential (Hilding-Rydevik and Bjarnadottir, 2007; Runhaar, 2009). Implementation and functioning of Natura 2000 in various Member States is linked to multiple processes at different policy levels and depends on case-specific interplay (Borrass et al., 2015). A large diversity of approaches to implementation can be seen as a strength, as it can enable learning for improved future functioning of Natura 2000 (Winkel et al., 2015). However, to utilise this potential, there is a need for improved platforms and mechanisms of learning across the Member States (Winkel et al., 2015).

Some studies underlined the temporal aspects of Natura 2000 implementation. As Natura 2000 was implemented very quickly in many countries, it was not surprising that the process was not ideal (Kati et al., 2015). However, as Europe currently faces the next step of the network's implementation, i.e. creation and implementation of management plans for specific sites, the process could be improved by taking better consideration of the local context. Guidelines concerning organisation of the stakeholder involvement process (e.g. Bots et al., 2011; Hiedanpää, 2002) could be helpful in that respect.

Finally, the review has shown many implementation problems related to the low capacity of local actors. This suggests that a better flow of know-how from the EU to the local level, a larger number of better qualified staff and adequate funding are necessary components of successful implementation and functioning of the network. In their survey of conservation scientists on the functioning of Natura 2000 implementation, Kati et al. (2015) also underlined the low political will of both national and local authorities to fulfil the goals of Natura 2000. They underlined the need for mechanisms strengthening the linkages between EU policy and national, regional and local administration levels.

4.2. Research gaps

Our analysis has shown unequal distribution of social-science research about Natura 2000 among the different EU countries. In general, there were fewer studies addressing the countries that entered the EU in 2004 or later (i.e. the non-EU-15 countries). Obviously, this could be a result of a later implementation of Natura 2000 in these countries, leading to a delay in associated research. However, as discussed by Popescu et al. (2014), this issue is more complex. According to these authors, the "new" EU countries only lagged behind EU-15 by a relatively short time (3 to 5 years) in the designation of Natura 2000 sites. Nevertheless, even this short time lag could have contributed to the observed differences in research effort. An additional contributing factor could be the relatively lower levels of research funding in the countries in economic transition compared to the EU-15 countries. However, there were also exceptions, where some of the late-accession countries (e.g. Poland) were represented in more papers than some of the EU-15 countries, which possibly could be explained by the higher importance of particular social issues in these countries (e.g. linked to more conflictual situations), or the presence of particularly productive research groups in some countries. Moreover, it must be kept in mind that our review only includes peer-reviewed scientific articles in English. This could have led to some bias, as some issues may have been covered in the grey literature or in references published in other languages. Particularly, this could have led to underrepresentation of findings of practical relevance, such as e.g. local-specific challenges faced by various stakeholders groups (e.g. the site managers) or best-practice solutions to particular cases on the ground. Still, our review presents a reliable overview of the body of knowledge which is broadly available to the international scientific community. As such, it could contribute to the EU fitness check and to the recommendations for improving Natura 2000 implementation and functioning; however, one should keep in mind the limitations of such review, and whenever possible complement our findings with existing local recommendations and guidelines.

Several additional gaps could be identified in the body of social-science research concerning Natura 2000. First of all, in spite of the widely recognised importance of the participation of various stakeholders in the implementation and operation of the network, relatively few studies have evaluated in detail the participation processes linked to Natura 2000. It is possible that such information could be found in grey literature for the local studies but such literature was not a focus of our review. Particularly, there is a need for more research on the importance of participation for actual conservation outcomes, i.e. the extent to which participation affects biodiversity on the ground. Rauschmayer et al. (2009) suggested that both the process and outcomes of natural resources governance need to be investigated if we are to judge its effectiveness. In the case of participation, some studies evaluated the process itself (e.g. in terms of good or deliberative participation), but its effects on biodiversity were rarely scrutinised (Reed, 2008). Young et al. (2013) have investigated the correlation between the quality of stakeholders' involvement and the future biodiversity outcomes as perceived by the stakeholders, but they could find clear relationship between the process quality and the perceived outcome only in some cases. Although it was confirmed that in general a better quality of participation had a positive impact on social outcomes and particularly trust and justice, more studies are needed to confirm if the improved participation also leads to improved ecological outcomes. As public participation is still rather undeveloped in the majority of the EU countries, insights from such studies could provide useful knowledge for improving the further steps of Natura 2000 implementation and functioning. However, one needs to keep in mind that not only the participation process, but also different external factors may influence the ultimate conservation outcomes. Nevertheless, participatory approaches could be useful in the development of management plans for Natura 2000 (Hochkirch et al., 2013), as they increase trust among stakeholders and enable better integration of their different values, potentially allowing for better conservation outcomes (Williams, 2011; Young et al., 2013).

Better participation may practically lead to improved engagement in conservation and increased awareness of the conservation needs. Also, participatory process may contribute to Natura 2000 managers' understanding of the potential reasons for the resistance towards the network. At the same time, there is a need for studies investigating the potential effects of education and increasing awareness on people's perceptions of Natura 2000 and potential attitude changes. Although cognitive approaches alone proved not to be sufficient in furthering attitude change (Heberlein, 2012), they are an important component of strategies for dealing with environmental issues (Gardner and Stern, 1996). The importance of increasing the public awareness on Natura 2000, especially at the local level, was also underlined in a large survey of conservation scientists recently carried out by Kati et al. (2015). Our review has shown that there is still low acceptance of the Natura 2000 network in society, and a lack of knowledge on the network operation can be a factor contributing to it. As social acceptance is an important prerequisite for the implementation of conservation policies, there is a need for increased efforts, e.g. in terms of education and information, aiming at raising this acceptance (Kati et al., 2015). Still, although education and information are important, they are not sufficient for facilitating social acceptance. There is thus a need to also explore what other factors (in addition to low awareness) contribute to the resistance against the network in many places.

In addition, the low acceptance of the network by landowners may suggest that there is a need for compensatory measures, such as reimbursement of the conservation costs incurred by the private land owners (Kamal and Grodzinska-Jurczak, 2014; Schröter-Schlaack et al., 2014). For example, Stancioiu et al. (2010) suggested the need for compensatory financial mechanisms to cover the costs of Natura 2000 for the land owners. Also, conservation scientists surveyed by Kati et al. (2015) highlighted the need for an independent funding mechanism entirely devoted to supporting implementation of Natura 2000 goals. Also Winkel et al. (2015) suggested the need for development of a coherent funding strategy for Natura 2000 based on comprehensive assessment of both current spending and financial needs for the network. This may be particularly important for the CEE countries with extensive rural areas, large coverage of Natura 2000 sites and lower level of economic development compared to the EU-15 countries (Pavasars, 2013; Stancioiu et al., 2010). To design effective financing mechanisms that support the network, we see a need for more studies analysing the effects of alternative compensatory approaches in a range of socio-economic settings, on e.g. acceptance of conservation or biodiversity outcomes; however our review have revealed that such studies are still rare.

The issue of effectiveness has been largely neglected in the social research about Natura 2000. Very few studies looked at the costs or the benefits of the network, and comprehensive economic analyses were entirely missing in the reviewed publications. Surprisingly, the concept of ecosystem services was very rarely utilised in social-science research about Natura 2000, although it may seem particularly well fitted to analysing the complex socio-ecological systems of Natura 2000 sites (Primmer et al., 2015; Soane et al., 2012). Ecosystem service research could, for example, aim to identify and quantify potential benefits from the protection of the Natura 2000 sites, which in term could contribute to wider acceptance of the network (Cruz et al., 2011). Research on the effectiveness of the Natura 2000 network should also involve studies developing and testing indicators of effectiveness, including both ecological indicators as well as indicators of the social dimension encompassing human actions, institutions, organisations and networks (Salafsky et al., 2002). Such indicators are urgently needed to evaluate the success (or failure) of the network.

Conservation does not operate in an empty space. Rather, it is an integral part of complex socio-ecological systems. Consequently, insufficient consideration of social aspects risks undermining conservation effectiveness, while integrating local human context in the protected areas facilitates achieving biological conservation and socioeconomic development outcomes (Oldekop et al., 2016). Although Natura 2000 is generally seen as a successful conservation endeavour (Kati et al., 2015), our review points to different shortcomings affecting practically all EU Member States. Social science research has a great potential to contribute to the knowledge base necessary for improving the situation. Particularly, the knowledge derived from the social science investigations could contribute to the ongoing Natura 2000 fitness check (EC, 2015b), by pointing to the areas in the network's implementation and functioning that need to be improved.

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Appendix A. Supplementary data

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Mainstreaming the social sciences in conservation

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Keywords: conservation social science, environmental social science, conservation science, human dimensions, conservation biology, social-ecological systems, conservation planning, natural resource management

Abstract

Despite broad recognition of the value of social sciences and increasingly vocal calls for better engagement with the human element of conservation, the conservation social sciences remain misunderstood and underutilized in practice. The conservation social sciences can provide unique and important contributions to society's understanding of the relationships between humans and nature and to improving conservation practice and outcomes. There are 4 barriers – ideological, institutional, knowledge, and capacity – to meaningful integration of the social sciences into conservation. We provide practical guidance on overcoming these barriers to mainstream the social sciences in conservation science, practice, and policy. Broadly, we recommend fostering knowledge on the scope and contributions of the social sciences to conservation, including social scientists from the inception of interdisciplinary research projects, incorporating social science research and insights during all stages of conservation planning and implementation, building social science capacity at all scales in conservation organizations and agencies, and promoting engagement with the social sciences in and through global conservation policy-influencing organizations. Conservation social scientists, too, need to be willing to engage with natural science knowledge and to communicate insights and recommendations clearly. We urge the conservation community to move beyond superficial engagement with the conservation social sciences. A more inclusive and integrative conservation science - one that includes the natural and social sciences - will enable more ecologically effective and socially just conservation. Better collaboration among social scientists, natural scientists, practitioners, and policy makers will facilitate a renewed and more robust conservation. Mainstreaming the conservation social sciences will facilitate the uptake of the full range of insights and contributions from these fields into conservation policy and practice.

Calls for a More Social Conservation Science and Practice

Pointing to the critical importance of the social sciences to the global conservation agenda is now routine. Everyone working in conservation, it seems, recognizes that natural science alone cannot solve conservation problems (e.g., Mascia et al. 2003; Chan et al. 2007; Schultz 2011; Kareiva & Marvier 2012; Hicks et al. 2016). Sandbrook et al. (2013:1488) argue that "…the natural science methods of conservation biology are insufficient to find solutions to complex conservation problems that have social dimensions." De Snoo et al. (2013:68) suggest "close involvement of social researchers with their expertise, theories and methods, into conservation biology is a prerequisite for progress in the field." Most recently, at the 2015 International Congress for Conservation Biology of the Society for Conservation Biology (SCB) in Montpellier, France, incoming SCB president James Watson announced that "Conservation science is evolving…both natural and social sciences are crucial to solve conservation problems." Similar declarations about the need for greater consideration of the human dimensions are now common in conservation meetings around the world.

The conservation social science fields have grown significantly over the last few decades. This is evidenced by the growing application of different social science fields to understand and ultimately improve conservation practice and an increasing institutionalization of the social sciences in conservation organizations. Formed in 2003, SCB's Social Science Working Group (SSWG) became the second-largest group of all sections and working groups by 2011. Conservation social science publications and textbooks are growing in number (e.g., Vaccaro et al. 2010; Newing et al. 2011; Decker et al. 2012; Manfredo et al. 2014; Bennett & Roth 2015); natural resource departments in universities increasingly include social science in their curriculum; many conservation organizations and agencies have hired social scientists;

numerous environmental management bodies have formed social science working groups; a growing number of funders support conservation social science; and international conservation bodies are creating social science units. For example, the International Union for the Conservation of Nature (IUCN) has recently created a Global Economics and Social Science Programme (GESSP) that is aiming to further promote and develop the use of the social sciences in conservation.

Yet, we assert that the social sciences have not yet achieved the same level of recognition and acceptance in conservation science, practitioner, and policy circles as the natural sciences. This is evidenced, for example, by the relative imbalance of social to natural science presentations at conservation conferences and the imbalance of articles on social versus natural sciences in conservation-focused journals. Further, it is the norm for conservation organizations and agencies to employ natural scientists, whereas it is less common for such organizations to hire social scientists and, when present, they are often in the minority. On the ground, far too often, social science is not embedded in the design, implementation, monitoring, and assessment of conservation interventions (Sievanen et al. 2012). Underpinning all this is that the breadth and role of conservation social science is often not clear to conservation scientists, organizations, practitioners, and funders. In short, we claim that the social sciences are still far from mainstream in conservation and as a result their potential contributions to improving conservation policies and practice are not being realized fully.

Building on the momentum and increasing interest in the human dimensions of conservation, we urge the conservation community to move beyond a superficial engagement with the conservation social sciences toward a true mainstreaming of the social sciences in conservation science, policy, and practice. Drawing on the results of a focus-group meeting at the North American Congress for Conservation Biology in July 2014, we outline barriers to meaningful integration of the social sciences in conservation and provide practical guidance for mainstreaming the breadth of the social sciences with the aim of building a renewed, integrated, and more robust conservation science and practice.

The Conservation Social Sciences

A useful starting point for a discussion of mainstreaming the conservation social sciences is an appreciation of the breadth of the field and its purposes. The term *conservation social sciences* refers to diverse traditions of using social science to understand and improve conservation policy, practice, and outcomes. We take a broad view of the conservation social sciences. The conservation social sciences draw on the classic disciplines, such as anthropology, sociology, political science, economics, psychology, human geography, and on applied disciplines such as education, development studies, marketing, communication studies, and law. Many of these disciplines have subfields that focus specifically on the environment or conservation (e.g., environmental anthropology, environmental sociology, environmental governance, ecological economics, conservation psychology, environmental education, environmental geography and environmental law). Interdisciplinary fields, such as science and technology studies, conservation and development, human dimensions of natural resource management, human ecology, ethnoecology, and political ecology, draw upon various social sciences or both social and natural science. There are also strong traditions of conservation social science and interdisciplinary conservation science that have emerged from non-Western and non-English language academic traditions, for example, from European and Latin American scholars (e.g., Leff 1994; Escobar 1998; Reyes-García et al. 2006; Pascual et al. 2014) and indigenous scholars (Kimmerer 2013; Augustine & Dearden 2014). While qualitatively different, we recognize the importance of the environmental humanities (Castree et al. 2014), including environmental history, environmental philosophy and ethics, ecoliterary and ecocultural studies, and the arts to improving our understanding of, encouraging reflection upon and communicating about historical, current, and envisioned relationships between humans and nature. For overviews of the conservation social sciences see, for example, Vaccaro et al. (2010), Newing et al. (2011), and Bennett and Roth (2015).

The social sciences ask numerous questions that can improve our understanding of conservation policy and practice, from the individual, to the community, to the international scale (Table 1). In doing so, the conservation social sciences can serve vastly different purposes (Lowe et al. 2009; Sandbrook et al. 2013), which we categorize as instrumental, descriptive, reflexive, and generative. The conservation social sciences might serve an instrumental role, for example, in determining what constitutes effective management, governance, or communications strategies for conservation. They can also serve a descriptive role, for example, by providing a historical account or describing the diverse ways in which conservation occurs in different contexts. The social sciences may also play a reflexive role, for example, by asking critical questions about the way different conservation models are framed, justified, and determined to be culturally appropriate. Finally, the conservation social sciences have a generative role, for example, when they produce innovative conservation concepts, policies, practices, and models. Of course, individual projects that apply conservation social science can serve overlapping and complementary purposes.

We contend the role of social science is often misunderstood. Conservation social scientists are often employed as meeting facilitators, planners, public educators, survey designers, project evaluators, behavior changers, or implementers (Welch-Devine & Campbell 2010). However, even in the most applied aspects of the tradition, conservation social scientists are problem formulators, data collectors, analysts, and theory developers who can provide insights that can guide the social processes associated with conservation. Furthermore, while there is increasing attention to interdisciplinarity (e.g., Campbell 2005; Fox et al. 2006; Christie 2011; Sievanen et al. 2012), the social sciences should not be just an add on to interdisciplinary conservation research projects after the project has already been conceived (Viseu 2015:291). This misunderstanding and lack of early involvement in projects undermines the potential contributions of social science and interdisciplinary conservation science to better science or more complete solutions.

Barriers to Engaging with the Conservation Social Sciences

To realize their full contribution, we assert that the social sciences need to be mainstreamed in conservation policy and practice. By arguing for this mainstreaming, we seek to draw consistent and prioritized attention to the social dimensions of conservation in all social and ecological contexts and at all organizational levels with the ultimate goal of achieving a more robust, effective, and socially just conservation practice. This is a momentous but essential task.

Is conservation ready to mainstream social science? Simply doing more social science will not necessarily lead to better conservation unless that social science is assimilated into a hospitable environment. By ready we do not simply mean willing. Rather, are conservation organizations, institutions, and associations capable of truly integrating diverse insights from the social sciences? In practice social science may be watered-down and potential insights ignored resulting in policy evaporation, meaning a supportive high-level policy environment yields little implementation on the ground (see Moser and Moser [2005] for similar concerns relative to gender mainstreaming). Many conservation scientists, organizations, and funders currently employ an ad hoc approach to engaging with the conservation social sciences. Realizing the full value of the conservation social sciences requires knowledge of and commitment to social sciences across scales. For example, high-level offices to field practitioners in conservation organizations need adequate social science expertise to inform all aspects of their operations. Fulfilling the need for more and better social science in conservation may require a transformation of the entire approach, agenda, culture, and ethos of the conservation community.

Thus, prior to suggesting steps for mainstreaming at various scales, we acknowledge some perceived or real barriers to integrating social and interdisciplinary sciences as a means of explaining how it is, after more than a decade of calls to better integrate the social sciences (Mascia et al. 2003), that the conservation community still struggles with exactly how to make that happen. We present the results of a focus-group workshop on the conservation social sciences at the North American Congress for Conservation Biology in 2014 and the literature on interdisciplinary research (e.g., Fox et al. 2006; Welch-Devine & Campbell 2010; Clark et al. 2011; Christie 2011; Moon & Blackman 2014). We summarize the barriers to social science mainstreaming under the following 4 categories: ideological barriers, institutional barriers, knowledge barriers, and capacity barriers (Fig. 1). Successful mainstreaming requires directly addressing all barriers simultaneously.

First, natural and social scientists often think quite differently about how the world operates and how scientists should engage with it. Such ideological barriers include differing philosophies, worldviews, or epistemologies (also called “theories of knowledge” [Moon & Blackman 2014]). Differing worldviews may produce distinct understandings of the connections between nature and humans. This can lead to incompatible ways of thinking about a problem or of approaching research. For example, social and natural sciences may prioritize different scales and units of analysis. A study of environmental change, for instance, may start with human action for the social scientist but ecological indicators for the natural scientist. Natural and social scientists may also view the nature and scope of knowledge differently, particularly what constitutes acceptable methods and valid data. As a result, social scientists often interact with nature and with human communities in different ways than natural scientists.

Second, conservation organizations and institutions are often configured for natural sciences, not social sciences. Such institutional barriers include organizational cultures, interests, and histories, as well as decision-making structures such as laws and regulation. Conservation organizations or funders may have an organizational culture that primarily employs, understands, or values the natural sciences. Historically, many conservation organizations and funders have focused solely or primarily on natural sciences, leading them to privilege studies that indicate deductive rather than inductive reasoning. There is often a resistance to changing this focus to include and fund more social science perspectives. Some individuals or organizations may even feel threatened by the insights social scientists provide, particularly when those insights challenge entrenched practices and narratives. Beyond individual organizations, structural institutions that shape how the environment is governed, such as law, often impede integrative conservation practice.

Third, all fields are steeped in disciplinary assumptions, theories, and methods. The ensuing knowledge barriers include training, experience, and knowledge of theories and methods. Conservation social scientists engage with discipline-specific language and different theories to understand topics under study, which can be inaccessible to nonspecialists, just as the language of natural sciences can be impenetrable to nonexperts. The application of conservation social science may also require training in social science theories and methods and experience with method application and analysis of results or, equally important, training in integrative approaches that can provide a platform for natural and social scientists to engage effectively without having to relinquish their own disciplinary expertise. The value of the range of social science methods (e.g., qualitative, quantitative, spatial, planning, evaluative, historical, meta-analytical, arts-based, and participatory methods) and related analytical techniques may not be immediately apparent to natural scientists, practitioners, or policy makers.

Fourth, it takes capacity to engage with the social sciences. The capacity barriers to a deeper integration of social sciences can include human capital, skills, and resources. Limited social science capacity within conservation organizations may mean conservation practitioners and organizations looking to fund conservation social sciences do not know where or how to begin engaging with social sciences. Without a clear understanding of the breadth of the conservation social sciences, the types of questions that each field of conservation social science poses, and the methods used by disciplinary specialists, conservation organizations and funders may not appreciate the potential contribution of each social science field to improving conservation practice and outcomes. This may also mean the necessary skills to carry out social science research projects or the necessary connections to social science expertise in other organizations may often be lacking within organizations. Finally, financial resources are almost always limited, and, when science is prioritized, it is often earmarked for natural science research. It is important that conservation scientists, organizations, and agencies aiming to integrate social sciences into their scope and work recognize and address these potential challenges and barriers to integration.

Mainstreaming the Conservation Social Sciences

Mainstreaming of the conservation social sciences will need to occur at different scales and in different communities of practice. We consider 3 different mainstreaming entry points (i.e., within the conservation science community, within conservation agencies and organizations, and within global conservation policy-influencing bodies) and outline a number of steps that might be taken at each level.

