



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

**Working Group  
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Puebla, Mexico**

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

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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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## Key Words

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).

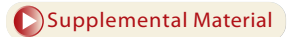
Reviews of SDM literature include those of Guisan & Zimmermann (2000), Stauffer (2002), Guisan & Thuiller (2005), Richards et al. (2007), and Schröder (2008). Several books have either been recently published or are in preparation (Franklin 2009; A.T. Peterson & A. Guisan, personal communication). Instructional 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.



## 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.

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**Spatial autocorrelation:**

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

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## Models across Terrestrial, Freshwater, and Marine Environments

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 toposcals (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).

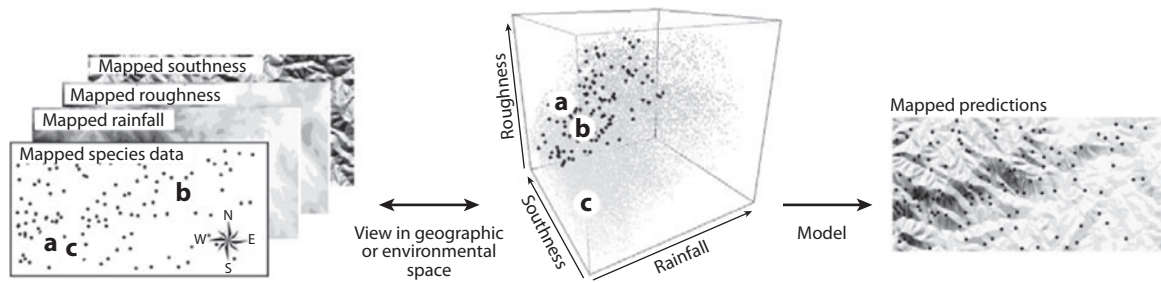
Although these are long-standing concepts, there is as yet little consensus on how to deal with scale disparities when fitting SDMs. Several methods, mostly from landscape ecology, focus on describing scales of pattern in ecological data. These include lacunarity, spectral analysis, and wavelet-coefficient 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.


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.

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

 Supplemental Material

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

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## 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.

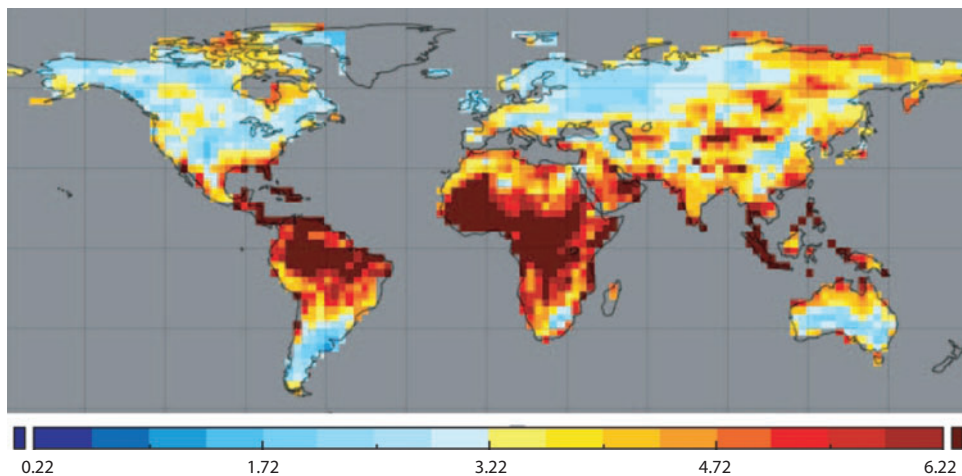
Several approaches can improve the use of models for extrapolation, and reduce or expose errors. Differences between the sampled and prediction spaces can be quantified (e.g., similarity measures, Williams et al. 2007; **Figure 2**); species data can be weighted to represent the invasion process or the 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 (Bertheaux 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.

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

### ▶ Supplemental Material

& 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.

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

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## 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.

### 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**).

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

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 [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 *Notofagus* 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 nonequilibrium 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 hierarchical 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.

## 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,

 Supplemental Material

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.

## DISCLOSURE STATEMENT

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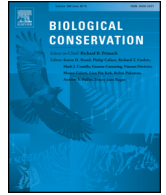
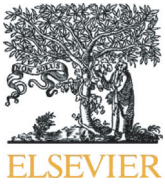
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## Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://ecolsys.annualreviews.org/errata.shtml>