First, regarding mainstreaming in conservation science, our initial suggestion is the least bold, but it may be the most contentious. Perhaps it is time for applied and mission-driven professional conservation organizations to signify a move away from isolated areas of conservation science toward a community of practice united in its desires to improve conservation using all available approaches and methods. Because the conservation sciences include the natural sciences, the social sciences, and interdisciplinary endeavors, we propose that the Society for Conservation Biology consider rebranding itself as the Society for Conservation Science. Significant steps are needed within the conservation science community to increase knowledge of the definitions, focal areas, theories, methods, and contributions of the diversity of conservation social sciences, not just those that are instrumental to conservation. This includes a deeper understanding of the philosophical differences underpinning social and natural sciences and the implications of these differences (Moon & Blackman 2014). For example, it is important to understand that the potential insights of social science are not always amenable to quantitative methods or models (Drury et al. 2011). Such knowledge, however, is not enough. Specific actions need to be taken to overcome institutional and capacity barriers within the conservation science community. Suggested steps include increasing the breadth of social science content within undergraduate and graduate conservation biology and environmental management (e.g., forestry, fisheries, and agriculture) programs; ensuring that conservation journals equally support the publication of natural, social, and interdisciplinary articles and that these journals have social-science editors and reviewers; improving the representation of social scientists in conservation-related departments and research institutes, including in leadership positions (e.g., department heads, deans); rethinking funding structures so that there is greater financial support for the social sciences (commensurate to the need); taking steps to ensure greater participation, better exposure, and more comprehensive treatment of the social sciences at conservation conferences; selecting natural and social scientists equally for conservation fellowship programs; and placing social science on an equal footing in interdisciplinary research projects by ensuring that social scientists are not an afterthought and are equally represented at all stages of project design, implementation, analysis, and writing.

Because capacity begets capacity, taking steps such as these will stop the chicken-or-egg phenomenon currently occurring in conservation science. However, changing the ideologies and culture of the conservation science community may be more challenging than simply changing a name or the membership. Conservation science will increasingly need to make room for different worldviews, opinions, and approaches and for deliberations on results that conflict with each other (Green et al. 2015). Yet as Viseu (2015:291) argues, “We must insist on the value of complexity, so that divergent thinking is not eclipsed in the effort to speak with one voice. We must make room for the disputes that are at the center of knowledge production.” Fundamental to this process will be open-mindedness, patience, humility, honesty, listening, willingness to differ, and clear communication (Winowiecki et al. 2011).

Second, conservation organizations often recognize the importance of the social sciences and are increasingly engaging in and funding conservation social science research. Government conservation agencies are also taking into account social science research when making decisions about the environment, for example when evaluating an environmental assessment or the potential of creating a new national park. Yet at some level, many agencies and organizations are still grappling with the what, how, and why, which requires considerable evidence of the distinct value proposition of specific conservation social sciences to key aspects of their missions in order to contemplate the path to incorporating or mainstreaming. Thus, developing an understanding of the social sciences and their organizational and conservation benefits is an important first step for many conservation agencies and organizations. Once the case has been made, specific actions are needed to strategically increase social science capacity within conservation organizations and agencies. We propose 6 practical steps: recognize agency, organizational, and financial barriers to incorporating conservation social sciences; take steps to overcome these barriers by building understanding of and support for the conservation social sciences within the organization; identify the conservation problem or problems that the agency or organization aims to address and highlight their social dimensions, partnering with social scientists from the beginning of the process to frame key topics, questions, and approaches; brainstorm key topics for investigation or research questions and prioritize them to establish a conservation social science agenda; partner with, contract, or hire conservation social scientists to carry out the work; and appoint one person to be accountable for ensuring social science is continually incorporated into projects and that results will inform decision making (Bennett & Roth 2015).

This entire process may require organizations to revisit their theory of change and, while doing so, to examine where social science insights may be useful. Doing so with social scientists could generate new insights into unquestioned assumptions about values, mental models (including about history), cognition, human or organizational behavior, and social dynamics and help identify where conservation efforts are likely to yield unintended side effects because of individual, collective, or organizational realities or responses that were previously unforeseen by the organization. Pragmatically, conservation organizations could establish dedicated funding streams for social science programs or personnel or create mechanisms to fund external social science research. Organizations seeking to engage the social sciences should develop a clear idea of the social science approach that suits their needs and recognize that engaging with all manner of and approaches to conservation social sciences can improve conservation policies and practice. It makes sense to start with a pilot social science initiative before scaling up.

We recognize that there are a number of conservation organizations and agencies that actively incorporate the social sciences at various levels in the organization as part of monitoring and evaluation processes or throughout the project cycle (e.g., The Nature Conservancy, Conservation International, Wildlife Conservation Society, Rare, Ecotrust, the U.S. Fish and Wildlife Service and National Park Service). Yet the scope and scale of engagement within these large and well-known organizations is not readily apparent. A review of how, at what stages, and the extent and efficacy with which conservation organizations of different sizes use the social sciences is beyond the purview of this paper, but it would be an insightful endeavor.

Third, in the global conservation policy arena, mainstreaming would be supported by promoting social sciences in and through global conservation policy-influencing organizations such as the United Nations Environment Program and the International Union for Conservation of Nature (IUCN), which can uniquely advance a global community of practice around the conservation social sciences. Although the SSWG of the SCB plays an important role as a professional organization, there is also a need for better integration of the conservation social sciences in policy development. The IUCN Global Economics and Social Science Program (GESSP) may take a leading role in promoting and highlighting the role of the social sciences in improving the policy and practice of conservation. A promising recent initiative of the IUCN GESSP is to launch the IUCN Social Science for Conservation Fellowship Program to investigate and demonstrate where and how social science perspectives, methods, and approaches can improve understanding of and address challenges related to the human dimensions of conservation. Additional steps that could be taken by such organizations for the conservation social sciences are writing and distributing position papers or policy briefs that demonstrate the value of applying the social sciences in conservation; leading the way in demonstrating and documenting the role of the social sciences through codeveloping or facilitating interdisciplinary, multi-benefit, high-impact partnerships with global development organizations and agencies (e.g., United Nations, Oxfam or U.S. Agency for International Development); collaborating with the Global Environment Facility and other global conservation financing agencies to guide and incentivize conservation organizations and government agencies to use the social sciences to understand, improve, and document the human context and impact of interventions; advocating for enhanced social science integration in future global sustainability agreements (e.g., Convention on Biological Diversity); using conservation meetings such as the World Conservation Congress, World Parks Congress, and International Congress for Conservation Biology to promote a better understanding of the role of social sciences in conservation; and providing practical guidance for how conservation organizations can integrate methods, practitioners, and approaches from the social sciences into their mandates, projects, capacity, and funding streams to design more effective conservation, better understand impacts of conservation, etc. Such a body could support broad and systematic reviews of social science perspectives on different pressing or emerging conservation challenges (e.g., wildlife crime, social conditions for conservation success, large scale marine protected areas) to identify lessons learned, make recommendations, and propose directions for future research. At the same time, central hubs or bodies that might support the integration of social sciences into conservation need adequate seed and core funding and sufficient capacity to persist and successfully promote this mandate. The conservation funding community thus has a clear role in enabling such a global conservation social science initiative; the IUCN GESSP is only one such example.

Finally, we turn the mirror on ourselves and highlight the important role social scientists must play in the mainstreaming process. Conservation social scientists need to be willing and able to better engage with natural scientists and conservation practitioners. Academic training can produce social scientists who are challenged to communicate their research outcomes with diverse non-specialist audiences or to provide politically realistic and action-oriented recommendations. The way social scientists communicate may be too academic or theory laden to be accessible, which will likely interfere with initial and ongoing engagements with natural scientists, conservation organizations, and policy makers. The academic focus on research and publications may also interfere with conservation social scientists' abilities to take sufficient time to collaborate meaningfully and to make efforts to influence conservation practice. Finally, conservation social scientists often neglect to integrate ecology into their training programs and their research – often relying instead on proxies such as perceptions or behaviors – leaving natural scientists and others wondering about the real-world ecological implications of this research. To connect and gain traction, social scientists may need to reflect on their outreach strategies (e.g., explaining their theory and methods, communicating clearly in outputs, translating insights into understandable and actionable recommendations) and grapple with how their work links to conservation biology and ecological outcomes throughout the research process. This does not mean the theory and language of social science should be abandoned; rather, it means social scientists need to learn to communicate for different audiences and purposes. Specifically, we propose that social scientists would benefit from science communication courses. In short, conservation social science remains an emerging field of practice that will need to meet natural science and practitioner colleagues part way in order for more effective integration to take place.

Toward a Collaborative and Integrated Conservation Science and Practice

Conservation science needs to be inclusive, integrative, and collaborative in order to understand and address the conservation challenges of the 21st century. We argue that the social sciences play a critical role in improving marine and terrestrial conservation and more broadly in the theory and practice of environmental management. We are not suggesting that conservation social science alone can solve conservation problems or that social and natural scientists with their tools and methods should sit side by side and use research to solve conservation problems. Conservation as a practice is necessarily multi- and interdisciplinary; that is, it requires an understanding of both natural and social systems and collaboration between natural and social scientists. It is also transdisciplinary, meaning it requires collaboration among researchers, practitioners, policy makers, and stakeholders (Fig. 2). We assert that good interdisciplinary and transdisciplinary conservation scholarship requires a solid understanding of and attention to disciplinary differences and contributions. Discussions across disciplinary and science-to-action boundaries are challenging but worth undertaking because these efforts, at the very least, will lay the groundwork for better mutual understanding and, at best, will contribute to better conservation outcomes. This disciplinary and real-world integration should be done at all stages in the conservation research-to-action cycle while making allowances for the need to balance feasibility, efficiency, and effectiveness.

The time is right to take active steps to mainstream the social sciences in conservation at all scales, from individual initiatives to national or global policies, and in different types of organizations and projects. There is widespread recognition of the need to understand social dimensions and support for engaging the conservation social sciences. Although each subfield of the conservation social sciences has a distinct contribution to make, they remain underutilized and their potential contributions largely unrealized. There is thus a need to intentionally and carefully increase knowledge of the diversity of the social sciences and to build social-science capacity in the conservation science, practice, and policy arenas. We suggest a number of actionable steps to mainstream the social sciences in conservation in order to overcome ideological, institutional, knowledge, and capacity barriers to integration. Yet, there is still much to learn. We recommend a review of past successes and failures in integrating social science into real-world conservation projects (i.e., not just into interdisciplinary research projects) and organizations and documentation of best practices to facilitate better incorporation in the future. This would promote learning and help social scientists have a more meaningful impact in the future of conservation. It would also be worthwhile to document strategies to balance feasibility, efficiency, and effectiveness in integrated conservation science projects. A productive engagement with the conservation social sciences will likely require long-term ongoing partnerships, knowledge and capacity building, open dialogue, clear communication, reflection on past and present practice, and a willingness to adapt programs of work. A more inclusive conservation science (i.e., one that includes methods and insights from the natural sciences, the social sciences, and the humanities) will enable the conservation community to produce more ecologically effective and socially just conservation. Mainstreaming the conservation social sciences will facilitate the uptake of the full range of insights and contributions from these fields into conservation policy and practice.

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Table 1 - Conservation problems at different scales and relevant fields of social science.

Locus and scale of problem	People and groups or topics of study*	Examples of problems or questions at this scale	Possible fields of social science
Society at national and international	general public, advocacy groups, international NGOs and ENGOs, national agencies,	How do different groups in society understand and relate to nature? What ways of thinking inform particular	sociology, anthropology, history, conservation education, science studies, political ecology,

scales	international bodies such as the IUCN ideas, metaphors, philosophies, narratives, beliefs, ethical stances	conservation practices or resistance to them? What broad social and material factors shape the way society approaches conservation? What are the social, ecological, behavioral, and cognitive outcomes of conservation education efforts? In what ways might ethics guide conservation actions?	humanities and ethics
Federal or state laws and policies	politicians, legislators, policy makers, scientists laws, governance, incentives, regulations, knowledge building	Are laws efficient and effective at supporting conservation? How do science and other factors guide conservation decision making? What is the impact of a proposed environmental law or policy on conservation or society? Do existing educational policies facilitate learning environmental science and knowledge effectively? How might law and policy support conservation while fostering sustainable prosperity?	environmental law, political science, science studies, conservation education, ecological economics
Midlevel multijurisdiction management unit	tribes, NGOs, management boards planning, regional policy creation, brokering of management actions	How does decision making occur in management boards? Who is involved in environmental governance? What is the role of science in management? How and by whom has an area been used historically? What are the main conflicts over resource management and why do these conflicts occur? How do different funding models – e.g., corporate funding, national funding - influence the conservation agenda?	human geography, political science, science studies, anthropology, sociology, history, human dimensions, political ecology
Local governments	elected leaders, planning departments, technical agencies political grounding, best practices, applied	Is environmental conservation a local-election issue? How might cities plan their green space and parks for the health of both nature and people?	political science, ecological economics, planning

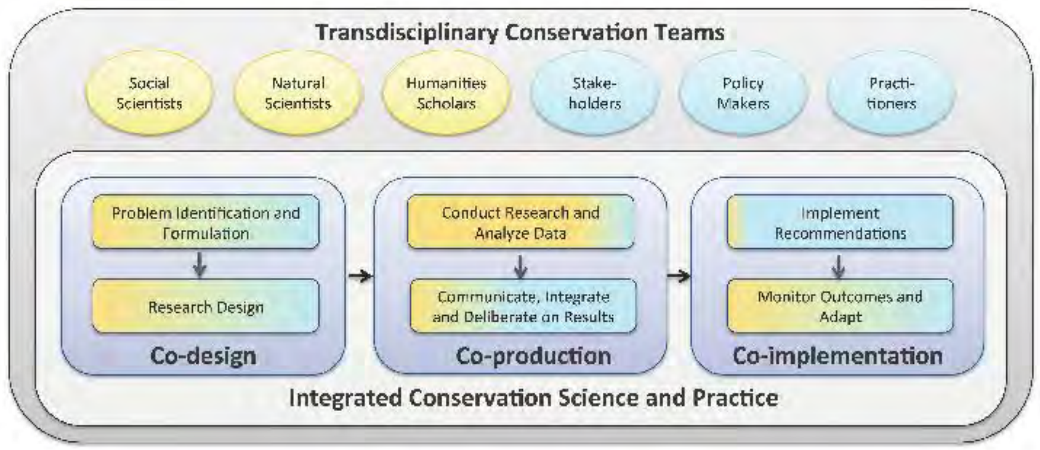
	technologies		
Management initiative, e.g., protected area	managers, comanagement boards, adjacent communities best practices, participation, governance	What management actions are being taken? By whom? How? How are community livelihoods and economics impacting or being impacted by a protected area? How is a management initiative being received or resisted? What cultural models are being employed to shape conservation policy and practice?	anthropology, political science, psychology, conservation and development, ecological economics, political ecology, science studies
Private sector and businesses	resource-dependent corporations, local businesses and sectors best practices, goods & services, sustainability programs	What governance or economic mechanisms might be used to guide corporate behavior? How can environmental messaging be used to guide consumer behavior?	conservation and development, ecological economics, education, psychology
Community, neighborhood, or group	resource-dependent communities, civic organizations, associations, schools, livelihood group civic engagement, social networking, place making, social norms	How do local social practices or cultural norms and social identities affect conservation behaviors? What factors give rise to different levels of civic engagement? What competing visions for conservation exist among local people or between local people and outside organizations? How can outreach be improved through understanding social networks? How do cultural practices relating to the environment figure in resource use conflicts?	anthropology, conservation and development, conservation education, communication and marketing, psychology, history
Household or individual	residents, individual resource users, homeowners, visitors/tourists, private landowners, recreationists awareness, knowledge, attitudes, values, personal norms, emotions, behavior,	How are individuals likely to respond to a particular conservation initiative or management action? How can we develop effective communications to build local support for conservation efforts? How can we change consumer decisions to reduce environmental impacts? How can we facilitate knowledge development and behavior	psychology, ecological economics, conservation education, political science, history, communication and marketing

	stewardship, conflict	change of resource users?	

*Abbreviations: NGO, nongovernmental organization; ENGO, environmental nongovernmental organization; IUCN, International Union for Conservation of Nature.

Figure 1 - Barriers to mainstreaming the social sciences in conservation.

Figure 2 – Framework for a collaborative and integrated conservation science and practice.


Transdisciplinary Conservation Teams
Social Scientists
Natural Scientists
Humanities Scholars
Stake-holders
Policy Makers
Practi-tioners
Problem Identification and Formulation
Research Design
Co-design
Conduct Research and Analyze Data
Communicate, Integrate and Deliberate on Results
Co-production
Implement Recommendations
Monitor Outcomes and Adapt
Co-implementation
Integrated Conservation Science and Practice

Genetic Rescue

Working Group
2016 CBSG Annual Meeting
Puebla, Mexico

Genetic Rescue

Convenors: Oliver Ryder, Dalia Conde and Johanna Staerk

Background: In 2015 at the CBSG meeting in Al-Ain, we had the first GENETIC RESCUE workshop. This year we will follow up focusing on developing a decision framework for which species we need to urgently store live cells. This may depend on many different factors, not only on species threats, population size, but access to samples and possibilities to infrastructure development. We have invited Dr. Melissa A. Kenney to help us developing this framework. Dr. Kenney is an Assistant Research Professor in Environmental Decision Analysis and Indicators at the University of Maryland, Earth System Science Interdisciplinary Center (ESSIC) and Cooperative Institute for Climate and Satellites - Maryland.

Introduction to Genetic Rescue
GENETIC RESCUE is defined as *an increase in population-level viability through the re-introduction of previously lost genetic material by cell-based human intervention.*
Genetic rescue involves utilizing preserved and banked tissue samples, both reproductive and somatic across a variety of technological means to add genetic diversity and/or producing viable offspring for critically endangered animals and plants. They include artificial insemination, *in vitro* fertilization, etc., along with induced stem cell development and applications of cloning technology.

Rationale – Genetic Rescue is the response to an extinction crisis. It has the greatest potential for impact where traditional means of species recovery by live animal transfer are not practical or possible. Emerging technologies in genetics and assisted reproduction will be crucial for some species sustainability. Numerous challenges exist in moving from proof of principle to making these technologies practicable. Two examples are methods of species choice for rescue, and another is the lack of availability of suitable samples.

Sources:
Full description of genetic rescue:
Definition from revive and restore
http://reviverestore.org/what-we-do/genetic-rescue/

Genetic rescue and biodiversity banking, Oliver Ryder at TEDxDeExtinction:
http://tedxtalks.ted.com/video/Genetic-rescue-and-biodiversity

The alluring simplicity and complex reality of genetic rescue
http://www.uas.alaska.edu/artssciences/naturalsciences/biology/faculty/tallmon/Tallmonetal_TREE.pdf
Cited by Edmands (2007): Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management http://onlinelibrary.wiley.com/doi/10.1111/j.1365-294X.2006.03148.x/epdf

2009 Genetic rescue guidelines with examples from Mexican wolves and Florida panthers
http://link.springer.com/article/10.1007/s10592-009-9999-5

2005 TREE Genetic restoration:' a more comprehensive perspective than 'genetic rescue
http://www.sciencedirect.com/science/article/pii/S0169534705000078

2001 TREE Restoration of genetic variation lost – the genetic rescue hypothesis
http://www.sciencedirect.com/science/article/pii/S0169534700020656

Expanding Options for Species Survival: Establishing a Global Wildlife GeneBank of Viable Cell Cultures – presentation by Oliver Ryder
http://iucncongress.ipostersessions.com/?s=D5-24-E1-A7-26-30-69-B9-F6-4F-6A-8A-0C-58-02-09

IUCN

Species Survival Commission

CONSERVATION BREEDING SPECIALIST GROUP

Addressing human population and behavior in the design of conservation planning processes

Working Group
2016 CBSG Annual Meeting
Puebla, Mexico

Addressing human population and behavior in the design of conservation planning processes

CONVENOR: Phil Miller

AIM: The aim of this working group session is to explore how we can better incorporate knowledge around human population growth dynamics and behavior-driven activities that threaten wildlife persistence into our species conservation planning workshops. This effort will extend the discussions on a similar topic that began at the 2015 CBSG Annual Meeting in Al Ain, UAE.

BACKGROUND: We have only rarely incorporated human demographic analysis into the risk assessment component of our conservation planning workshops. Furthermore, we do not include a detailed analysis of human activities on the landscape – and the behaviors that drive those activities – and how they impact local wildlife populations. From the perspective of developing a vision of the future for threatened wildlife populations, we need to understand how threatening activities may change in the future as human populations continue to grow. As pointed out by a growing number of conservation professionals, the real issue with human population is their mechanisms and ever-increasing rate of natural resource consumption, particularly as nations evolve along the socio-economic continuum.

Therefore, successful planning for endangered species conservation requires identifying means by which human activities can be modified to maintain viable populations. For more than 20 years, CBSG's Population and Habitat Viability Assessment (PHVA) workshops have featured recommendations that are developed in the spirit of moderating our negative impacts on species and habitats. But we have not systematically addressed the issue of increasing human population abundance and how to face the dynamic impacts of this threat.

At the 2015 CBSG Annual Meeting in Al Ain, a working group began to address this issue. The participants enthusiastically supported the general proposal to incorporate these aspects of "the human dimension" into future CBSG-facilitated species conservation workshops. We focused our subsequent discussion in the context of a potential workshop opportunity in Chile, where Humboldt penguins are impacted by a variety of human-mediated activities. Discussions among Humboldt penguin biologists and other interested parties have been ongoing after the Al Ain session.

PROCESS: The working group will begin by revisiting the discussion of concepts initiated in the 2015 Al Ain working group, and will expand ideas and concepts from that session that are most relevant to our long-term aim. We will also build on appropriate themes discussed by other working groups meeting earlier in the 2016 agenda that are addressing the larger topic of human population and species conservation. Finally, we will revisit the Chile Humboldt penguin workshop opportunity to generate a more clear vision of an expanded conservation planning process that can be promoted and facilitated by CBSG.

OUTCOMES: The group will produce a set of guidelines that describe how such an expanded process can be applied, with an emphasis on the resources required to increase its chances for successful application.

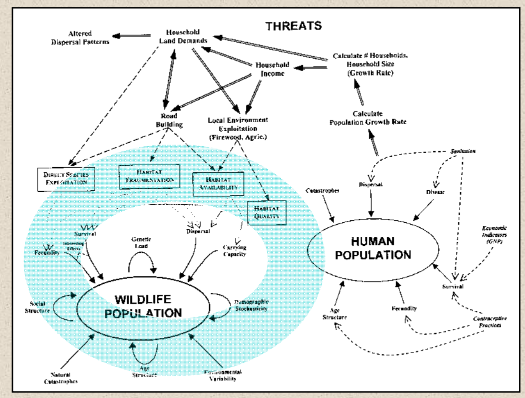
CBSG Annual Meeting 2015: Al Ain, UAE

Advancing CBSG process design through incorporating human behaviour change

Initiator, facilitator & flip charterer: Philip S Miller
Reporter: Andrea Fidgett
Time keeper: Kirsten Pullen
Presenter: Heribert Hofer

People: Not just numbers, also activities

Lacy & Miller 1999 unpublished



Proposed working group tasks

- Review the breadth and depth of goals and actions created in past CBSG conservation planning workshops. ✗
- Explore the nature of an expanded set of goals that more explicitly address human population dynamics and activities. ✓
- Consider the design of an expanded conservation planning process incorporating these considerations: ✓
  - How do we adjust our current process mechanics?
  - Are there new facilitation tools and processes to adopt when considering an expanded design?
  - With whom should we be communicating and collaborating to design such a process?

Questions

- Should we pursue this?
- If so, HOW???
  - human population projections
  - functional relationships
  - predicting future impacts
  - making management recommendations
  - workshop process modifications

a hypothetical workshop: conservation plan for Humboldt penguins in Peru

- Direct and indirect interaction with local fisheries
  - ⇒ direct: mortality through by-catch in nets
  - ⇒ indirect: competition for food
- El Niño events more frequent and severe
  - ⇒ fish supply drops, followed by reproductive failure / starvation of penguins [and local fisheries]
- guano harvesting for fertilisers
  - ⇒ literally takes away the base for nesting

Issues in designing recommendations which potentially involve behaviour change

- Need to know who wants the workshop and why
- Identify appropriate participants (beyond the usual suspects)
- Have a detailed [Vortex-like] checklist
  - ⇒ ensure appropriate coverage of potential aspects in economic, cultural, social dimensions
- Improve threat analysis by paying more detailed attention to the human component

Improving threat analysis: detailed attention to the human component

- quantitative estimates of intensity of threat
- temporal dynamics of threat
- economic drivers
- social drivers
- cultural drivers

recognizing that not everyone in the community is the same (gender!!!!!)

- external impacts on local economies (local fisheries)
- additional external environmental drivers (acidification)
- data on local / regional human population dynamics and migration patterns (past dynamics, projections for future)

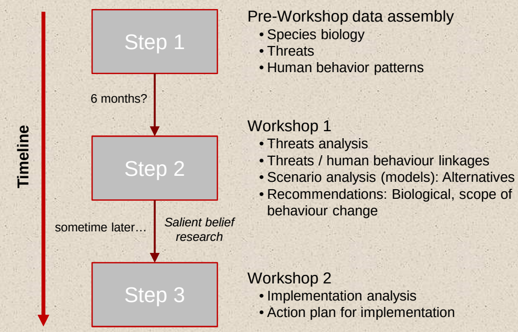
Issues in designing recommendations which potentially involve behaviour change

- Ethical dimension
  - stop a starving person from eating that endangered plant?
  - Contraception / castration: no right to reproduce?
- Behaviour change recommendations: do you want to make them work?
  - Recommending legislation / regulations: are they enforceable?
  - Salient belief research – avoid wrong assumptions, identify incentives
    e.g. Melbourne / Perth guano: toilet paper hygiene vs flimsiness
- Implementation is a long process – with or without CBSG involvement ?

Design of workshop process: issues

- ❖How much change of human behaviour do we need to improve the viability of the species of concern?
  e.g. how much more knowledge does the local community need in order to change its behaviour?
- ❖Do we have enough time within the workshop setting?
  ⇒ usually not…
- ❖Requires people in the room who know about drivers and threats.
  ⇒ They often think they know the solution…

Proposed expanded workshop design & schedule



Benefits of this schedule

- ❖Immediacy: short-term emergency conservation action possible
- ❖Pulls in people with (to conservation experts) novel expertise
- ❖Permits setting and management of expectations by stakeholders in an appropriate way
- ❖Encourages implementation by a group of dedicated people

More about Humboldt penguins in Peru…

- ❖Proyecto Punta San Juan
- ❖www.puntasanjuan.org – Video!

CBSG Annual Meeting 2015: Al Ain, UAE

Working Group Report:

Advancing CBSG conservation planning process design to incorporate information on human population dynamics and behaviour

AIM

The aim of this Working Group is to explore the feasibility of expanding our practical vision for endangered species conservation planning, with an explicit focus on local human population abundance, growth rate, and ecological consequences of individual/community behavior and impacts to endangered species persistence.

BACKGROUND

In late 2011, CBSG Chair Onnie Byers challenged our Strategic Committee to identify the next "Big Idea" that could shape a segment of our future activities. Bob Lacy responded with an essay outlining the dire threat that continued human population growth poses to the planet's biodiversity, and proposed that all CBSG risk assessment processes explicitly include consideration of this threat:

> …I would suggest that every risk assessment we undertake should include deliberate and explicit analysis of the projections for changes in human population numbers *and activities* [emphasis added] in the area of concern.

We have only rarely incorporated human demographic analysis into our risk assessment workshops. Even more conspicuously absent from our risk assessment work is a detailed treatment of the nature of human activities on the landscape and how those activities impact associated wildlife populations. Especially important from a risk assessment perspective is the need to understand how those threatening activities may change in the future as human populations continue to grow (hence the added emphasis in Lacy's quote above). As pointed out by a growing number of conservation professionals, the real issue with human population is their mechanisms and rate of natural resource consumption, particularly as nations evolve along the socio-economic continuum.

Therefore, successful planning for endangered species conservation requires identifying means by which human activities can be modified to maintain viable populations. For more than 20 years, CBSG's Population and Habitat Viability Assessment (PHVA) workshops have featured recommendations that are developed in the spirit of moderating our negative impacts on species and habitats. But we have not systematically addressed the issue of increasing human population abundance and how to face the dynamic impacts of this threat.

Working Group Human population: Notes

Phil's additional thoughts

- Different strands of thinking already in the literature
  - Accelerated human population growth and protected area edges
  - Conservation in the Anthropocene (Peter Kareiva)
  - Global biodiversity conservation and the alleviation of poverty

Plan of 1999 of Bob Lacy and Phil Miller

- How do changes of habitat quality affect carrying capacity
- How does poaching affect survivorship and fecundity
- But then how to link into the human-generated threats and the dynamics of human population

A lot of data out there on population growth projections (global and regional) – World population prospects – the 2012 revision

Examples:

- threats to Sumatran rhino pop growth PVA 16-18 Feb 15: direct threats and drivers of those threats (e.g. poaching driven by demand for rhino horns)
- Colorado pikeminnow PVA: explicit links of human activities, their impact on the environment and their impact on target pop (impact of mercury – generated by coalfire power generation); % injury as a function of mercury accumulation; and have rate of change of mercury input into the river system, and have a sense of the reproductive rate as a function of age and mercury accumulation
- Example re-introduction of Arabian oryx in Oman (M S-P): mid 80s, then mid 90s facing poaching (450 => 200); initially thinking of human element was not done carefully; now government fenced reserve the size of 2800 km^2
- Tried it out on woolly monkeys in Alto Mayo Protected Forest Peru
-

Perspective of risk assessment – then we do have to go through this process

Recognizing the consequences of behavior; incentives

CBSG, PVA & the theory of change

Knowledge + attitude + interpersonal communication + barrier removal => behaviour change => threat reduction => conservation result

- CBSG knows conservation result and go back to threat reduction
- Other collaborators (IFAW, Rare) think about behaviour change
- Stimulated by the question: Can you use vortex to model behavior change in people?

Several theories of behaviour change, e.g. – breakdown of these models

- Community based social marketing
- … (Kirsten Pullen)

What is the question? Several options

- Formalizing the functional relationships in threat analysis
- Improve the level of detailed threat analysis
- Improve the quality of developing the details and chance of successful implementation of recommendations {on the basis of good solutions for behaviour change}
- Improve the scope of recommendations

Conceptual issues

- Not just a question of what you are good at but also what you need to be good at to save species
- Need to include the human component where necessary

Implementation

- Bring in additional / external expertise? (e.g. social scientists)
- Need the people who make you buy things that you do not want
- Use examples from health sector which have had two decades of experience
- Do we have enough time within the workshop setting? Usually not. Requires people in the room who know about the drivers and threats. Often they also think they know the solution.
- How much change of behaviour do we need to change to have a demographic impact? (e.g. how much more knowledge does the local community need to gain in order to change behaviour)
- Use each arrow in the graphic model of causal chains as a potential intervention point
- A scale issue – local – regional – global

Phil questions:

Should we do this and if so how?

- Human pop projections
- Functional relationships
- Predicting future impacts
- Making management recommendations
- Workshop process modifications

<u>Part 2: try out a hypothetical workshop</u>

Humboldt penguin conservation plan

Workshop 18 years ago in Peru

Want to redo one with a big picture –

- basic interaction with local fisheries, including competition for food,
- El Niño becoming more frequent and severe, which have the consequence that the fish supply drops, followed by reproductive failure of penguins,
- guano harvesting for fertilisers takes away the basis for nesting,

How to do it?

- Need to know who wants the workshop and why
- Identify appropriate participants which either participate in early analytical parts
- Have a detailed Vortex-like checklist to ensure appropriate coverage of potential aspects for the economic, cultural and social dimensions {requires at least a generic detailed "model" of what might affect human activities}
- Improve threat analysis by paying more detailed attention to the human component
    - quantitative estimates of intensity of threat
    - temporal dynamics of change of that intensity
    - social and cultural drivers, recognizing that not everyone in the community is the same
    - external impacts on local economies such as local fisheries
    - additional external environmental drivers such as acidification
    - invoke or use data on local and if necessary regional human population dynamics (past as well as future projections)

- This implies collecting some data in advance to prepare well
- Find out whether community cares about the species in question; and if not do not assume that behavior change may not be possible because
- Design expanded modeling analysis and create scenarios in the risk assessment context which incorporate various degrees of behavioural change as well as population dynamics
- New issues in designing recommendations which potentially involve behaviour change
    - Ethical dimensions: stop a starving person from eating that endangered plant, tell a person that they have no right to reproduction
    - Identifying appropriate behaviour and the changes required from current behaviour often makes numerous assumptions (and thus are a potentially dangerous way)
    - Salient belief research – identifying misconceptions or incentives (Melbourne vs Perth guano: loo paper hygiene and appearance vs flimsiness)
    - Enforceability of regulations
    - Recommendation may include the starting of a process with or without the involvement of CSBG which may include another workshop on implementation options
    - Resembles (in a very generic way) decision steps of Ex situ Guidelines
- Scenario of time line
    - Gathering information (Workshop 0)
    - Diagnosis along traditional PHVA lines (Workshop 1)
    - Do salient belief research
    - Recognizing the limits of immediate behavior change recommendations: Workshop 2 on implementation, include marketeers
- Advantages:
    - Fulfills the need for immediacy, also allowing for short-term emergency action
    - Pulls in other kinds of people
    - Allows the management of expectations in an appropriate way
    - Supports a line of thought that the only successful projects invoke groups of dedicated people who see it all through (rather than bits of modules done by various bits of people)
- Conservation psychology
- Did the group consider dynamics of human behaviours that cannot be changed? Part of behavioural maintenance…

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Editorial

What Every Conservation Biologist Should Know about Human Population

At the 25th meeting of the Society for Conservation Biology in 2011, Thomas Lovejoy was asked in the opening plenary session why few talk about human population as the root of environmental degradation. The question is a reminder of how little conservation biologists have incorporated current understanding of human population into their everyday thinking about environmental problems. We are not the first to highlight human population in this journal (Grossman 2010; Prichard 2011). However, we would like to highlight some of the most critical points about human population from a human-demography perspective.

First, human population has only recently become an environmental problem. Before 1800, there was no sign of an approaching population crisis. Mortality and fertility were high, with life expectancy at birth around 35 years and a total fertility rate over 6 births per woman. Thus, there was little to no population growth and the world's population was less than one billion. Such a small population could have consumed unlimited resources for a long period of time and not faced today's environmental problems.

However, in the early 1800s mortality began to decline in more developed countries. People began to live longer due to improved sanitation and water supplies, better hygiene, and higher living standards. Mortality began to decline in less developed countries about 100 years later. The same factors, along with medical interventions such as immunizations, reduced mortality rapidly. Today global life expectancy at birth is 70 years [PRB 2011]. However, fertility remained high and there were many more births than deaths, which resulted in population growth. Living longer is widely seen as a desirable achievement, but it was this achievement that brought population growth.

Second, the world population growth rate peaked in the early 1960s. In fact, it was already declining when Paul Ehrlich (1968) published *The Population Bomb*, which brought widespread attention to the negative effects of population. By the time conservation biologists were calling attention to the "missing agenda" of human population control in this journal (Meffe et al. 1993), population growth rates had already been declining for 3 decades.

The population growth rate declined because fertility began to decline. Fertility began falling in the late 1800s in more developed countries and around 1950 in less developed countries. Fertility declined for a variety of reasons, but one important reason was the decline in mortality (Mason 1997). Because parents became confident their children would survive, they reduced births to achieve their desired family size. Today the global total fertility rate is 2.5 children per woman (PRB 2011).

Third, this pattern of population change, known as the demographic transition, is universal (Bongaarts and Bulatao 2000). Once the demographic transition begins, the path to a stable, larger population, characterized by low mortality and fertility, is a matter of time. More developed countries have completed the demographic transition and most less developed countries are nearing the end of it. Sub-Saharan Africa stands out as the only region where fertility has not yet declined substantially. Scherbov et al. (2011) estimate there is an 84% probability that world population growth will end by 2100. The United Nations (2011) forecasts a population of 10.1 billion for 2100, although the pace of remaining fertility decline will determine the eventual population size. If fertility declines faster than currently anticipated, it is likely that the global population will peak and then decline substantially by 2100 (UN 2011).

So, here we are in 2012 with a world population of 7 billion. The good news is the growth rate is falling rapidly, world population is stabilizing, and it should never again double in size. And – here is the fourth point –the world has survived the population bomb by coming through the last 50 years of rapid growth much better than predicted in the 1960s (Lam 2011). So far, neither mass starvation nor economic collapse has come to pass as was predicted. The bad news is the population will stabilize at a much larger size than that of before 1800.

Given today's demographic context, how might conservation biologists constructively approach the issue of human population? Conservation biologists could call for and support the following policies and programs.

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1. Maintain support of family planning. Now that fertility has declined to 2.5 children per woman, the population agenda is largely seen as complete by the international community. Thus, family planning was not included among the Millennium Development Goals. However, there is still an unmet need for contraception. The proportion of women in unions who want to avoid a pregnancy, but are not using contraception, is as high as one-third in some Sub-Saharan countries (ORC Macro 2012). Worldwide, this translates into 215 million women with an unmet need for contraception (Singh et al. 2009). Furthermore, access to contraception needs to be maintained in the future. Maintaining such access will help women realize their reproductive choices and minimize population growth.
2. Move the population and environment agenda toward population distribution and composition. The notion that population is the root of environmental problems has focused on population size; that is, people are bad for the environment and the more people there are, the worse it must be. However, connections between population size and the environment are complex and shaped by a host of mediating factors (Axinn & Ghimire 2011). Some of these factors are other aspects of population, namely the distribution of populations across space and their composition. For example, the concentration of people in cities or away from key habitat can reduce environmental effects (Hunter et al. 2003). Furthermore, the number of households is more strongly associated with consumption than the number of people (Liu et al. 2003). In turn, the household composition of a population is important. Thus, the focus on population size should shift to a more comprehensive approach to population.
3. Address consumption separately from its connections to population size. The challenge now is consumption. Addressing this challenge, it can be argued, has too often been derailed by the call to reduce population growth. Our understanding of how and why population growth has changed over the last 2 centuries may provide some clues to how consumption patterns may change. Most people did not reduce their individual fertility because they had a worldview that population growth was a global problem. Instead, fertility declined for many varied and context-specific reasons, but a core component was that people were making individual, rational choices that met their needs (Mason 1997). The pathways to reduced consumption will probably also be numerous and context-specific, and ultimately, people will make individual choices that make sense in their social and economic environment. (Pearce 2012).

As with population issues, conservation biologists should ensure that we, as individuals and a professional society, understand the current state of knowledge about consumption and encourage constructive dialogues on consumption and its effects on biodiversity. We are not the first to highlight the issue of consumption (Baltz 1999) in this journal. Although conservation biologists may debate whether U.S. consumption is excessive (Ehrlich & Goulder 2007), the answer is more clear to some. Two months after the 2011 Society for Conservation Biology meeting mentioned above, the first author was in India attending a presentation by Elinor Ostrom (2012), who won the Nobel Prize for her work on management of the commons. At the end of the presentation, a participant asked Dr. Ostrom how we can get the world to talk about consumption as the root cause of the world's environmental problems. This is the question conservation biologists should ask more often.

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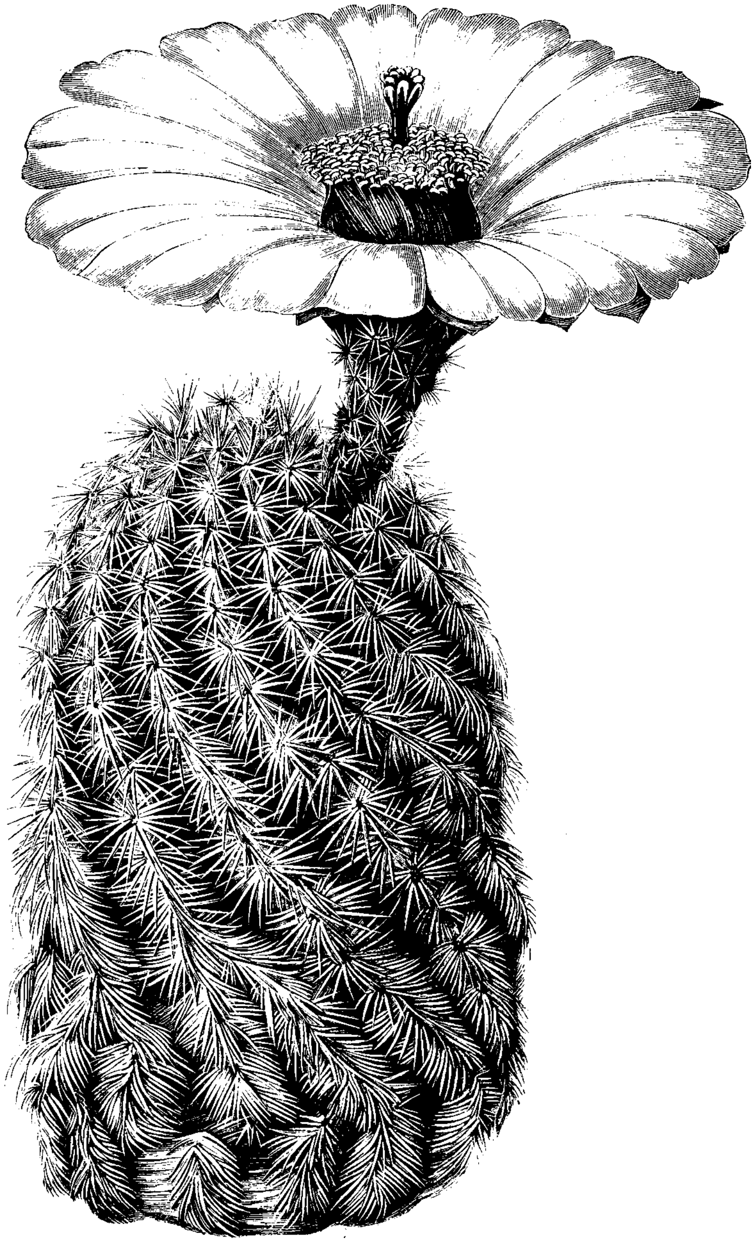

Human population reduction is not a quick fix for environmental problems

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The inexorable demographic momentum of the global human population is rapidly eroding Earth's life-support system. There are consequently more frequent calls to address environmental problems by advocating further reductions in human fertility. To examine how quickly this could lead to a smaller human population, we used scenario-based matrix modeling to project the global population to the year 2100. Assuming a continuation of current trends in mortality reduction, even a rapid transition to a worldwide one-child policy leads to a population similar to today's by 2100. Even a catastrophic mass mortality event of 2 billion deaths over a hypothetical 5-y window in the mid-21st century would still yield around 8.5 billion people by 2100. In the absence of catastrophe or large fertility reductions (to fewer than two children per female worldwide), the greatest threats to ecosystems—as measured by regional projections within the 35 global Biodiversity Hotspots—indicate that Africa and South Asia will experience the greatest human pressures on future ecosystems. Humanity's large demographic momentum means that there are no easy policy levers to change the size of the human population substantially over coming decades, short of extreme and rapid reductions in female fertility; it will take centuries, and the long-term target remains unclear. However, some reduction could be achieved by midcentury and lead to hundreds of millions fewer people to feed. More immediate results for sustainability would emerge from policies and technologies that reverse rising consumption of natural resources.

demography | fertility | catastrophe | war | mortality

The size of the global human population is often considered unsustainable in terms of its current and future impact on the Earth's climate, its ability to distribute food production equitably, population and species extinctions, the provision of adequate ecosystem services, and economic, sociological, and epidemiological well-being (1–8). Others argue that technology, ingenuity, and organization are stronger mediators of the environmental impact of human activities (9–11). Regardless, *Homo sapiens* is now numerically the dominant large organism on the planet. According to the United Nations, the world human population reached nearly 7.1 billion in 2013, with median projections of 9.6 billion (range: 8.3–11.0 billion) by 2050 and 10.9 billion (range: 6.8–16.6 billion) by 2100 (12), with more recent refinements placing the range at 9.6 to 12.3 billion by 2100 (13). So rapid has been the recent rise in the human population (i.e., from 1.6 billion in 1900), that roughly 14% of all of the human beings that have ever existed are still alive today (14).

Worldwide, environmental conditions are threatened primarily because of human-driven processes in the form of land conversion (agriculture, logging, urbanization), direct exploitation (fishing, bushmeat), species introductions, pollution, climate change (emissions), and their synergistic interactions (15). Although it is axiomatic that a smaller human population would reduce most of these threatening processes (16), separating consumption rates and population size per se is difficult (17) because of their combined effects on the loss of biodiversity and nonprovisioning natural capital (3, 18, 19), as well as the variation in consumption patterns among regions and socio-economic classes (20, 21). Sustainability requires an eventual stabilization of Earth's human population because resource demands and living space increase with population size, and proportional ecological damage increases even when consumption patterns stabilize (22, 23); it is therefore essential that scenarios for future human population dynamics are explored critically if we are to plan for a healthy future society (24).