## 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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## 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 <sup>a</sup>	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 <sup>b</sup> = 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	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	SDM: 11 Non-SDM: 16	
Species range maps (expert-drawn or other, e.g. IUCN Red List maps)	Presence/ absence map; Species richness	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	SDM: 2 Non-SDM: 10	
SDM: presence-only (e.g. MaxEnt, GARP)	Relative P(occurrence) or threshold conversion to presence/ absence	Black	Black	Black	Black	Black	Black	Black	Black	Grey	Grey	Black	Black	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	Black	Black	Black	Black	Black	Black	Black	Black	Grey	Grey	Black	Black	SDM: 4 Non-SDM: 0	
SDM: presence-absence (repeat surveys per site; e.g. occupancy models)	P(occurrence), threshold conversion to presence/ absence	Black	Black	Black	Black	Black	Black	Black	Black	Grey	Grey	Black	Black	SDM: 0 Non-SDM: 0	
SDM: abundance data	Prediction of abundance	Black	Black	Black	Black	Black	Black	Black	Black	Grey	Grey	Black	Black	SDM: 2 Non-SDM: 0	
HSI: Expert-derived habitat suitability index	Relative suitability ranking/ score, or binary distribution	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	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	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	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 )	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	SDM: 3 Non-SDM: 20	
Simple habitat maps (e.g. satellite-derived vegetation, bathymetry)	Threshold conversion to presence/ absence	Black	Black	Black	Black	Black	Black	Black	Black	Grey	Grey	Black	Black	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)	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	Black	SDM: 4 Non-SDM: 19	

<sup>a</sup> Many publications either did not specify the type of input data, or were vague. Further interrogation of supporting information was carried out where possible.

<sup>b</sup> Detectability refers to the probability that a species will be detected at a site, given that it is present.

<sup>c</sup> Threshold set too high.

<sup>d</sup> 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).

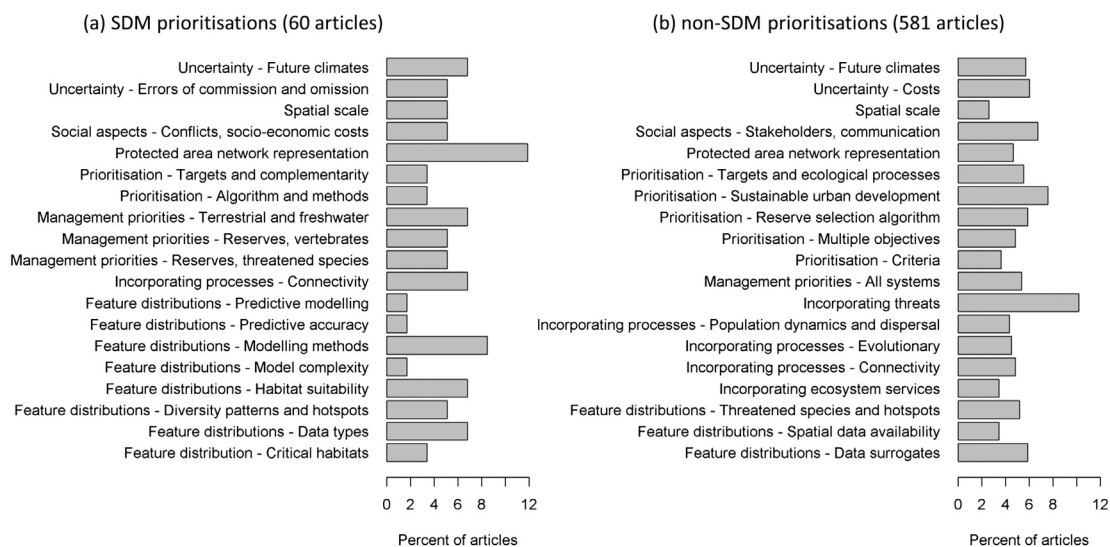
Knowing when and why conservation planners choose different biodiversity feature data inputs for informing decisions would provide insight into which data are most useful for solving which objectives. Despite a significant body of knowledge on SDMs having been assembled more than a decade ago, and repeated 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