There have been repeated calls for rapid action to reduce the world population humanely over the coming decades to centuries (1, 3), with lay proponents complaining that sustainability advocates ignore the "elephant in the room" of human overpopulation (25, 26). Amoral wars and global pandemics aside, the only humane way to reduce the size of the human population is to encourage lower per capita fertility. This lowering has been happening in general for decades (27, 28), a result mainly of higher levels of education and empowerment of women in the developed world, the rising affluence of developing nations, and the one-child policy of China (29–32). Despite this change, environmental conditions have worsened globally because of the overcompensating effects of rising affluence-linked population and consumption rates (3, 18). One of the problems is that there is still a large unmet need for more expansive and effective family-planning assistance, which has been previously hindered by conservative religious and political opposition, premature claims that rapid population growth has ended, and the reallocation of resources toward other health issues (33). Effective contraception has also been delayed because of poor education regarding its availability, supply, cost, and safety, as well as opposition from family members (33). Notwithstanding, some argue that if we could facilitate the transition to lower fertility

Significance

The planet's large, growing, and overconsuming human population, especially the increasing affluent component, is rapidly eroding many of the Earth's natural ecosystems. However, society's only real policy lever to reduce the human population humanely is to encourage lower per capita fertility. How long might fertility reduction take to make a meaningful impact? We examined various scenarios for global human population change to the year 2100 by adjusting fertility and mortality rates (both chronic and short-term interventions) to determine the plausible range of outcomes. Even one-child policies imposed worldwide and catastrophic mortality events would still likely result in 5–10 billion people by 2100. Because of this demographic momentum, there are no easy ways to change the broad trends of human population size this century.

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rates, most of the sustainability problems associated with the large human population would be greatly alleviated (3, 34–36).

Even in an ideal socio-political setting for lower birth-rate policies and the commitment to global-scale family planning, however, several questions remain: (*i*) How quickly could we achieve a smaller human population by adjusting such sociological levers (or via unexpected, large-scale stressors), and (*ii*) where in the world are human populations likely to do the most damage to their supporting environment over the coming century? To address the first of these questions on population trajectories, we built deterministic population models for humans, based on broad, multiregion geographical data drawn from the World Health Organization (WHO) and the United States Census Bureau. Using a Leslie-matrix approach, we projected the 2013 world population through to the year 2100 with several adjustments to fertility, mortality, and age at first childbirth (primiparity) to investigate the relative importance of different vital rates (representing possible policy interventions or stressors) on the trajectory and population size at the end of this century, and on the ratio of the "dependent" component of the population (<15 and >65 y) to the remainder (28). Existing projections of the human population typically do not include mass mortality events, of which there has been no prior experience, such as worldwide epidemics, nuclear wars, or climate change (32). We therefore also added four "catastrophe" scenarios to simulate the possible effects of climate disruption, world wars, or global pandemics on population trends. Our aim was not to forecast the actual population size at the end of this century; rather, we sought to compare the sensitivity of population trajectories to plausible and even unlikely social phenomena, and consider how these might influence long-term human demography.

To address the second question on environmental impacts of future populations, we focused on 14 region-specific projections of the human population, and related these to the areas of the planet most in need of environmental protection from the perspective of unique ecosystems: Biodiversity Hotspots (37). Although there are other ways of measuring regional patterns in environmental degradation and susceptibility (18), today's 35 Biodiversity Hotspots are internationally recognized as regions containing the most unique (endemic) species that are currently experiencing the greatest threats from human endeavors (37, 38). Previous studies have shown that current human population densities and growth rates are higher on average in Biodiversity Hotspots than elsewhere (39, 40), contributing to higher rates of deforestation and species loss (41). We used a similar framework to consider future human population trajectories of different regions relative to the distribution of global Biodiversity Hotspots, with the goal of assessing the relative change in threat to these unique environments after accounting for geographical differences in growth rates.

Methods

Demographic Data. Most published human demographic data are expressed as mortality and birth rates per 5-y age class, often with the first year of life provided separately. The most reliable age-specific mortality rates are reported by the WHO under the auspices of the WHO-CHOICE project (www.who.int/choice). Although originally compiled for modeling the progression of diseases in the human population, we opted to use these data because they are conveniently expressed as mortality rates per yearly age class and per WHO subregion (42), and so do not require smoothing or interpolation. The 14 WHO-CHOICE subregions, based on geographical location and demographic profiles and their constituent countries (www.who.int/choice), are listed in the legend of Fig. 4.

For globally averaged, age-specific (0–100+ y) mortalities, we aggregated the mean mortalities across each WHO subregion, with each age-specific (x) mortality (M_x) weighted by its population size vector (N_x) for each subregion. We estimated the 2013 N_x from the 2005 N_x provided by the WHO-CHOICE project by multiplying each N_x by the ratio of N_{2013}:N_{2005}, with N_{2013} sourced for each subregion from the US Census Bureau International Database (www.census.gov/population/international/data/idb).

We accessed 2013 fertility data by 5-y age groups from the US Census Bureau International Database. We converted the births per 1,000 women into age-specific fertilities (m_x) by dividing the 5-y classes equally among their constituent years and accounting for breeding female mortality within each of the 5-y classes. All age-specific population size, mortality, and fertility data we derived from these sources are available online at dx.doi.org/10.4227/05/5386F14C65D34.

Leslie Matrix. We defined a prebreeding 100 (i) × 100 (j) element, Leslie matrix (**M**) for females only, multiplying the subsequent projected population vector by the overall sex ratio to estimate total population size at each time step. Fertilities (m_x) occupied the first row of the matrix (ages 15–49), survival probabilities (1 – M_x) were applied to the subdiagonal, and the final diagonal transition probability ($\mathbf{M}_{i,j}$) represented survival of the 100+ age class. Complete R code (43) for the scenario projections is provided in Datasets S1 and S2.

Global Scenarios. For each projection, we multiplied the N_x vector by **M** for 87 yearly time steps (2013–2100, except for one fertility-reduction scenario that was extended to 2300). All projections were deterministic. Scenario 1 was a business-as-usual (BAU) "control" projection, with all matrix elements kept constant at 2013 values. Scenario 2a was a "realistic" projection with a linear decline in M_x, starting in 2013, to 50% of their initial values by 2100 (i.e., via improving diet, affluence, medicine, female empowerment, and so forth). We also emulated a shift toward older primiparity by allocating 50% of the fertility in the youngest reproductive age class (15–24) evenly across the older breeding classes (25–49), following a linear change function from 2013 to 2100 (as per the decline in M_x). We then implemented a linear decline in total fertility from the 2013 starting value of 2.37 children per female to 2.00 by 2100 (to simulate the ongoing trend observed in recent decades). The rate of fertility decline was thus 0.0042 children per female per year. Scenario 2b was identical to Scenario 2 in all respects except mortality remained constant over the projection interval. Scenario 3 was similar to Scenario 2a, except that we reduced total fertility more steeply, to one child per female by 2100 to emulate, for example, a hypothetical move toward a worldwide one-child policy by the end of the century. This rate of fertility decline was thus 0.0157 children per female per year. In scenario 4, we reduced fertility even more rapidly to one child per female by 2045 (fertility decline rate = 0.0427) and kept it constant thereafter to 2100; we also removed the assumption that mortality (M_x) would decline over the projection interval, so we maintained M_x at 2013 values. In Scenario 5, we examined how a global avoidance of unintended pregnancies resulting in births, via reproduction education, family planning, and cultural shift (3), would affect our projections to 2100. Using data from 2008, there were 208 million pregnancies globally, of which an estimated 86 million were unintended (44). Of these 86 million, ∼11 million were miscarried, 41 million aborted, and 33 million resulted in unplanned births (44). In this scenario, therefore, we assumed that 33 of 208 (15.8%) births per year of the projection would not occur if unwanted pregnancies were avoided entirely.

Scenarios 6–9 represent a comparative "what if?" exploration of different levels of chronic or acute elevated mortality rates, spanning the plausible through to the highly unlikely. Scenario 6 used the BAU matrix, but with childhood mortality increasing linearly to double the 2013 values by 2100 to simulate food shortages caused by, for example, climate-disruption impacts on crop yields (45). Scenario 7 implemented a broad-scale mortality event equivalent to the approximate number of human deaths arising from the First and Second World Wars and the Spanish flu combined (Σ = 131 million deaths; http://necrometrics.com) as a proportion of the midway (i.e., 2056) projected population size (9.95 billion) (*Results*). Based on a world population of 2.5 billion at the end of the Second World War, this combined death toll from these historical events represented 5.2% of the global population; thus, we applied this proportional additional mortality to the 2056 (midway) world population estimate, which equates to about 500 million deaths over 5 y. For Scenario 8, we implemented a mass mortality event that killed 2 billion people worldwide (again, implemented over a 5-y period from 2056 onwards). Scenario 9 was identical to Scenario 8, only we increased the death toll substantially, to 6 billion, and implemented the catastrophe one-third of the way through the projection interval (i.e., 2041) to allow for a longer recovery from its consequences. A summary of the initial parameter values and their temporal changes for all scenarios is provided in Table S1.

Although potentially exaggerated, we also assumed that the demographic rates of the overall human population would shift markedly following such large mortality events, thus mimicking a type of postwar condition similar to that observed in the 1950s (i.e., the "baby boom"). Following the final year of the mass mortality catastrophe, we (arbitrarily) assumed that fertility would double, but then decline linearly to 2013 values by 2100. We also assumed that overall

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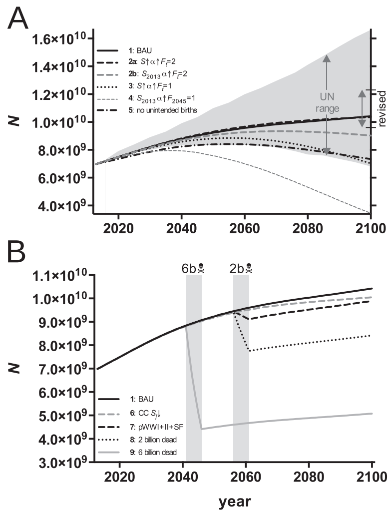

Fig. 1. Scenario-based projections of world population from 2013 to 2100. (*A*) Scenario 1: BAU population growth (constant 2013 age-specific vital rates); Scenario 2a: reducing mortality (M), increasing age at primiparity (α), declining fertility to two children per female ($F_t = 2$) by 2100; Scenario 2b: same as Scenario 2a, but without reduced mortality; Scenario 3: same as Scenario 2a, but $F_t = 1$; Scenario 4: same as Scenario 3, but without reduced mortality and $F_t = 1$ by 2045 and thereafter constant to 2100; Scenario 5: avoiding all unintended pregnancies resulting in annual births. High and low projections by the United Nations (12) are shown as a grayed area, and the revised range for 2100 (13) is also indicated. (*B*) Scenario 6: elevated childhood mortality (M_j) from climate change (CC); Scenario 7: mass mortality event over a 5-y period starting 2056, equal to the proportion of combined number of deaths from World War I, World War II, and Spanish flu scaled to the mid-21st century population; Scenario 8: 2 billion people killed because of a global pandemic or war spread over 5 y, starting midway (i.e., 2056) through the projection interval; Scenario 9: 6 billion people killed because of a global pandemic or war spread over 5 y and initiated one-third of the way through the projection interval (i.e., 2041). The mass mortality windows are indicated as gray bars.

mortality would double following the final year of the catastrophe (e.g., to emulate lingering effects such as food shortages, disrupted social interactions and disease epidemics), but then decline linearly to 2013 values by 2100.

For all scenario-based projections, we calculated the yearly total population size (males and females), and the proportion of the population <15-y-old or >65-y-old. The sum of this proportion (i.e., the proportion in the 15- to 65-y classes) relative to the remainder represents the "dependency ratio," which is a metric of the population generally considered to be dependent on the productivity of used society (28). To test the sensitivity of the choice of the upper-age boundary on the overall ratio (e.g., 65 y), we repeated the calculation for the upper "dependant" age of 75 y.

Subregional Scenarios. We alternatively projected each of the WHO subregions separately using their subregion-specific mortalities and US Census Bureau fertilities and population vectors, without assuming any changes over time to the component vital rates or migration between regions. Indeed, interregional migration remains one of the most difficult parameters to predict for the human population (32). For comparison, we also repeated the subregional projections assuming the same linear change in vital rates as per Scenario 2a for the global projections. For each region, we overlaid the extent of the latest 35 Conservation International Biodiversity Hotspots (37, 38) (shapefile available from databasin.org) to determine which Hotspots were associated with the most rapid projected expansion of the human population over the coming century, and the areas of highest human population density in 2100.

Results

Projection Scenarios. The population projections for the BAU (Scenario 1) and realistic changes in vital rates (Scenario 2a) produced similar 2050 [9.23 and 9.30 billion, respectively; difference (Δ) = 68 million] and end-of-century populations (10.42 and 10.35 billion, respectively; Δ = 70 million) (Fig. 1*A*). The more draconian fertility reduction to a global one child per woman by 2100 (Scenario 3) resulted in a peak population size of 8.9 billion in 2056, followed by a decline to ~7 billion by 2100 (i.e., a return to the 2013 population size) (Fig. 1*A*). Enforcing a one child per female policy worldwide by 2045 and without improving survival (Scenario 4) resulted in a peak population size of 7.95 billion in 2037, 7.59 billion by 2050, and a rapid reduction to 3.45 billion by 2100. Avoiding the approximate 16% of annual births resulting from unintended pregnancies (Scenario 5) reduced the projected population in 2050 to 8.39 billion (compared to, for example, 9.30 billion in Scenario 2a; Δ = 901 million), and in 2100 to 7.3 billion (compared to, for example, 10.4 billion in Scenario 2a; Δ = 3014 million) (Fig. 1*A*).

The most striking aspect of the "hypothetical catastrophe" scenarios was just how little effect even these severe mass mortality events had on the final population size projected for 2100 (Fig. 1*B*). The climate change (childhood mortality increase) (Scenario 5), future proportional "World Wars" mortality event (Scenario 6), and BAU (Scenario 1) projections all produced between 9.9 and 10.4 billion people by 2100 (Fig. 1*B*). The catastrophic mass mortality of 2 billion dead within 5 y half-way through the projection interval (Scenario 7) resulted in a population size of 8.4 billion by 2100, whereas the 6 billion-dead scenario (Scenario 8) implemented one-third of the way through the projection still led to a population of 5.1 billion by 2100 (Fig. 1*B*).

Projecting Scenario 3 (worldwide one-child policy by 2100, assuming no further reduction in total fertility thereafter) to 2300, the world population would fall to half of its 2013 size by 2130, and one-quarter by 2158 (Fig. 2). This result is equivalent to an instantaneous rate of population change (r) of −0.0276 once the age-specific vital rates of the matrix stabilize (i.e., after we imposed invariant vital rates at 2100 and onwards).

Another notable aspect of the noncatastrophe projections (Scenarios 1 and 3) was the relative stability of the dependency ratio during the projection interval (Fig. 3). The ratio varied from 0.54 to a maximum of 0.67 (Scenario 3) by 2100, with the latter equating to ~1.5 (1/0.67) working adults per dependant. Increasing the older dependency age to 75 only stabilized the dependency ratio further (Scenario 1: 0.38–0.44; Scenario 3: 0.33–0.44) (Fig. S1).

Subregions. Region 4 (Americas B) overlaps the highest number of Biodiversity Hotspots (9), although it is projected to have the fourth lowest population density by 2100 (44.8 persons km^{-2}) (Table S2). The regions with the next-highest number of Hotspots are Regions 2 (Africa E) and 14 (Western Pacific B) (eight each) (Fig. 4 and Table S1). Although Region 14 had the largest human population in 2013, Region 2 had the second-highest projected rate of increase of all regions (Fig. 4). Furthermore, two Hotspots in Region 2 (Eastern Afromontane, Horn of Africa) are also found in Regions 6 and 7 (Eastern Mediterranean), with the sixth- and third-highest rates of increase, respectively (Table S2). Both African regions (Regions 1 and 2) are also projected to have the second- (Region 1: 246.4 persons km^{-2}) and third-highest (Region 2: 241.3 persons km^{-2}) population

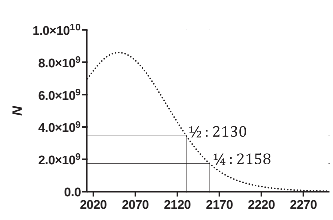

Fig. 2. Long-term outlook. Scenario-based projection of world population from 2013 to 2300 based on constant 2013 age-specific vital rates but declining fertility to one child per female (F_t = 1) by 2100 (fertility held constant thereafter). Population reduces to one-half of its 2013 size by 2130, and one-quarter by 2158.

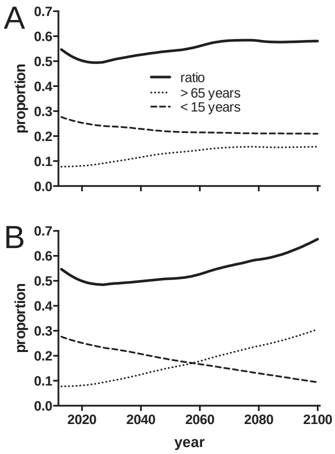

Fig. 3. Size of dependent population. Proportion of people <15 y or >65 y per time step, and their ratio to the (most productive) remainder of the population (dependency ratio) for (*A*) Scenario 1 (BAU), and (*B*) Scenario 3 (decreasing mortality, increasing age at primiparity, decreasing fertility to one child per female). See *Methods* for detailed scenario descriptions.

densities by 2100 (Fig. 4 and Table S1). The Biodiversity Hotspots of Region 12 (Southeast Asia D: Himalaya, Indo-Burma, Western Ghats, and Sri Lanka) are also a particular concern because the region currently has the second-largest population size and is projected to double by the end of this century, producing the highest projected human population density of any subregion (656 persons km^{-2}) (Fig. 4 and Table S1). If we alternatively assumed linear declines in fertility and mortality, and increasing age at primiparity (i.e., Scenario 2a conditions), the subregional rankings according to projected rate of increase were nearly identical (except for the relative ranking of the last two regions) (Table S3). For these projections, the final mean population densities were between 16% and 37% lower (Table S3) than those predicted assuming constant vital rates (Fig. 4 and Table S2).

Discussion

Although not denying the urgency with which the aggregate impacts of humanity must be mitigated on a planetary scale (3), our models clearly demonstrate that the current momentum (28) of the global human population precludes any demographic “quick fixes.” That is, even if the human collective were to pull as hard as possible on the total fertility policy lever (via a range of economic, medical, and social interventions), the result would be ineffective in mitigating the immediately looming global sustainability crises (including anthropogenic climate disruption), for which we need to have major solutions well under way by 2050 and essentially solved by 2100 (3, 46, 47). However, this conclusion excludes the possibility that global society could avoid all unintended births or that the global average fertility rate could decline to one child per female by 2100. Had humanity acted more to constrain fertility before this enormous demographic momentum had developed (e.g., immediately following World War II), the prospect of reducing our future impacts would have been more easily achievable.

That said, the projections assuming all unintended pregnancies resulting in births were avoided each year resulted in a global human population size in 2100 that was over 3 billion people smaller than one assuming no similar reduction in birth rates (compare, for example, Scenarios 5 and 2a). Similarly, a global move toward one child per female by 2100 or, more radically, by 2045, indicated that there could be theoretically billions fewer people by the end of the century. More realistically, if worldwide average fertility could be reduced to two children per female by 2020 (compared with 2.37 today), there would be 777 million fewer people to feed planet-wide by 2050 (compared with the BAU; scenario not shown in *Results*). Although these scenarios would be challenging to achieve, our model comparisons reveal that effective family planning and reproduction education worldwide (48) have great potential to reduce the size of the human population and alleviate pressure on resource availability over the long term, in addition to generating other social advantages, such as fewer abortions, miscarriages, and lower maternal mortality (3).

This finding is particularly encouraging considering that even the population reduction attributed to China’s controversial one-child policy might have been assisted by an already declining fertility rate (49), much as the world’s second most-populous country, India, has demonstrated over the last several decades (50). Perhaps with a more planned (rather than forced) approach to family planning, substantial reductions in future population size are plausible. Better family planning could be achieved not only by providing greater access to contraception, but through education, health improvements directed at infant mortality rates, and outreach that would assuage some of the negative social and cultural stigmas attached to their use (33). A greater commitment from high-income countries to fund such programs, especially in the developing world, is a key component of any future successes (51).

Our aim was not to forecast a precise trajectory or size of the human population over the coming century, but to demonstrate what is possible when assuming various underlying dynamics, so as to understand where to direct policy most effectively. Although all projections lacked a stochastic component (notwithstanding the prescribed trends in vital rates and mass mortality catastrophes imposed), such year-to-year variation is typically smoothed when population sizes are large, as is the case for humans. Catastrophic deaths arising from pandemics or major wars could, of course, lead to a wide range of future population sizes. Our choice of the number of people dying in the catastrophe scenarios illustrated here were therefore necessarily arbitrary, but we selected a range of values up to what we consider to be extreme (e.g., 6 billion deaths over 5 y) to demonstrate that even future events that rival or plausibly exceed past societal cataclysms cannot guarantee small future population sizes without additional measures, such as fertility control. Furthermore, we did not incorporate any density feedback to emulate the effects of a planet-wide human carrying capacity on vital rates (3), apart from scenarios imitating possible demographic consequences of reduced food supply or resource-driven war or disease, because such relationships are strongly technology-dependent and extremely difficult and politically sensitive to forecast (26, 52). Furthermore, regional comparisons should be considered only as indicative because we did not explicitly model interregional migration, and the projected rates of change and final densities are dependent on whether vital rates are assumed to be constant or change according to recent trends. Local population densities do not necessarily correlate perfectly with regional consumption given world disparity in wealth distribution, environmental leakage, and foreign land grabbing (18). Despite these simplifications, our results are indicative of the relative influence of particular sociological events on human population trajectories over the next century.

Globally, human population density has been shown to predict the number of threatened species among nations (53–55), and at a national scale, there is a clear historical relationship between human population size and threats to biodiversity (56, 57). However, because of the spatial congruence between human population size and species richness, a lack of data on extinctions, and variability across methods, there is only a weak correlation globally between human density and observed species extinctions (58). Nonetheless, the pressures are clear, with half of world protected areas losing their biodiversity (59) because of high human stressors—including population growth rates and locally or foreign-driven consumption (60)—at their edges.

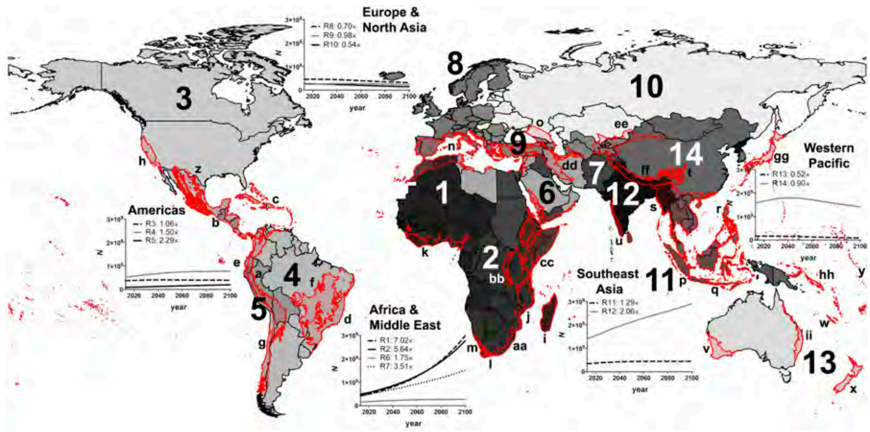

Fig. 4. Regional variation and impacts. Human population projections under the BAU levels of population growth (2013 matrix; Scenario 1) for 14 subregions (R1–R14; see below for country composition). Regional shading indicates relative mean population density projected for 2100: white shading = 0 persons km^{-2} to darker shading = 656.6 persons km^{-2}). Values next to each region line (legends) indicate the ratio of the projected 2100 population (N_{2100}) to the 2013 start population (N_{2013}). Red hatched overlay indicates position of global Biodiversity Hotspots (a–ii: see below for full Hotspot list). Full Hotspot listing per region and associated projected values are also provided in Table S2. Subregion country composition (boldface indicates region number on the map): Africa D, **Region 1**: Angola (AGO), Benin (BEN), Burkina Faso (BFA), Cameroon (CMR), Cape Verde (CPV), Algeria (DZA), Gabon (GAB), Ghana (GHA), Guinea (GIN), Gambia (GMB), Guinea-Bissau (GNB), Equatorial Guinea (GNQ), Liberia (LBR), Madagascar (MDG), Mali (MLI), Mauritania (MRT), Mauritius (MUS), Niger (NER), Nigeria (NGA), Senegal (SEN), Sierra Leone (SLE), Sao Tome and Principe (STP), Seychelles (SYC), Chad (TCD), Togo (TGO); Africa E, **Region 2**: Burundi (BDI), Botswana (BWA), Central African Republic (CAF), Côte d'Ivoire (CIV), The Democratic Republic of the Congo (COD), Congo (COG), Eritrea (ERI), Ethiopia (ETH), Kenya (KEN), Lesotho (LSO), Mozambique (MOZ), Malawi (MWI), Namibia (NAM), Rwanda (RWA), Swaziland (SWZ), United Republic of Tanzania (TZA), Uganda (UGA), South Africa (ZAF), Zambia (ZMB), Zimbabwe (ZWE); Americas A, **Region 3**: Canada (CAN), Cuba (CUB), United States (USA); Americas B, **Region 4**: Argentina (ARG), Antigua and Barbuda (ATG), Bahamas (BHS), Belize (BLZ), Brazil (BRA), Barbados (BRB), Chile (CHL), Colombia (COL), Costa Rica (CRI), Dominica (DMA), Dominican Republic (DOM), Grenada (GRD), Guyana (GUY), Honduras (HND), Jamaica (JAM), Saint Kitts and Nevis (KNA), Saint Lucia (LCA), Mexico (MEX), Panama (PAN), Paraguay (PRY), El Salvador (SLV), Suriname (SUR), Trinidad and Tobago (TTO), Uruguay (URY), Saint Vincent and the Grenadines (VCT), Venezuela (VEN); Americas D, **Region 5**: Bolivia (BOL), Ecuador (ECU), Guatemala (GTM), Haiti (HTI), Nicaragua (NIC), Peru (PER); Eastern Mediterranean B, **Region 6**: United Arab Emirates (ARE), Bahrain (BHR), Cyprus (CYP), Islamic Republic of Iran (IRN), Jordan (JOR), Kuwait (KWT), Lebanon (LBN), Libyan Arab Jamahiriya (LBY), Oman (OMN), Qatar (QAT), Saudi Arabia (SAU), Syrian Arab Republic (SYR), Tunisia (TUN); Eastern Mediterranean D, **Region 7**: Afghanistan (AFG), Djibouti (DJI), Egypt (EGY), Iraq (IRQ), Morocco (MAR), Pakistan (PAK), Somalia (SOM), Sudan (SDN), Yemen (YEM); Europe A, **Region 8**: Andorra (AND), Austria (AUT), Belgium (BEL), Switzerland (CHE), Czech Republic (CZE), Germany (DEU), Denmark (DNK), Spain (ESP), Finland (FIN), France (FRA), United Kingdom (GBR), Greece (GRC), Croatia (HRV), Ireland (IRL), Iceland (ISL), Israel (ISR), Italy (ITA), Luxembourg (LUX), Monaco (MCO), Malta (MLT), The Netherlands (NLD), Norway (NOR), Portugal (PRT), San Marino (SMR), Slovenia (SVN), Sweden (SWE); Europe B, **Region 9**: Albania (ALB), Armenia (ARM), Azerbaijan (AZE), Bulgaria (BGR), Bosnia and Herzegovina (BIH), Georgia (GEO), Kyrgyzstan (KGZ), The Former Yugoslav Republic of Macedonia (MKD), Montenegro (MNE), Poland (POL), Romania (ROU), Serbia (SRB), Slovakia (SVK), Tajikistan (TJK), Turkmenistan (TKM), Turkey (TUR), Uzbekistan (UZB); Europe C, **Region 10**: Belarus (BLR), Estonia (EST), Hungary (HUN), Kazakhstan (KAZ), Lithuania (LTU), Latvia (LVA), Moldova (MDA), Russian Federation (RUS), Ukraine (UKR); Southeast Asia B, **Region 11**: Indonesia (IDN), Sri Lanka (LKA), Thailand (THA), East Timor (TLS); Southeast Asia D, **Region 12**: Bangladesh (BGD), Bhutan (BTN), India (IND), Maldives (MDV), Myanmar (MMR), Nepal (NPL), Democratic People's Republic of Korea (PRK); Western Pacific A, **Region 13**: Australia (AUS), Brunei Darussalam (BRN), Japan (JPN), New Zealand (NZL), Singapore (SGP); Western Pacific B, **Region 14**: China (CHN), Cook Islands (COK), Fiji (FJI), Federated States of Micronesia (FSM), Cambodia (KHM), Kiribati (KIR), Republic of Korea (KOR), Lao People's Democratic Republic (LAO), Marshall Islands (MHL), Mongolia (MNG), Malaysia (MYS), Niue (NIU), Nauru (NRU), Philippines (PHL), Palau (PLW), Papua New Guinea (PNG), Solomon Islands (SLB), Tonga (TON), Tuvalu (TUV), Vietnam (VNM), Vanuatu (VUT), Samoa (WSM). **Biodiversity Hotspots**: a, Tropical Andes; b, Mesoamerica; c, Caribbean Islands; d, Atlantic Forest; e, Tumbes-Chocó-Magdalena; f, Cerrado; g, Chilean Winter Rainfall-Valdivian Forests; h, California Floristic Province; I, Madagascar and the Indian Ocean Islands; j, Coastal Forests of Eastern Africa; k, Guinean Forests of West Africa; l, Cape Floristic Region; m, Succulent Karoo; n, Mediterranean Basin; o, Caucasus; p, Sundaland; q, Wallacea; r, Philippines; s, Indo-Burma, India and Myanmar; t, Mountains of Southwest China; u, Western Ghats and Sri Lanka; v, Southwest Australia; w, New Caledonia; x, New Zealand; y, Polynesia-Micronesia; z, Madrean Pine-Oak Woodlands; aa, Maputaland-Pondoland-Albany; bb, Eastern Afromontane; cc, Horn of Africa; dd, Irano-Anatolian; ee, Mountains of Central Asia; ff, Eastern Himalaya, Nepal; gg, Japan; hh, East Melanesian Islands; ii, Forests of East Australia.

The socio-political argument for encouraging high fertility rates to offset aging populations (61) that would otherwise put a strain on the productive (working) component of the population is demonstrably weak. This is because focusing solely on the growing aged component of a population ignores the concomitant reduction in the proportion of young dependants as the affluence level and fertility rates of women shift to older primiparity and fewer children. Thus, our projections show that even an aging population maintains an approximately constant number of dependants per working-age person, even under scenarios or in regions of relatively rapid projected decline (e.g., Regions 8, 10, and 13) (Fig. 4).

The broader question of what constitutes an optimum human population size (and how long it would take) is fraught with uncertainty, being so highly dependent on technological and sociological advances (9, 62). It has been suggested that a total world population between 1 and 2 billion might ensure that all individuals lived prosperous lives, assuming limited change in per capita consumption and land/materials use (1, 62). According to our basic fertility-reduction model (to one child per female by 2100), and excluding mass mortality events, achieving such a goal would take a minimum of 140 y (2 billion by 2153) (Fig. 1*B*), but realistically much longer given decreasing mortality rates and the intractability and questionable morality of enforcing a worldwide one-child policy as fertility control. A considerably larger optimal human population size is also feasible if society embraces technological improvements (including sustainable energy) that allow for decoupling of impacts and near-closed-system recycling, and so can vastly reduce consumption rates of primary resources (63, 64).

Conclusion

There are clearly many environmental and societal benefits to ongoing fertility reduction in the human population (3, 48, 58), but here we show that it is a solution long in the making from which our great-great-great-great grandchildren might ultimately benefit, rather than people living today. It therefore cannot be argued to be the elephant in the room for immediate environmental sustainability and climate policy. A corollary of this finding is that society's efforts toward sustainability would be directed more productively toward adapting to the large and increasing human population by rapidly reducing our footprint as much as possible through technological (63, 64) and social innovation (3, 65), devising cleverer ways to conserve remaining species and ecosystems, encouraging per capita reductions in consumption of irreplaceable goods (58), and treating population as a long-term planning goal.

It is therefore inevitable that the virtually locked-in increase in the global human population during the 21st century—regardless of trends in per capita consumption rates—risks increasing the threat to the environment posed by humans because of growing aggregate and accumulated demands. Apart from efforts to accelerate (rather than reverse) ongoing declines in fertility, ameliorated especially by effective family planning, female empowerment, better education, and political and religious endorsement of sustainability in the developing world (48), the only other immediate control on regional population trends could take the form of (politically and morally contentious) country-specific immigration policies. Accepting the difficulty of this, the question of how many more species we lose, ecosystem services we degrade, and natural capital we destroy will therefore depend mostly—at least over the coming century—on how much we can limit the damage through timely and efficient technological and social advances. However, this is not an excuse for neglecting ethical measures for fertility reduction now; it could avoid millions of deaths by midcentury and possibly keep the planet more habitable for *Homo sapiens* in the next.

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Supporting Information

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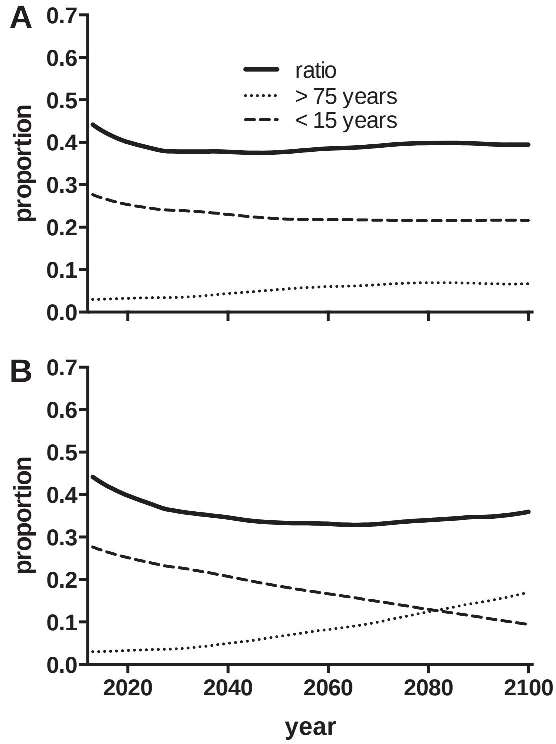

Fig. S1. Testing sensitivity of scenario assumptions: Proportion of people <15 y or >75 y per time step, and their ratio to the remainder of the population (dependency ratio) for (*A*) Scenario 1 (BAU), and (*B*) Scenario 3 (decreasing mortality, increasing age at primiparity, decreasing fertility to one child per female). See main text for detailed scenario descriptions.

Table S1. Summary of initial parameter values and temporal changes for the 10 scenarios considered

Scenario	Fertility (m) (children per female)	Primiparity	Mean juvenile mortality ($\overline{M}_{0-5}$)	Mean adult mortality ($\overline{M}_{6-100}$)	Catastrophic deaths
1	2.37 (constant)	unchanged	0.0131 (constant)	0.0490 (constant)	0
2a	2.37 (2013) → 2.00 (2100)	50% $m_{15-24} \rightarrow m_{25-49}$*	0.0131 (2013) → 0.0066 (2100)	0.0490 (2013) → 0.0245 (2100)	0
2b	2.37 (2013) → 2.00 (2100)	50% $m_{15-24} \rightarrow m_{25-49}$	0.0131 (constant)	0.0490 (constant)	0
3	2.37 (2013) → 1.00 (2100)	50% $m_{15-24} \rightarrow m_{25-49}$	0.0131 (2013) → 0.0066 (2100)	0.0490 (2013) → 0.0245 (2100)	0
4	2.37 (2013) → 1.00 (2045, constant to 2100)	50% $m_{15-24} \rightarrow m_{25-49}$	0.0131 (constant)	0.0490 (constant)	0
5	2.37–15.8% births per year[†] (constant)	Unchanged	0.0131 (constant)	0.0490 (constant)	0
6	2.37 (constant)	Unchanged	0.0131 (2013) → 0.0262 (2100)	0.0490 (constant)	0
7	2.37 (constant)	Unchanged	0.0131 (constant)	0.0490 (constant)	500 million deaths 2056–2061
8	2.37 (constant)	Unchanged	0.0131 (constant)	0.0490 (constant)	2 billion deaths 2056–2060
9	2.37 (constant)	Unchanged	0.0131 (constant)	0.0490 (constant)	6 billion deaths 2041–2045

An arrow (→) indicates the parameter value changes (linearly) to the new value indicated by the year given.

*For example, 50% of the fertility resulting from 15- to 24-y-olds shifts to that of 25- to 49-y-olds.

[†]For example, each year, 15.8% of births deemed "unwanted" are subtracted from total fertility.

Table S2. BAU population growth and its implications for Biodiversity Hotspots

Subregion	N_{2013} (millions)	N_{2100}/N_{2013}	$\overline{D}_{2100}$ (ppl km^{-2})	Biodiversity Hotspots
1-Africa D	425	7.02	246.4	Guinean Forests of West Africa
				Mediterranean Basin
2-Africa E	491	5.64	241.3	Cape Floristic Region
				Succulent Karoo
				Maputaland-Pondoland-Albany
				Madagascar & Indian Ocean Islands
				Coastal Forests of Eastern Africa
				Eastern Afromontane
				Horn of Africa
				Guinean Forests of West Africa
7-Eastern Mediterranean D	432	3.51	215.4	Eastern Afromontane
				Horn of Africa
				Mediterranean Basin
				Irano-Anatolian
5-Americas D	87	2.29	67.7	Tropical Andes
				Tumbes-Choco-Magdalena
				Caribbean Islands
				Mesoamerica
12-Southeast Asia D	1405	2.06	656.6	Himalaya
				Indo-Burma
				Western Ghats and Sri Lanka
6-Eastern Mediterranean B	158	1.75	44.7	Eastern Afromontane
				Horn of Africa
				Mediterranean Basin
				Irano-Anatolian
4-Americas B	518	1.50	44.8	Chilean Winter Rainfall and Valdivian Forests
				Atlantic Forest
				Cerrado
				Tropical Andes
				Tumbes-Choco-Magdalena
				Caribbean Islands
				Mesoamerica
				California Floristic Province
				Madrean Pine-Oak Woodlands
11-Southeast Asia B	346	1.29	177.1	Indo-Burma
				Sundaland
				Wallacea
3-Americas A	373	1.06	20.0	Caribbean Islands
				California Floristic Province
9-Europe B	241	0.98	75.1	Mediterranean Basin
				Irano-Anatolian
				Caucasus
				Mountains of Central Asia
14-Western Pacific B	1571	0.90	107.5	Mountains of Central Asia
				Himalaya
				Mountains of Southwest China
				Indo-Burma
				Sundaland
				Philippines
				East Melanesian Islands
				Polynesia-Micronesia
8-Europe A	460	0.70	82.7	Mediterranean Basin
10-Europe C	270	0.54	7.0	Caucasus
				Mountains of Central Asia
13-Western Pacific A	166	0.52	10.4	Southwest Australia
				Forests of East Australia
				New Caledonia
				New Zealand
				Japan

Current human population size and structure (N_{2013}), ratio of population change based on our midrange BAU demographic projections (N_{2100}/N_{2013}), mean population density (people km^{-2}) in 2100 across all countries per region ($\overline{D}_{2100}$) and the Biodiversity Hotspots contained within each of 14 WHO-defined population subregions. Regions are ordered (descending) by N_{2100}/N_{2013}. Subregion country composition (see legend to Fig. 4 for country code expansion): Africa D (Region 1: AGO, BEN, BFA, CMR, CPV, DZA, GAB, GHA, GIN, GMB, GNB, GNQ, LBR, MDG, MLI, MRT, MUS, NER, NGA, SEN, SLE, STP, SYC, TCD, TGO), Africa E (Region 2: BDI, BWA, CAF, CIV, COD, COG, ERI, ETH, KEN, LSO, MOZ, MWI, NAM, RWA, SWZ, TZA, UGA, ZAF, ZMB, ZWE), Americas A (Region 3: CAN, CUB, USA), Americas B (Region 4: ARG, ATG, BHS, BLZ, BRA, BRB, CHL, COL, CRI, DMA, DOM, GRD, GUY, HND, JAM, KNA, LCA, MEX, PAN, PRY, SLV, SUR, TTO, URY, VCT, VEN), Americas D (Region 5: BOL, ECU, GTM, HTI, NIC, PER), Eastern Mediterranean B (Region 6: ARE, BHR, CYP, IRN, JOR, KWT, LBN, LBY, OMN, QAT, SAU, SYR, TUN), Eastern Mediterranean D (Region 7: AFG, DJI, EGY, IRQ, MAR, PAK, SOM, SDN, YEM), Europe A (Region 8: AND, AUT, BEL, CHE, CZE, DEU, DNK, ESP, FIN, FRA, GBR, GRC, HRV, IRL, ISL, ISR, ITA, LUX, MCO, MLT, NLD, NOR, PRT, SMR, SVN, SWE), Europe B (Region 9: ALB, ARM, AZE, BGR, BIH, GEO, KGZ, MKD, MNE, POL, ROU, SRB, SVK, TJK, TKM, TUR, UZB), Europe C (Region 10: BLR, EST, HUN, KAZ, LTU, LVA, MDA, RUS, U.K.R), Southeast Asia B (Region 11: IDN, LKA, THA, TLS), Southeast Asia D (Region 12: BGD, BTN, IND, MDV, MMR, NPL, PRK), Western Pacific A (Region 13: AUS, BRN, JPN, NZL, SGP), Western Pacific B (Region 14: CHN, COK, FJI, FSM, KHM, KIR, KOR, LAO, MHL, MNG, MYS, NIU, NRU, PHL, PLW, PNG, SLB, TON, TUV, VNM, VUT, WSM).

Table S3. Effects of declining fertility and mortality by region

Subregion	N_{2013} (millions)	N_{2100}/N_{2013}	$\bar{D}_{2100}$ (ppl km^{-2})
1-Africa D	425	4.45	156.1
2-Africa E	491	3.61	154.7
7-Eastern Mediterranean D	432	2.31	141.8
5-Americas D	87	1.56	46.1
12-Southeast Asia D	1405	1.41	448.5
6-Eastern Mediterranean B	158	1.24	31.7
4-Americas B	518	1.08	32.2
11-Southeast Asia B	346	0.96	132.1
3-Americas A	373	0.77	14.7
9-Europe B	241	0.74	56.4
14-Western Pacific B	1571	0.68	81.5
8-Europe A	460	0.54	64.3
13-Western Pacific A	166	0.44	8.7
10-Europe C	270	0.42	5.4

Shown are the current human population size and structure (N_{2013}), ratio of population change based on our midrange demographic projections (N_{2100}/N_{2013}), mean population density (people km^{-2}) in 2100 across all countries per region ($\bar{D}_{2100}$). This scenario assumes a linear trend to halving the initial (2013) fertilities and mortalities (juvenile and nonjuvenile), and increasing age at primiparity (following Scenario 2 conditions) by 2100. Regions are ordered (descending) by N_{2100}/N_{2013}. Subregion country composition (see Fig. 4 for expansion of country abbreviations): Africa D (Region 1: AGO, BEN, BFA, CMR, CPV, DZA, GAB, GHA, GIN, GMB, GNB, GNQ, LBR, MDG, MLI, MRT, MUS, NER, NGA, SEN, SLE, STP, SYC, TCD, TGO), Africa E (Region 2: BDI, BWA, CAF, CIV, COD, COG, ERI, ETH, KEN, LSO, MOZ, MWI, NAM, RWA, SWZ, TZA, UGA, ZAF, ZMB, ZWE), Americas A (Region 3: CAN, CUB, USA), Americas B (Region 4: ARG, ATG, BHS, BLZ, BRA, BRB, CHL, COL, CRI, DMA, DOM, GRD, GUY, HND, JAM, KNA, LCA, MEX, PAN, PRY, SLV, SUR, TTO, URY, VCT, VEN), Americas D (Region 5: BOL, ECU, GTM, HTI, NIC, PER), Eastern Mediterranean B (Region 6: ARE, BHR, CYP, IRN, JOR, KWT, LBN, LBY, OMN, QAT, SAU, SYR, TUN), Eastern Mediterranean D (Region 7: AFG, DJI, EGY, IRQ, MAR, PAK, SOM, SDN, YEM), Europe A (Region 8: AND, AUT, BEL, CHE, CZE, DEU, DNK, ESP, FIN, FRA, GBR, GRC, HRV, IRL, ISL, ISR, ITA, LUX, MCO, MLT, NLD, NOR, PRT, SMR, SVN, SWE), Europe B (Region 9: ALB, ARM, AZE, BGR, BIH, GEO, KGZ, MKD, MNE, POL, ROU, SRB, SVK, TJK, TKM, TUR, UZB), Europe C (Region 10: BLR, EST, HUN, KAZ, LTU, LVA, MDA, RUS, U.K.R), Southeast Asia B (Region 11: IDN, LKA, THA, TLS), Southeast Asia D (Region 12: BGD, BTN, IND, MDV, MMR, NPL, PRK), Western Pacific A (Region 13: AUS, BRN, JPN, NZL, SGP), Western Pacific B (Region 14: CHN, COK, FJI, FSM, KHM, KIR, KOR, LAO, MHL, MNG, MYS, NIU, NRU, PHL, PLW, PNG, SLB, TON, TUV, VNM, VUT, WSM).

Other Supporting Information Files

Dataset S1 (PDF)
Dataset S2 (PDF)

Harnessing values to save the rhinoceros: insights from Namibia

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Abstract The rate at which the poaching of rhinoceroses has escalated since 2010 poses a threat to the long-term persistence of extant rhinoceros populations. The policy response has primarily called for increased investment in military-style enforcement strategies largely based upon simple economic models of rational crime. However, effective solutions will probably require a context-specific, stakeholder-driven mix of top-down and bottom-up mechanisms grounded in theory that represents human behaviour more realistically. Using a problem-oriented approach we illustrate in theory and practice how community-based strategies that explicitly incorporate local values and institutions are a foundation for combating rhinoceros poaching effectively in specific contexts. A case study from Namibia demonstrates how coupling a locally devised rhinoceros monitoring regime with joint-venture tourism partnerships as a legitimate land use can reconcile individual values represented within a diverse stakeholder group and manifests as both formal and informal community enforcement. We suggest a social learning approach as a means by which international, national and regional governance can recognize and promote solutions that may help empower local communities to implement rhinoceros management strategies that align individual values with the long-term health of rhinoceros populations.

Keywords Community-based conservation, conservation tourism, incentives, poaching, policy, rhinoceros, values

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Introduction

The rate at which the poaching of rhinoceroses has escalated (Knight, 2012) since 2010 poses a threat to the long-term persistence of extant rhinoceros populations (Duffy et al., 2013). Resurgent global trade and unprecedented black market prices for rhinoceros horn are implicated as the major drivers of the killing (Ferreira & Okita-Ouma, 2012; Biggs et al., 2013). Although rhinoceros conservation scientists and practitioners promote a variety of strategies to safeguard the rhinoceros (Duffy et al., 2013), military-style law enforcement and demand reduction (Ferreira & Okita-Ouma, 2012; Biggs, 2013; Challender & MacMillan, 2014; IUCN et al., 2015) have dominated the response to protect Africa's remaining 20,000 white rhinoceros *Ceratotherium simum* and 5,000 black rhinoceros *Diceros bicornis*. Despite courageous efforts to combat poaching, and some positive trends in end-user behaviour (Coghlan, 2014), rhinoceros poaching rates continue to rise, with a reported 184% increase across Africa during 2008–2012 (Standley & Emslie, 2013). We investigated what and how community-based strategies make military-style protection more effective but also provide innovative, longer-term solutions that are more resilient to the changing type and magnitude of threat. We use the Namibian experience to make a case for rhinoceroses and other wildlife as a legitimate land use that embodies both collective and individual values, creating the social foundation that enforcement-based strategies require to be successful. This is preferable to the prioritization of military-style strategies, and more successful. Although we affirm that effective and reliable rhinoceros protection should be supported by governmental enforcement, we illustrate both in theory and practice that investing in community-based strategies that are founded explicitly on local values and rights, and facilitated through locally devised institutions, can improve our collective efforts to combat rhinoceros poaching.

What is the problem?

Rhinoceros poaching is a complex problem (Rittel & Webber, 1973; Brown et al., 2010) that is interconnected with other problems across multiple scales, making solutions elusive. Military-style protection strategies focus narrowly on poaching (Ferreira & Okita-Ouma, 2012) and often cause anger, resentment and a sense of disenfranchisement among local people (Dowie, 2009). This approach does not contextualize the problem, and reinforces fortress conservation, a product of Africa's late-colonial and independence history that reserved wild areas primarily for European leisure activities (Adams & Hulme, 2001; Brockington, 2002). Military-style protection, which is sometimes promoted by transnational conservation organizations (Dowie, 2009), tends to reinforce the benefits of biodiversity for powerful local and international elites. Fortress conservation has had significant political, social and cultural effects on indigenous people, including restricted access to, or exclusion from, both policy processes and areas important for their livelihood and cultural practices, and sometimes even physical relocation (Dowie, 2009). The erosion of culture, language and ultimately human dignity has resulted in retaliatory illegal hunting and other unsustainable use of resources, often referred to by conservationists as poaching (Sullivan & Homewood, 2004; Dowie, 2009). Thus, the response to conflict with local people, who are typically framed by conservationists as being part of the problem, has often been to tighten control through more weapons, fences and fines (Dowie, 2009). This approach has resulted in mistrust and a sense of alienation among local people, and established barriers that compromised local support for conservation; for example, resettlement plans for communities residing in Mozambique's Limpopo National Park caused anger and distrust (Dressler & Büscher, 2008; Milgroom & Spierenburg, 2008) and may have contributed to the upsurge in poaching in neighbouring South Africa's Kruger National Park. In some cases, measures to increase militarization of government-led enforcement and anti-poaching activity have undermined the efforts of conservationists working to build trust and cooperation with communities (IUCN et al., 2015).

The social injustices of fortress conservation have inhibited multi-stakeholder responses to the poaching problem. Addressing these injustices in the search for solutions will require a shift in the way practitioners orient themselves to natural resource management problems, and a broadening of perspective. Motivational instruments are fundamental in fostering positive changes in local attitudes and behaviours that align with conservation objectives and facilitate collective action (Berkes, 2004). Whereas the military-style approach to governance typically does not enrich or motivate local people, illicit trade and organized crime often do, to the extent that marginal increases in security investment and effectiveness are unlikely to be a significant deterrent; for example, a sworn affidavit from a poaching case in north-west Namibia indicates that poaching syndicates offer up to three times the mean annual household income (National Planning Commission, 2007) for a single set of rhinoceros horns. Models of speculative behaviour suggest that when in situ population numbers approach the minimum viable population size (as is the case with the black rhinoceros) it is more profitable for buyers to collude by employing a 'bank on extinction' strategy than to reduce consumption. Banking on extinction encourages an increase in poaching to extirpate the species in the wild while achieving a private stockpile monopoly scenario to maximize returns (Mason et al., 2012). Thus, without appropriate incentives to motivate compliance with government-imposed regulation and conservation objectives it is not surprising that in most cases local communities are unable or unwilling to stem the tide of organized criminal poaching, and are sometimes complicit in poaching activity. Lasting solutions depend on the availability of adequate resources, and changing the behaviour of local people in a manner that promotes rhinoceros conservation.

The poaching problem is often framed as a war against criminals, with response strategies seeking to catch poachers (Neumann, 2004). We suggest reframing the problem through two pragmatic questions: (1) What mix of instruments, incentives and institutions could maximize the values local people attach to conserving the rhinoceros? (2) Who decides how rhinoceroses are managed? This framing shifts the focus from militaristic to community-based approaches, acknowledging the complex systems in which multiple stakeholders operate. Solutions emanating from this approach will promote strategies that keep poaching from becoming a normative behaviour. We make a case for initiating behavioural change in local communities by developing an economic and socio-political relationship between the rhinoceros and local communities that harnesses human values to deliver greater return on investment for rhinoceros conservation initiatives.

Behavioural change: more than just deterrence

In addition to detection and prevention, military-style enforcement attempts to change behaviour by means of

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coercion, in the belief that threats and punishment will deter rule-breaking behaviour. Knowingly or not, these strategies are based on a simple model of rational crime; that is, crime results when an individual chooses to contravene rules where the benefits are perceived to be greater than the costs of their rule-breaking behaviour (Becker, 1968). When applied to rhinoceros poaching, this model assumes that poachers consider the anticipated financial benefits directly against the risk of being caught and the severity of potential punishment (Milner-Gulland & Leader-Williams, 1992). More recent expansions of the model explicitly incorporate a poacher's ability to calculate and trade-off the benefits of poaching against the likelihood of being shot and killed (Messer, 2010). However, observations and experimentation suggest that human behaviour, including acts of dishonesty, is typically not an outcome of a simple, rational cost–benefit analysis (Kahneman, 2011; Ariely, 2012; Shogren, 2012).

Criminal and dishonest behaviour in general is a product of influences more complex and fundamental to an individual's decision making than those comprising a purely rational economic cost-to-benefit trade-off. Values are the basic medium of exchange in all human interactions and underline the things and events that people desire and demand (Lasswell, 1971). People seek to shape and share values through exchanges structured on the norms embedded within societal institutions (Lasswell & Holmberg, 1992), which have a significant influence on behaviour (Keane et al., 2008; Kahler & Gore, 2012). Relationships, norms and values reduce the likelihood of individuals acting in their short-term self-interest (Ostrom, 2000). Mattson et al. (2012) provide an overview within a natural resource management and policy context of two dominant value concept schemes (Lasswell, 1943; Schwartz & Bilsky, 1987), with reference to Maslow's hierarchy of needs (Maslow, 1954). Each scheme has its own merits but we adopt Lasswell's policy-oriented value concept because it creates an explicit linkage between values and institutions, which we feel is critical in the context of rhinoceros conservation. Lasswell's value classification states human motivations are underpinned by personal, group and institutional values and can be categorized, regardless of age, gender, nationality or culture, as power, wealth, respect, well-being, affection, rectitude, skills or intelligence (Lasswell, 1971; Clark, 2002), and people use these base values to accumulate other sought-after values through institutions that use and have an impact on resources (Lasswell, 1971). Changing how the rhinoceros is valued, while developing or strengthening local institutions that embody these values, can become the basis for a shift in social norms, even after rhinoceros poaching has become a normative behaviour.

Other approaches that may be used to understand the complex factors that drive human behaviour include the theory of planned behaviour (Ajzen, 1991), value–belief–norm theory (Stern et al., 1999), and insights from conservation psychology on community-based social marketing (McKenzie-Mohr, 2000) and pro-environmental behaviour, including bounded rationality, willpower and self-interest (Steg & Vlek, 2009; Shogren, 2012). These may be applied to understand why poaching occurs and to design more effective and cost-efficient strategies for rhinoceros conservation.

Social capital is also critical to the power and continuity of social values and norms. Trust, cooperation and mutual support provide the foundation for the civil discourse required to secure solutions in the common interest (Putnam, 2000) and make values and norms explicit, agreed and observed. Social values, norms and capital commonly explain pro-environmental behaviour and collective action (Ostrom, 2000). Coercive deterrence of illicit behaviour does not harness the values and norms of local communities or have positive outcomes for social capital; for example, incarcerated community members can reduce social capital by breaking relationships or creating financial dependencies that may motivate retribution and retaliatory action. Strategies that recognize individual and communal values, harness normative behaviour, and invest in social capital are likely to hold greater promise for changing and sustaining pro-rhinoceros behaviour.

Increasing local intolerance to poaching

Top-down rule making and enforcement that ignores local norms and institutions can produce negative outcomes, particularly where government and law enforcement officials lack the necessary resources for effective implementation (Lejano et al., 2007). Conversely, monitoring and enforcement systems that are devised and build capacity at the local level have been found to be more successful over longer time periods (Berkes et al., 2006; Ostrom, 2007). Military-style responses are understandable and necessary but could deliver more effective conservation if they were motivated by and incorporated local values. A balance between top-down military-style strategies and bottom-up community-based mechanisms is needed to ensure behaviour in the common interest prevails over individuals' short-term financial gains. Fundamental to this rebalancing is the need for our understanding of human behaviour to be applied within a practical decision making framework. Engaging established frameworks from the policy sciences can provide a comprehensive understanding of rhinoceros poaching across multiple temporal and spatial scales (Clark, 2002).

Understanding the individual and community values that motivate pro-conservation behaviour is central to solving natural resource management problems. Common-interest solutions require that resources (e.g. rhinoceros horn) are used and managed through local institutions, which is a critical factor in reducing over-exploitation, excluding roving bandits (Ostrom, 1990; Berkes et al., 2006) and mobilizing local support for rhinoceros conservation. Thus, an optimal combination of instruments, incentives and institutions that promote pro-rhinoceros behaviour should ensure that community values and the institutions within which they are shaped and shared are maintained or enhanced.

Namibia's practice-based approach

Namibia's community-based natural resource management programme was founded and formalized in the mid 1990s following a series of socio-ecological surveys with residents of communal land, and policy reform that would return rights over wildlife and tourism to these residents through the establishment of a common property regime called a conservancy (Jones & Murphree, 2001). Based on Ostrom's design principles for effective, sustainable common property natural resource management institutions (Jones, 2010), Namibia's community-based natural resource management framework seeks to create conditions that promote pro-conservation behaviour by rural communities. This is achieved primarily through provision of property rights and incentives through locally accrued and distributed benefits from wildlife and tourism (MET, 2013). Benefits are typically realized in power-sharing or financial terms whereby rural residents registered with a gazetted conservancy receive clearly defined, conditional user rights over wildlife and tourism development (Jones et al., 2015). These devolved rights have been used to help secure significant local income and jobs. In 2013 communal conservancies received NAD 72,200,000 (c. USD 6.5 million) and facilitated 6,472 jobs through 167 joint ventures with conservancies (NACSO, 2014). To date, 79 conservancies have been registered in Namibia, incorporating 8.3% of the population (> 175,000 people) and 19.4% of the land area (c. 16 million ha; NACSO, 2014). Although not without criticism (Sullivan, 2002; Hoole, 2010), these conservancies have probably contributed to a decrease in poaching (Owen-Smith, 2010) and a general widespread increase in wildlife on communal land, including threatened mammals such as the black-faced impala *Aepyceros melampus petersi*, Hartmann's mountain zebra *Equus zebra hartmannae*, cheetah *Acinonyx jubatus*, lion *Panthera leo* and black rhinoceros (IUCN, 2014; NACSO, 2014).

Collaborative efforts to establish local value-based institutions that secure the common interest in conserving the black rhinoceros were initiated formally in north-west Namibia in the early 1980s (Owen-Smith, 2010) and included a locally devised and managed auxiliary game guard system (Loutit & Owen-Smith, 1989). A series of stakeholder engagement workshops helped strengthen the foundation for long-term strategic partnerships between government, local communities, NGOs and, more recently, private-sector tourism operators, based on a recognition and understanding of local values, perspectives and desired outcomes for rhinoceros conservation (Hearn et al., 2004). Namibia's community-oriented approach has helped to instil in local communities a sense of ownership and acceptance of the rhinoceros, despite all black rhinoceroses being owned by the state (!Uri-≠Khob, 2004).

In 2005 the innovative Rhino Custodianship Programme established by Namibia's Ministry of Environment and Tourism spearheaded a large-scale initiative to achieve biological management and rural development goals by restoring the black rhinoceros to its historical rangelands while meeting an emerging demand from local communities to engage in rhinoceros tourism (!Uri-≠Khob et al., 2010). This provided an opportunity to strengthen existing local values and institutions that supported rhinoceros conservation, demonstrated by the government's willingness to share key values identified by communities, including power (through the establishment of co-management institutions that have granted custodial rights to landholders or communal conservancies that wish to utilize the rhinoceros for tourism on their land), wealth (through rights for local people to benefit from non-consumptive use of rhinoceroses, without any requirement to share profits with central government) and respect (through assigning joint responsibility for local conservation activities). Other values sought by local people, notably skills, knowledge and well-being, have been fulfilled through partnerships with local and international NGOs, and with tourism operators that have contributed towards rhinoceros conservation, especially through co-financing rhinoceros monitoring. Since the reform of Namibia's community-based conservation policy in the mid 1990s (Owen-Smith, 2010), and the adoption and expansion of joint-venture tourism enterprises, the rhinoceros population has more than doubled (Beytell & Muntifering, 2009) and sustained consistent positive growth rates (Brodie et al., 2011) despite persisting almost entirely on formally unprotected lands. Although 51% of the rhinoceros population persists on communal conservancy land, only 4 of the 18 confirmed incidents of poaching in 2014 occurred in these areas (Muntifering et al., 2015).

Designing a tourism product that serves as an effective community-based conservation mechanism requires reconciling the individual values of a diverse group of stakeholders, in particular those of local communities. The rhinoceros tourism model developed in north-west Namibia has evolved through learning what approaches are effective in practice, and through an inclusive and comprehensive decision making process. Aligned with conservation tourism principles (Buckley, 2010), best practices have been developed to minimize disturbance of rhinoceroses, maintain tourist satisfaction, and sustain sufficient profit to produce net conservation benefits. Allowing local

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trackers to showcase their tracking skills and local knowledge has instilled a sense of pride in traditional skills and rhinoceros protection. In one conservancy, benefits from rhinoceros tourism have significantly improved local attitudes towards rhinoceroses (/Uiseb, 2007), and intolerance of poaching has contributed towards formal and informal community enforcement. In December 2012 a rhinoceros poacher was identified, apprehended, arrested and had a firearm and horns confiscated within 24 hours of the discovery and immediate reporting of the carcass by a local farmer near the north-east boundary of the Palmwag Tourism Concession Area. Tourism initiatives currently finance ongoing monitoring of 25% of Namibia's north-west free-ranging rhinoceroses. Of the 18 confirmed cases of rhinoceros poaching that have occurred in north-west Namibia during 2012–2014, none were in an area where rhinoceros tourism is practised, or in a conservancy wildlife tourism area with permanent activity and direct benefit-sharing agreements between the private sector operator and the host conservancy.

As the demand for rhinoceros tourism opportunities increases it will become essential to design and implement benefit-sharing mechanisms that ensure security, quality monitoring, and community support for rhinoceroses. One promising policy intervention that has emerged through an extended social context mapping of local values (Clark, 2002) has been the development of a conservancy-led rhinoceros ranger initiative. Since 2012 26 rangers have been appointed by and accountable to 13 communal conservancies. These Conservancy Rhino Rangers have been provided with training, state-of-the art monitoring equipment and field gear, and performance-based bonus payments to improve the quantity and quality of conservancy-led rhinoceros patrols (Muntifering et al., 2015). The number of trained, equipped rhinoceros monitoring personnel in Namibia's north-west has tripled since 2012 and the number of conservancies actively engaged in monitoring has increased twelve-fold; in 2014 there were 1,013 ranger patrol days and 727 rhinoceros sightings by rangers in the 13 participating conservancies.

The sustainability of the initiative will depend on an institutional arrangement ensuring that the benefits from rhinoceros tourism return to the conservancy. Under a user-pays principle the local communities that bear the monitoring and opportunity costs of rhinoceros conservation would receive royalty payments. The initiative would thus not only enhance the quality and quantity of community-led monitoring efforts but would also reinforce rhinoceros tourism as a legitimate and profitable land use. Successful implementation will require an integrated, comprehensive, inclusive and transparent decision-making process that includes planning, open debate, and setting rules and guidelines that secure the common interest (Clark, 2002). Rigorous appraisals of contextual, practice-based prototypes will help facilitate the identification of best practices (Hohl & Clark, 2010), quantify causal effects (Ferraro & Hanauer, 2014), and apply lessons learned to evolving contexts.

Let the locals lead

Understanding local perspectives and values is fundamental to solving complex natural resource management problems effectively (Clark, 2002). Yet the top-down command and control approach, with associated emphasis on military-style regulatory and enforcement strategies, continues to drive the discourse in the search for solutions to poaching (Biggs, 2013; Challender & MacMillan, 2014). We recognize that law enforcement is critical to effective prevention of wildlife crime but our experience in Namibia suggests that bolstering investments that seek to engage and empower local communities in rhinoceros protection efforts will probably yield greater returns than continuing to focus narrowly on fighting fire with fire. However, shifting our priorities will probably require a reassessment of how we orient ourselves to the poaching problem and the theories we apply towards devising strategies. To do this we need to unlearn much of what traditional economic theory and the simple model of rational crime have taught us regarding how people think and behave, by acknowledging the evidence, embracing new insights on human decision making from behavioural economics and applying them to conservation problems (Cowling, 2014). By refocusing from a simplistic cost–benefit world view to incorporating cognitive, emotional and social factors, in particular values and institutions, to drive behavioural change, longer-term solutions can be developed.

We have argued for the role of values, norms, social capital and institutions in changing the pay-off structures of wildlife crime, and illustrated its application in north-west Namibia. Although much of the theory is universally transferable in terms of both location and target species, it should be noted that this case study is context-specific and may be influenced by contextual factors such as the region's high tourism draw, low human population density, arid and rugged terrain less suitable for domestic livestock, and cohesive social and institutional networks. Replication in other locations may be confounded by different political, social and ecological environments. We therefore emphasize that harnessing local community values to save the rhinoceros should not be viewed as a universal panacea for poaching but rather as a fundamental factor that provides the necessary social foundation for other policy instruments, incentives and institutions (Young & Gunningham, 1997). Policies that do not engage, empower and benefit local communities living alongside rhinoceroses will have limited success. We assert the fundamental importance of letting the locals lead (Smith et al., 2009), as it has been demonstrated that the long-term effectiveness of biodiversity conservation programmes depends on the support of local people, the ability to harness local knowledge and cooperative capacity, and the degree to which solutions are devised and owned by local people (Young & Gunningham, 1997; Ostrom, 2000, 2007; Berkes, 2004; Lejano et al., 2007; Brooks et al., 2012).

Although solutions ultimately depend on creating and sustaining pro-rhinoceros behaviour at the local level, the problem must be addressed at multiple scales (Berkes, 2007). International, regional, national (notably major horn markets and rhinoceros range countries) and local governance bodies need to recognize and promote local governance and resource rights regimes that align individual self-interest with the long-term health of rhinoceros populations (Berkes et al., 2006). This may best be achieved through a social learning process that disseminates information on a regular basis to solve the problem in a way that is consistent with local practices. Such a multi-tiered approach will help design and deliver bottom-up strategies underpinned by human values and facilitated through local institutions that, when combined with top-down regulation, will be more effective in securing a future for the rhinoceros.

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Biographical sketches

Jeff Muntifering is a conservation biologist who has worked on community-based rhinoceros conservation in Namibia for 12 years. Wayne Linklater's research focuses on the ecology, behaviour and management of wildlife. Susan Clark is an expert on policy science. Simson !Uri-≠Khob leads rhinoceros monitoring operations. John Kasaona works to improve community-based conservation strategies. Kenneth /Uiseb has researched community attitudes towards rhinoceroses. Pierre Du Preez is Namibia's National Rhino Coordinator. Kapoi Kasaona has worked in rhinoceros conservation and tourism. Petrus Beytell's research focuses on rhinoceros, lion and crocodile ecology. Jermain Ketji leads community engagement for private-sector tourism. Boas Hambo is a guide and leads the Rhino Ranger Support Group. Matthew Brown is Conservation Director for The Nature Conservancy's Africa Programme. Chris Thouless leads support services for community conservation projects. Shayne Jacobs' research focuses on ecosystem ecology. Andrew Knight's research focuses on improving conservation-related decision making.

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Population and Habitat Viability Assessment (PHVA)
Workshop Process Reference Packet

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About CBSG

The Conservation Breeding Specialist Group (CBSG) (www.cbsg.org) is a global volunteer network of over 500 conservation professionals, coordinated by a headquarters staff of six and assisted by nine Regional and National Networks on six continents. This network is dedicated to saving threatened species by increasing the effectiveness of conservation efforts worldwide. CBSG is recognized and respected for its use of innovative, scientifically sound, collaborative processes that bring together people with diverse perspectives and knowledge to catalyze positive conservation change. CBSG is a part of the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN), and is supported by a non-profit organization incorporated under the name Global Conservation Network.

Since its inception in 1979, CBSG has assisted in the development of conservation plans involving over 190 species through more than 340 workshops held in 67 countries. CBSG has collaborated with more than 180 zoos and aquariums, 150 conservation non-governmental organizations (NGOs), 60 universities, 45 government agencies, and 30 corporations. By applying unique conservation tools, and training others in their use, CBSG contributes to the long-term sustainability of endangered species and ecosystems around the globe.

Our Approach to Conservation

CBSG promotes effective and comprehensive conservation action by emphasizing the exchange of information across diverse groups to reach agreement on the important challenges facing humans and wildlife. Our interactive, participatory workshops provide an objective environment, expert knowledge, and thoughtful group facilitation designed to systematically analyze problems and develop focused solutions using sound scientific principles. This process enables workshop participants to produce meaningful and practical management recommendations that generate political and social support for conservation action at all levels – from local communities to national political authorities. Rapid dissemination of these recommendations allows them to be used almost immediately to influence stakeholders and decision-makers, and maintains the momentum generated at the workshop.

CBSG Regional Networks

Regional Networks take CBSG tools and principles deep into the local institutions of a region or country, allowing stakeholders to work with our basic conservation techniques and adapt them to meet their own needs. This level of freedom to shape a Network according to the needs of the culture, society, and services of the individual country or region is a requirement for success. Regional and National Networks of CBSG are not just desirable but necessary due to the sheer magnitude of the problem of biodiversity loss on this planet, as

IUCN

The International Union for Conservation of Nature (IUCN) (www.iucn.org) brings together states, government agencies, and a diverse range of nongovernmental organizations in a unique world partnership that seeks to influence, encourage and assist societies throughout the world in conserving the integrity and diversity of nature and to ensure that any use of natural resources is equitable and ecologically sustainable.

SSC

The Species Survival Commission (www.iucn.org/about/work/programmes/species) is the largest of IUCN's six volunteer Commissions, with a global membership of 8,000 experts. SSC advises IUCN and its members on the wide range of technical and scientific aspects of species conservation and is dedicated to securing a future for biodiversity.

well as to address the diversity in environment, culture, economic conditions, governance, and philosophies encountered in different countries and regions.

Species Conservation Planning: Our Philosophical Approach

Traditional approaches to endangered species conservation planning have tended to emphasize our lack of information and the need for additional research. This has been coupled with a hesitancy to make explicit risk assessments of species status, and a reluctance to specify immediate or non-traditional management recommendations. The result has been long delays in preparing action plans, loss of momentum, and dependency on crisis-driven actions or broad recommendations that do not provide useful guidance to management authorities. Furthermore, there is a lack of generally accepted tools to evaluate the interaction of biological, physical, and social factors affecting the population dynamics of threatened species and populations. Consequently, we recognize an urgent need for tools and processes to characterize such things as: the risk of species and habitat extinction; the possible impacts of future events on populations; the predicted effects of management interventions on future population stability; and how to develop and sustain learning-based cross-institutional management programs.

Effective conservation action is best built upon a synthesis of available biological information, but is dependent on actions of humans living within the range of the threatened species, as well as established national and international interests. In this context, we also observe deficiencies in conservation planning methods when we view the system through the lens of sociological dynamics. Local management agencies, external consultants, or local experts will often identify endangered species management actions that have a heavy emphasis on traditional principles of wildlife biology and ecology. However, these isolated and narrow professional approaches seem to have little effect on the political and social changes required for effective collaborative management of threatened species and their habitat. This focused, disciplinary approach is a natural consequence of our specialist academic training, but usually fails to produce truly integrated solutions that will appeal to a broad domain of stakeholders and – more importantly – achieve more effective conservation of biodiversity.

Recognizing these complex issues and needs related to endangered species conservation planning, CBSG has nearly 20 years of experience in developing, testing and applying a series of scientifically based tools and processes to facilitate and improve risk characterization and species management decision-making. These tools are rooted in the more traditional conservation scientific disciplines of population biology, genetics, and ecology, but are also explicitly linked to methods based in the dynamics of social learning. Information is analyzed and recommendations are made in intensive, problem-solving workshops to produce realistic and achievable recommendations for both *in situ* and *ex situ* population management.

Our workshop processes provide an objective environment, expert knowledge, and neutral facilitation that support the sharing of information across institutions and stakeholder groups, fostering agreement on the issues and information, and enabling stakeholder groups to make useful and practical management recommendations for the taxon and habitat system under consideration. This approach has been quite successful in unearthing and integrating previously unpublished information that is frequently of great value to the decision making process. The constant refinement, expansion, and heuristic value of the CBSG workshop processes have made them imaginative and productive tools for species conservation planning (Conway 1995; Byers and Seal 2003; Westley and Miller 2003).

There are characteristic patterns of human behavior that are cross-disciplinary and cross-cultural which affect the processes of communication, problem-solving, and collaboration. Some of these characteristic behavior patterns show themselves in:

- the acquisition, sharing, and analysis of information pertinent to the conservation needs of the situation;
- the perception and characterization of risk to the species in question resulting from human activities;
- the development of trust among individuals (stakeholders) tasked with conservation planning; and
- 'territoriality' (personal, institutional, local, national) that impedes effective collaboration.

Each of these patterns has strong emotional components that shape our interactions. CBSG's recognition of these patterns has been essential in the development of processes to assist people in working groups to reach agreement on needed conservation actions, to identify collaborative structures required to implement those actions, and to establish new working relationships.

CBSG workshops are organized to bring together the full range of stakeholders who share a strong interest in the conservation and management (or the consequence of such management) of a species in its habitat. One goal in all workshops is to reach a common understanding of the scientific knowledge available and its possible application to the decision-making process and to needed management actions. We have found that a workshop process driven by practical decision-making – replete with risk characterization methods, stochastic simulation modeling, management scenario testing, and deliberation among stakeholders – can be a powerful tool for extracting, assembling, and exploring information. This workshop process encourages the development of a shared understanding across a broad spectrum of training and expertise. These tools also support the creation of working agreements and instilling local ownership of the conservation problems at hand and the management decisions and actions required to mitigate those problems. As participants work as a group to appreciate the complexity of the conservation problems at hand, they take ownership of the process and of the ultimate management recommendations that emerge. This is essential if the management recommendations generated by the workshops are to succeed.

CBSG's interactive and participatory workshop approach supports and promotes effective conservation by fostering the creation of species management plans and the political and social support of the local people needed to implement these plans. In addition, simulation modeling is an important tool in this process, and provides a platform for testing assumptions, data quality, and alternative management scenarios. Workshop participants recognize that the present science is imperfect, and that management policies and actions need to be designed as part of a biological and social learning process. The CBSG workshop process provides a means for designing and implementing management plans and programs on the basis of sound science, while allowing new information and unexpected events to be used for learning and to adjust management practices.

The PHVA Workshop Process: An Introduction

Probably the most widely recognized workshop process conducted by CBSG is the Population and Habitat Viability Assessment, or PHVA. At its most basic level, the PHVA workshop process is based upon an explicit integration of biological and sociological science. Its closest intellectual relative – and the methodology from which its own name is derived – is the process of population viability analysis, or PVA. Population viability analysis describes a suite of quantitative methods used for evaluating extinction risk and informing strategic management planning for species threatened by human activities. PVA has been widely recognized as an important tool in the arsenal of the conservation biologist and natural resource manager. However, the methodology is often limited in its practical application because of its use within a narrow biological context, largely ignoring important information from other disciplines and perspectives that can enhance the input to the PVA as well as expand the utility of the recommendations that come from detailed analysis of the output.

The PHVA workshop process designed by CBSG directly addresses this important issue. The PHVA combines traditional PVA methodologies – most notably, the use of computer simulation models of the extinction process in small populations of threatened species – with structured tools for issue formulation and problem solving among a group of engaged workshop participants from a broad range of disciplines. Through this integrative process, stakeholders develop more effective recommendations for species conservation action, including the identification of personal responsibilities and timelines for action to ensure that the recommendations agreed upon by the participants become reality.

In general, each 3-4 day PHVA workshop process is defined by the following five elements:

- A pre-workshop planning phase, where broad workshop goals are identified, the workshop venue is chosen, critical participants (stakeholders) are identified and invited, and briefing materials are collected and distributed. More recently, this phase often includes the construction and interpretation of preliminary PVA simulation models that will form the basis of a comparative risk assessment conducted at the workshop itself.
- A workshop phase I – opening session, where local officials open the workshop, experts give short presentations on biological and sociological aspects of conservation of the focal species, and CBSG facilitators provide background material on workshop structure and process.
- A workshop phase II – working session, where participants typically function within small working groups defined by specific problems/topics. Working group activity focuses on problem analysis, information assembly, and formulating detailed recommendations. Interactions among groups, including those experts conducting the quantitative risk assessment using data and alternative management scenarios assembled by the other groups, is enhanced by periodic report-back in full plenary sessions. Each group creates a detailed report of their discussions and recommendations, which become the main components of the workshop report to be produced later (see below).
- A workshop phase III – closing session, where final recommendations are presented by each working group for acceptance by the full body of participants. Specific steps to be taken after the workshop are discussed and outlined by all in attendance.
- A post-workshop report production phase, where workshop organizers (in close consultation with CBSG staff) produce a draft report that is then sent to key participants for review and revision. The final report is then produced and distributed to all workshop participants and other interested parties.

To date, CBSG has conducted more than 180 PHVA workshops in nearly 40 countries. This statistic points to the robust nature of the process outlined above, which can be adapted to the specific cultural, linguistic, and sociopolitical environment within which the focal species is located. Reports from many of these workshops can be obtained online at www.cbsg.org.

Each of the two primary elements of a PHVA workshop – quantitative population viability analysis and participatory decision-making in a structured and facilitated environment – will be discussed in more detail in the following sections.

The PHVA Workshop Process: Quantitative Risk Assessment

Introduction

Thousands of species and populations of animals and plants around the world are threatened with extinction within the coming decades. For the vast majority of these taxa, this threat is the direct result of human activity. The particular types of activity, and the ways in which they impact wildlife populations, are often complex in both cause and consequence; as a result, the techniques we must use to analyze their effects often seem to be complex as well. But scientists in the field of conservation biology have developed extremely useful tools for this purpose, dramatically improving our ability to conserve the planet's biodiversity.

Conservation biologists involved in recovery planning for a given threatened species usually try to develop a detailed understanding of the processes that put the species at risk, and will then identify the most effective methods to reduce that risk through active management of the species itself and/or the habitat in which it lives. In order to design such a program, we must engage in some sort of predictive process: we must gather information on the detailed characteristics of proposed alternative management strategies and somehow predict how the threatened species will respond in the future. A strategy that is predicted to reduce the risk by the greatest amount – and typically does so with the least amount of financial and/or sociological burden – is chosen as a central feature of the recovery plan.

But how does one predict the future? Is it realistically possible to perform such a feat in our fast-paced world of incredibly rapid and often unpredictable technological, cultural, and biological growth? How are such predictions best used in wildlife conservation? The answers to these questions emerge from an understanding of what has been called "the flagship industry" of conservation biology: population viability analysis, or PVA. Most methods for conducting PVA are merely extensions of tools we all use in our everyday lives.

The Basics of PVA

To appreciate the science and application of PVA to wildlife conservation, we first must learn a little bit about population biology. Biologists will usually describe the performance of a population by describing its demography, or simply the numerical depiction of the rates of birth and death in a group of animals or plants from one year to the next. Simply speaking, if the birth rate exceeds the death rate, a population is expected to increase in size over time. If the reverse is true, our population will decline. The overall rate of population growth is therefore a rather good descriptor of its relative security: positive population growth suggests some level of demographic health, while negative growth indicates that some external process is interfering with the normal population function and pushing it into an unstable state.

This relatively simple picture is, however, made a lot more complicated by an inescapable fact: wildlife population demographic rates fluctuate unpredictably over time. For example, if we declare that, after some numbers of years of direct field study, an average of 50% of our total population of adult females are expected to produce offspring annually, it is quite likely that the number of adult females breeding in any one particular year **will not** be exactly 50%. The same can be said for most all other demographic rates: survival of offspring and adults, the numbers of offspring born, and the offspring sex ratio will almost always change from one year to the next in a way that usually defies precise prediction. These variable rates then conspire to make a population's growth rate also change unpredictably from year to year. When wildlife populations are very large – if we consider seemingly endless herds of wildebeest on the savannahs of Africa, for example – this random annual fluctuation in population growth is of little to no consequence for the future health and stability of the population. However, theoretical and practical study of population biology has taught us that populations that are already small in size (often defined in terms of tens to a few hundred individuals) are affected by these fluctuations to a much greater extent – and the long-term impact of these fluctuations is always negative. Therefore, a wildlife population that has been reduced in numbers will become even smaller through this fundamental principle of wildlife biology. Furthermore, our understanding of this process provides an important backdrop to considerations of the impact of human activities that may, on the surface, appear relatively benign to larger and more stable wildlife populations. This self-reinforcing feedback loop, first coined the "extinction vortex" in the mid-1980's, is the cornerstone principle underlying our understanding of the dynamics of wildlife population extinction.

Once wildlife biologists have gone out into the field and collected data on a population's demography and used these data to calculate its current rate of growth (and how this rate may change over time), we now have at our disposal an extremely valuable source of information that can be used to predict the *future* rates of population growth or decline under conditions that may not be so favorable to the wildlife population of interest. For example, consider a population of primates living in a section of largely undisturbed Amazon rain forest that is now opened up to development by logging interests. If this development is to go ahead as planned, what will be the impact of this activity on the animals themselves, and the trees on which they depend for food and shelter? And what kinds of alternative development strategies might reduce the risk of primate population decline and extinction? To try to answer this question, we need two additional sets of information: 1) a comprehensive description of the proposed forest development plan (how will it occur, where will it be most intense, for what period of time, etc.) and 2) a detailed understanding of how the proposed activity will impact the primate population's demography (which animals will be most affected, how strongly will they be affected, will animals die outright more frequently or simply fail to reproduce as often, etc.). With this information in hand, we have a vital component in place to begin our PVA.

Next, we need a predictive tool – a sort of crystal ball, if you will, that helps us look into the future. After intensive study over nearly three decades, conservation biologists have settled on the use of computer simulation models as their preferred PVA tool. In general, models are any simplified representation of a real system. We use models in all aspects of our lives; for example, road maps are in fact relatively simple (and hopefully very accurate!) 2-dimensional representations of complex 3-dimensional landscapes we use to get us where we need to go. In addition to making predictions about the future, models are very helpful for us to: i) extract important trends from complex processes, ii) allow comparisons among different types of systems, and iii) facilitate analysis of processes acting on a system.

Recent advances in computer technology have allowed us to create very complex models of the demographic processes that define wildlife population growth. But at their core, these models attempt to replicate simple biological functions shared by most all wildlife species: individuals are born, some grow to adulthood, most of those that survive mate with individuals of the opposite sex and then give birth to one or more offspring, and they die from any of a wide variety of causes. Each species may have its own special set of circumstances – sea turtles may live to be 150 years old and lay 600 eggs in a single event, while a chimpanzee may give birth to just a single offspring every 4-5 years until the age of 45 – but the fundamental biology is the same. These essential elements of a species' biology can be incorporated into a computer program, and when combined with the basic rules for living and the general characteristics of the population's surrounding habitat, a model is created that can project the demographic behavior of our real observed population for a specified period of time into the future. What's more, these models can explicitly incorporate the random fluctuations in rates of birth and death discussed earlier in this section. As a result, the models can be much more realistic in their treatment of the forces that influence population dynamics, and in particular how human activities can interact with these intrinsic forces to put otherwise relatively stable wildlife populations at risk.

Many different software packages exist for the purposes of conducting a PVA. Perhaps the most widely-used of these packages is *VORTEX*, developed by CBSG for use in both applied and educational environments. *VORTEX* has been used by CBSG and other conservation biologists for more than 15 years and has proved to be a very useful tool for helping make more informed decisions in the field of wildlife population management.

VORTEX Simulation Model Timeline

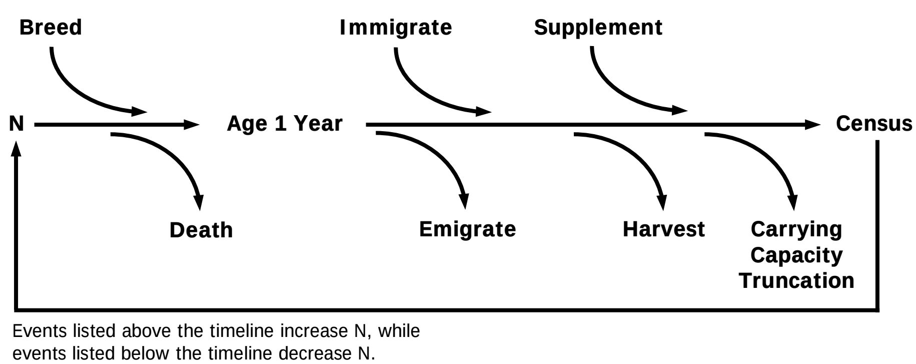

Figure 1. Simple timeline of components that make up a typical one-year timestep in the PVA package *VORTEX*. Population size N is calculated based on additions of individuals through births, immigration and supplementation from an outside source, and removals through mortality, emigration, harvest, and truncation to below ecological carrying capacity.

The *VORTEX* Population Viability Analysis Model

VORTEX models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. *VORTEX* also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations (Figure 1).

Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. The carrying capacity can be specified to change linearly over time, to model losses or gains in the amount or quality of habitat. Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size.

VORTEX models loss of genetic variation in populations by simulating the transmission of alleles from parents to offspring at a hypothetical genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. During the simulation, *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or "expected heterozygosity") relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

VORTEX is an *individual-based* model. That is, *VORTEX* creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *VORTEX* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of these events occur. Events occur according to the specified age and sex-specific probabilities. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because *VORTEX* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

Further information on *VORTEX* is available in Lacy (2000) and Miller and Lacy (2005).

Strengths and Limitations of the PVA Approach

When considering the applicability of PVA to a specific issue, it is vitally important to understand those tasks to which PVA is well-suited as well as to understand what the technique is not well-designed to deliver. With this enhanced understanding will also come a more informed public that is better prepared to critically evaluate the results of a PVA and how they are applied to the practical conservation measures proposed for a given species or population.

The dynamics of population extinction are often quite complicated, with numerous processes impacting the dynamics in complex and interacting ways. Moreover, we have already come to appreciate the ways in which demographic rates fluctuate unpredictably in wildlife populations, and the data needed to provide estimates of these rates and their annual variability are themselves often uncertain, i.e., subject to observational bias or simple lack of detailed study over relatively longer periods of time. As a result, the elegant mental models or the detailed mathematical equations of even the most gifted conservation biologist are inadequate for capturing the detailed nuances of interacting factors that determine the fate of a wildlife population threatened by human activity. In contrast, simulation models can include as many factors that influence population dynamics as the modeler and the end-user of the model wish to assess. Detailed interactions between processes can also be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes.

PVA models have also been shown to stimulate meaningful discussion among field biologists in the subjects of species biology, methods of data collection and analysis, and the assumptions that underlie the analysis of these data in preparation for their use in model construction. By making the models and their underlying data, algorithms, and assumptions explicit to all who learn from them, these discussions become a critical component in the social process of achieving a shared understanding of a threatened species' current status and the biological justification for identifying a particular management strategy as the most effective for species conservation. This additional benefit is most easily recognized when PVA is used in an interactive workshop-type setting, such as the Population and Habitat Viability Assessment (PHVA) workshop designed and implemented by CBSG.

Perhaps the greatest strength of the PVA approach to conservation decision-making is related to what many of its detractors see as its greatest weakness. Because of the inherent uncertainty now known to exist in the long-term demography of wildlife populations (particularly those that are small in size), and because of the difficulties in obtaining precise estimates of demographic rates through extended periods of time collecting data in the field, accurate predictions of the future performance of a threatened wildlife population are effectively impossible to make. Even the most respected PVA practitioner must honestly admit that an accurate prediction of the number of mountain gorillas that will roam the forests on the slopes of the eastern Africa's Virunga Volcanoes in the year 2075, or the number of polar bears that will swim the warming waters above the Arctic Circle when our great-grandchildren grow old, is beyond their reach. But this type of difficulty, recognized across diverse fields of study from climatology to gambling, is nothing new: in fact, the Nobel Prize-winning physicist Niels Bohr once said "Prediction is very difficult, especially when it's about the future." Instead of lamenting this inevitable quirk of the physical world as a fatal flaw in the practice of PVA, we must embrace it and instead use our very cloudy crystal ball for another purpose: to make **relative**, rather than **absolute**, predictions of wildlife population viability in the face of human pressure.

The process of generating relative predictions using the PVA approach is often referred to as <u>sensitivity analysis</u>. In this manner, we can make much more robust predictions about the relative response of a simulated wildlife population to alternate perturbations to its demography. For example, a PVA practitioner may not be able to make accurate predictions about how many individuals of a given species may persist in 50 years in the presence of intense human hunting pressure, but that practitioner can speak with considerably greater confidence about the relative merits of a male-biased hunting strategy compared to the much more severe demographic impact typically imposed by a female-biased hunting strategy. This type of comparative approach was used very effectively in a PVA for highly threatened populations of tree kangaroos (*Dendrolagus* sp.) living in Papua New Guinea, where adult females are hunted preferentially over their male counterparts. Comparative models showing the strong impacts of such a hunting strategy were part of an important process of conservation planning that led, within a few short weeks after a participatory workshop including a number of local hunters (Bonaccorso et al., 1999), to the signing of a long-term hunting moratorium for the most critically endangered species in the country, the tenkile or Scott's tree kangaroo (*Dendrolagus scottae*).

PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models often underestimate the threats facing the population, or the total risk these threats collectively impose on the population of interest. To address this limitation, conservation biologists must try to engage a diverse body of experts with knowledge spanning many different fields in an attempt to broaden our understanding of the consequences of interaction between humans and wildlife.

Additionally, models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed (see Lacy and Miller (2002), Nyhus et al. (2002) and Westley and Miller (2003) for more details).

Finally, it is also important to understand that a PVA model by itself does not define the goals of conservation planning of a given species. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance, must be defined by the management authorities before the results of population modeling can be used.

PVA and PHVA

While sounding quite similar in their acronyms, the generalized technique of population viability analysis and CBSG's workshop process known as Population and Habitat Viability Assessment (PHVA) have important differences that help us understand how each of them can be best used in conserving threatened biodiversity. A PVA is an analytical technique that is typically used to assess the current risk of decline or extinction of a given plant or animal population, and to investigate the most likely response of the population to changes in its rates of reproduction or survival from one year to the next. This investigation is conducted most effectively through the use of computer simulation models, and uses information gathered over many years by field researchers on the biological characteristics of the populations under study. These analyses can become quite complex and, therefore, they often remain in the confines of the conservation science community.

CBSG's Population and Habitat Viability Assessment, or PHVA, represents a significant extension of the more traditional PVA approach into the realm of practical conservation decision-making. Where a PVA is conducted with the expertise of population ecologists and geneticists and focuses intensively on the dynamics of population extinction, a typical PHVA workshop includes representatives and perspectives from a much more diverse body of interested parties, or stakeholders. These stakeholders utilize the results from a PVA analysis – performed during or immediately before the PVHA workshop – to improve the rigor and utility of very practical recommendations designed to effectively conserve the species or population that is the focus of the workshop. An outstanding example of effectively using a diversity of information to inform a PVA came in 1998 when local village chieftains and hunters were among those participating in the Papua New Guinea tree kangaroo PHVA workshop (Bonaccorso et al. 1999). Participatory Rural Appraisal (PRA) methods were used to determine the specifics of how these villagers hunted local tree kangaroos for food, with a special focus on the most endangered species known as the tenkile, or Scott's tree kangaroo. This information was not available from the standard scientific/academic community, instead residing as traditional knowledge in the communities that lived with the species. When incorporated into PVA models of tree kangaroo population dynamics, participants concluded that the hunting practices were unsustainable, and extinction of the tenkile was imminent unless drastic conservation measures were taken. Just weeks after the workshop, local village representatives signed a moratorium on tenkile hunting, and an Australian organization began working with the villages to adopt domestic animal farming as an alternative – and sustainable – protein source for the region. The moratorium is in effect to this day, and preliminary data indicate that the tenkile population is beginning to show signs of recovery. Without the input provided by those outside of the scientific community, the value of the analysis would have been greatly diminished.

In addition to the focused discussions on population dynamics, other discussions focusing on vital aspects of species conservation, such as legal issues, social acceptance, and human-wildlife interactions, form the basis of facilitated interactions between participants to a PHVA. So, the PVA forms the analytical "core" of the PHVA workshop, with expert participants from various disciplines encouraged to guide the use of the PVA models and adapt the results of the risk assessment to fit their own situations and needs as they develop species and habitat conservation strategies.

Perhaps the most visible difference between a PVA and a PHVA is in the number of experts needed to conduct one. A PVA can and often is completed by a single population biologist working with data gleaned from published sources. CBSG members and staff sometimes provide PVA consultant services, as do many other population biologists skilled in the modeling techniques. In contrast, a PHVA cannot be conducted by a single scientist, because by definition it involves the synthesis of concerns, ideas, data, and proposed conservation solutions from not only a range of population biologists, but also wildlife and land managers, social scientists, and others with knowledge needed for crafting a successful conservation plan for the species.

The PHVA Workshop Process: Design and Facilitation

Introduction

As discussed in the preceding section, a PHVA workshop is not defined merely by the presence of a stochastic simulation model of wildlife population dynamics. A broad diversity of stakeholders must be present to discuss a wide array of important topics affecting the future of the species, and the flow of information and ideas emanating from those experts must be assembled and managed in such a way that the group's productivity is maximized. These elements of successful collaboration can only be achieved through proper attention to workshop design and process facilitation. Westley and Byers (2003) refer to this process as "getting the right science and getting the science right". For our purposes here, we define *workshop design* as the construction of a chain of interactional tasks or elements that, when completed in their entirety, will help the participants achieve a predetermined workshop outcome that, in the case of a PHVA workshop, is the production of a species conservation management plan. Similarly, we define *facilitation* as the active management of the workshop process by trained individuals so that the participants can realize the workshop's objectives.

Workshop Design: Stakeholders

Once the workshop objectives and outcome have been clearly defined and understood by all involved in its organization, a critical first step in workshop design is the identification of key participants. A stakeholder is often defined by three primary characteristics:

- <u>Concern</u> – somebody with interest in the discussions around management of the focal species and the outcome of the PHVA workshop;
- <u>Expertise</u> – somebody with information or resources available to contribute to the workshop; and
- <u>Power</u> – somebody with the authority to support or block recommendations resulting from the workshop.

Ignoring any one of these characteristics will result in an erosion of collaborative spirit, a weak risk assessment of projected human impacts, or a degraded base of support for implementing important species conservation actions. Each one of these failures can seriously compromise the success of a PHVA workshop. Including a large diversity of stakeholders offers the greatest opportunity for creative collaboration – but also can mean a stiff challenge for a facilitator who is responsible for keeping all interested parties moving intellectually in the same direction. To do this, it is vitally important for all stakeholders to seek common ground in their deliberations around species conservation management issues.

Workshop Facilitation: The Divergent – Convergent Thinking Cycle

A basic principle of the PHVA workshop process is to encourage creative thinking around identification of alternative management options and the many ways in which they may be carried out. At the same time, the participants must use specific tools that assist them in choosing the best options in the spirit of action-based planning. The ideal workshop design explicitly includes at least three cycles of this type of convergent – divergent thinking (Figure 2). A variety of specific tools are introduced during a PHVA by the facilitator to help guide the participants through the appropriate element of the workshop design. A typical broad workshop design is described below. [It is important to recognize that each workshop will have its own needs that may require some degree of change from this basic format.]

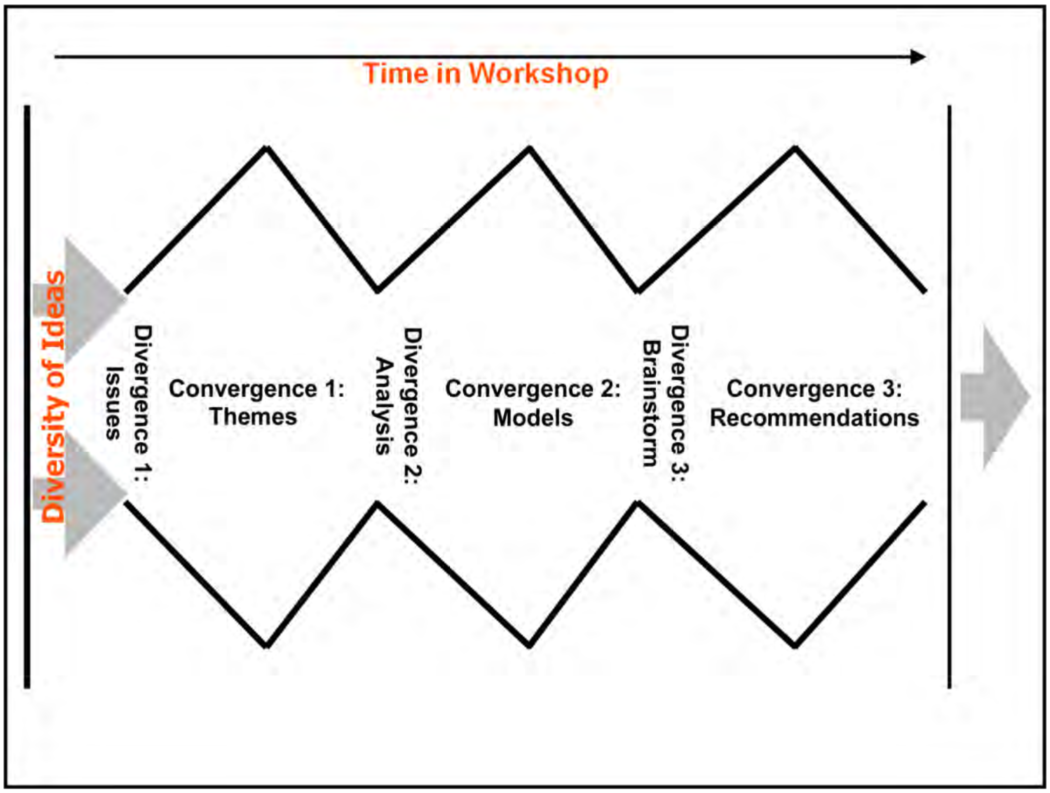

Figure 2. Generalized graphical depiction of process flow in working groups in a typical PHVA workshop. Adapted from Westley and Byers (2003).

Cycle 1: Issue identification and theme generation

Each participant comes to a PHVA workshop with their own experiences and issues, as well as concerns regarding how management of the species will impact their world. It is critical that they are able to express their opinions on the real problems surrounding conservation of the species – not only so that information is made available to the full group for discussion, but also so that each person feels involved in the workshop process from the beginning. This is accomplished by a brainstorming session where each person introduces himself or herself to the group and directly states their opinion about the most pressing issue facing conservation of the species in question. An important outcome of this process is the recognition that people from seemingly very different perspectives will often identify conservation of the species as a desirable outcome, thereby immediately defusing at least some level of tension between historically antagonistic stakeholders.

Once the full breadth of issues is identified, the facilitator must help the group cluster this list into a smaller collection of themed issues for discussion and analysis by smaller working groups. Human sociological research has determined that productive problem solving works best in groups of about six to eight people, with a focused set of issues to address. These themes typically are based on biological and sociological topics – habitat, genetics, disease, human/wildlife interactions, etc. – pertinent to the specific workshop at hand. Themes can also be based on taxonomy or geography in multi-species workshops. It is important that workshop participants are comfortable with the resulting consolidation of issues into themes, once again emphasizing stakeholder engagement throughout the process.

Workshop participants select the working group in which they wish to participate; the facilitator monitors this process so that one group does not become too large (say, > 15 people) at the expense of one or more other groups that become too small or even nonexistent. If this happens, the group revisits the choice of working group themes and adjusts as necessary to balance the distribution of participants among the groups. As a first task, each group expands upon their collection of brainstormed issues and produces a prioritized list of problem statements that form the basis of their upcoming deliberations.

Cycle 2: Data assembly and analysis

The next phase of divergence concentrates on another brainstorming process: the identification and assembly of information on the species and its conservation, in the specific context of each working group's theme. For those tasked with using the PVA simulation model, this phase consists of refining the basic demographic and genetic dataset used to create the preliminary risk assessment models. Other groups have the freedom to explore all relevant data, from population genetic data to information on the legislative environment for conservation in a given state, region or country. At this point in the workshop, it is critical to separate fact from assumption and to identify competing datasets so that information can be more effectively organized and interpreted.

During this phase of the workshop, working group participants often realize that other stakeholder have different perspectives on associated data (or more ambiguous assumptions), leading to difficulties in interpretation and agreement. Alternatively, a group may find there are very little hard data on their topic of interest, making if equally difficult to provide clear justification for conclusions that will form the basis of later recommendations. These complexities often make this the most difficult phase of the workshop – a period of maximum divergence sometimes referred to as the "groan zone" (Kaner 1996). The facilitator must be sensitive to this possibility and provide tools that can help groups make sense of the information at hand. These tools can include simple matrix templates or causal flow (influence) diagramming (see Appendix X for examples of products from these tools).

An especially valuable tool for data analysis is population viability simulation modeling. The use of such models, most commonly but not exclusively involving the *VORTEX* simulation, provides an environment within which alternative scenarios of human population activities and population/habitat management options can be constructed and tested. Where appropriate, each working group is encouraged to develop management scenarios that can be quantified for evaluation in *VORTEX*. This process thereby promotes interaction between working groups, enhancing the collaborative and participatory nature of the workshop process. Furthermore, the subsequent plenary report-back of results from the simulation modeling allows quick feedback to the various groups and provides them the information they need to proceed to the next step: conservation action planning.

Cycle 3: Developing recommendations and reaching consensus

As the working groups complete their analysis, they are once again asked to enter a divergent thinking phase and to brainstorm alternative solutions to the problems they have identified and analyzed. The workshop facilitator strives to keep the groups thinking first at a more strategic level, typically at the level of short- and long-term goals, before moving to the final step of constructing detailed action items. The identified goals are discussed, streamlined, and prioritized using techniques such as paired ranking, before moving to the final phase of action planning.

Working groups are asked to develop detailed action items for each of their goals, in order of priority. They are asked to apply the SMART criteria – Specific, Measurable, Achievable, Results-Oriented, Timely – to each action item so that they are fully characterized for later implementation. While this is the last element of the PHVA workshop process, it is the most critical as this is "where the rubber hits the road": this is the core of a long-term species conservation strategy. The facilitator must carefully monitor the presentation of these working group recommendations in the final workshop plenary, ensuring that full consensus is reached on the recommendations coming from the various groups. This consensus process is vital, as it enhances the sense of ownership among participants of the workshop product. This ownership will serve to promote timely and committed implementation of workshop recommendations.

CBSG has produced a set of task sheets that explain the various working group activities described above. These tasks are then typically assembled in a customized order – relevant to the specific workshop process required for a given project – to form a Workshop Handbook (see Appendix Y). This Handbook is distributed to all participants at the beginning of the workshop and serves as the main instrument for instructing them on the various tasks to be completed during the workshop. Throughout this divergent – convergent cycle of working group activity, PHVA workshop facilitators stress the importance of working group facilitation as a mechanism for productive discussion and effective development of recommendations. Before this cycle even begins, the facilitator explains the working group process and identifies various roles that working group participants must assume, perhaps on a rotating basis, in each working group session. These roles include working group *facilitator / discussion leader*; the *recorder*, who captures the core elements of the discussions on flip charts (this person could also be the facilitator); the *reporter*, who will present a summary of working group activity and output in plenary sessions; and the *timekeeper*, who will manage the amount of time spent on a given group activity and keep the group apprised of the time remaining for each task.

In conclusion, while we stress the importance of sound scientific logic and analysis as a core element of a PHVA workshop, the workshop will not succeed without equal attention given to sound process. Derivation of an effective process is predicated on the philosophy that stakeholders that participate in a complex species conservation planning project must be allowed to express their views and – more importantly – synthesize their views with those of others to collectively craft a set of conservation recommendations that will achieve endangered species stability while not excessively impacting the set of stakeholders who must live with the consequences of these recommendations. CBSG staff constantly work to refine the general process elements described here, and learn from others in the broad strategic planning community in order to bring the PHVA workshop process to an ever wider audience and, ultimately, to increase its effectiveness worldwide.

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Using the tools of the Species Conservation Toolkit Initiative

Working Group
2016 CBSG Annual Meeting
Puebla, Mexico

Using the tools of the Species Conservation Toolkit Initiative

CONVENORS: Jon Ballou, Bob Lacy, Taylor Callicrate

DESCRIPTION: The Species Conservation Toolkit Initiative is a partnership to ensure that the new innovations and tools needed for species risk assessment, evaluating conservation actions, and managing populations are developed, globally available, and *used effectively*. The tools in the toolkit include PMx, Vortex, Outbreak, MetaModel Manager, Vortex Adaptive Manager, and more. These are powerful tools for guiding species risk assessments and conservation planning, but it is not always easy to know how to use the many features in the software. In this working group, we will provide a short training session followed by discussion of further training needs. The specific tool(s) to be the focus of the training session will be identified by a survey of the meeting participants.

Survey of interest in training in SCTI tools at the 2016 CBSG annual meeting in Puebla

One of the working groups at the annual conference of the CBSG will provide a short training session on one or more of the tools of the Species Conservation Toolkit Initiative. (See above working group description.) To help identify which of the software programs and which features within the software should be the focus of the working group, we are asking for your feedback prior to the conference. If you might be interested in participating in this working group, please indicate on a 1 to 5 scale your level of interest in training in each of the following components of software packages (1 = little or no interest; 3 = moderate interest; 5 = very interested; blank = you don't know what the item refers to). Please respond by September 24th by emailing this document as an attachment to scti@vortex10.org .

Vortex (Population Viability Analysis)

____ use of studbooks and modeling ex situ populations

____ modeling genetics and genetic management options

____ other aspects of Vortex (Specify: _________________)

Outbreak (for modeling infectious disease in wildlife populations)

____ general overview

PMx (Pedigree analysis and management of breeding programs)

____ new Demographic tools

____ use of empirical kinships

____ customizing the Mate Suitability Index

____ Management Sets

____ integration with ZIMS; flow of data between studbooks and PMx

____ other aspects of PMx (Specify: _________________)

MetaModel Manager (for integrating other modeling tools)

____ modeling interacting species (i.e., linked Vortex analyses)

____ linking Vortex population model to Outbreak disease model

____ general overview

Vortex Adaptive Manager (for identifying optimal conservation actions under uncertainty)

____ general overview

Other?

____ other tools (Specify: _________________)

About SCTI

SCTI is led by Bob Lacy (Chicago Zoological Society), Jon Ballou (Smithsonian/National Zoo), and Onnie Byers (IUCN CBSG) in collaboration with other partners at conservation and research institutions around the world. SCTI currently employs a Conservation Science Programmer (Taylor Callicrate) and will soon be adding a Training Coordinator.

SCTI's managers work with the community of partners to shape the goals and functions of SCTI. In this way, SCTI adds tools and adapts existing ones to address changing conservation challenges.

SCTI builds innovative, accessible, and usable conservation tools and works with partners to develop effective training solutions.

SCTI holds a working group during the annual CBSG meeting and at other venues to update partners on progress and obtain input to adjust our goals and directives.

Contact us for the SCTI event schedule

This toolkit contains...

Vortex— A stochastic simulation of the extinction process.

PMx— Genetic and demographic management of pedigreed populations.

Outbreak— A stochastic simulation of disease dynamics.

MetaModel Manager— Link multiple models for simulation of interacting systems.

… and more! What conservation challenge can we help you with?

Please visit our website to see all tools, download software, donate, and make suggestions

www.vortex10.org

SCTI

The Species Conservation Toolkit Initiative

A partnership to ensure that the new innovations and tools needed for species risk assessment, evaluating conservation actions, and managing populations are developed, available, and used effectively.

Our Mission

SCTI was started with the vision of providing continuing, stable support for the development of conservation tools. We are currently focused on building the partnership and expanding support for SCTI tools.

Moving forward, specific goals & tasks will depend on the needs of the conservation community and the existence of financial support required to meet those goals. We will work to ensure that SCTI is:

- Creating innovative conservation tools
- Maintaining tools to reflect advances in research
- Supporting effective use of the tools by managers, scientists, and students
- Keeping conservation software freely available to the global community

Current Projects

- Collaboration with the ZIMS Studbook Module team to ensure smooth data transfer between PMx and ZIMS and to develop interactive ZIMS-PMx features
- Collaboration with San Diego Zoo and other partners to develop genomic management tools and integrate them into PMx
- Revision of manuals for PMx and Meta-Model Manager, and creating a manual for Outbreak.
- Restructuring of PMx demographic tools to accommodate species with incomplete data
- Revision of PMx genetic algorithms for empirical kinships and individuals with incomplete ancestry data
- Based on user input, identify support and training needs; in 2017, we will be adding a training coordinator position to help meet those needs

SCTI Partners

Financial commitments from our partners ensure that innovation in species conservation methodologies will be sustained and accelerated, and that the tools will be freely available to all.

Many partner organizations have chosen to make annual or multi-year financial commitments to SCTI, providing stability into the immediate future. We will continue to renew and seek new partners as time goes on.

Have questions, comments, or want to join the SCTI partnership?

Contact Bob Lacy
Robert.Lacy@czs.org
www.vortex10.org

Thanks to our current SCTI partners!

MetaModel Manager workshop at Brookfield Zoo