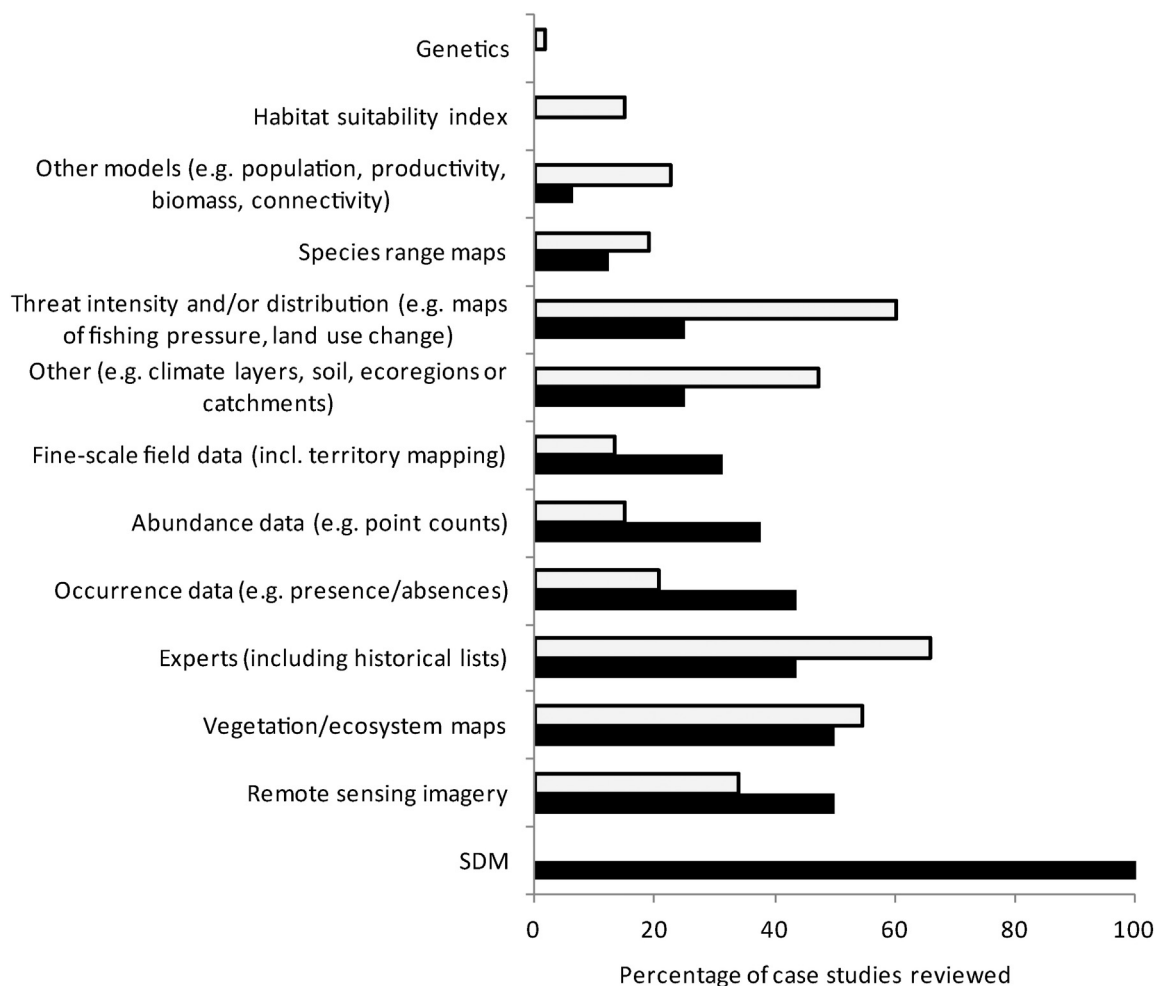
We sampled the peer-reviewed literature by searching the Web of Science, using the key words “conservation plan\*” or “land use plan\*” or “regional plan\*” (to select articles addressing conservation;  $n =$

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.

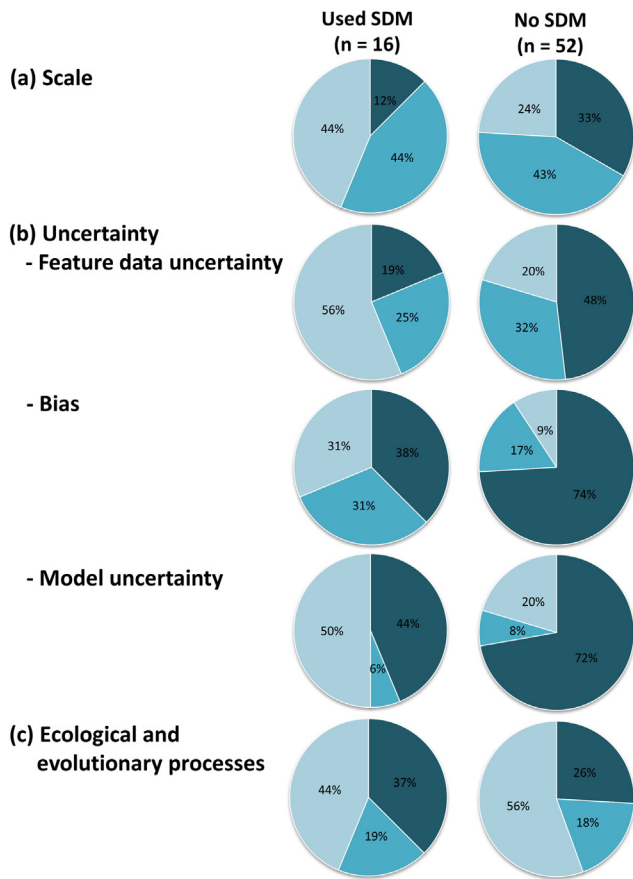
each classification using an unpaired two-sample t-test assuming unequal variances.

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](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?

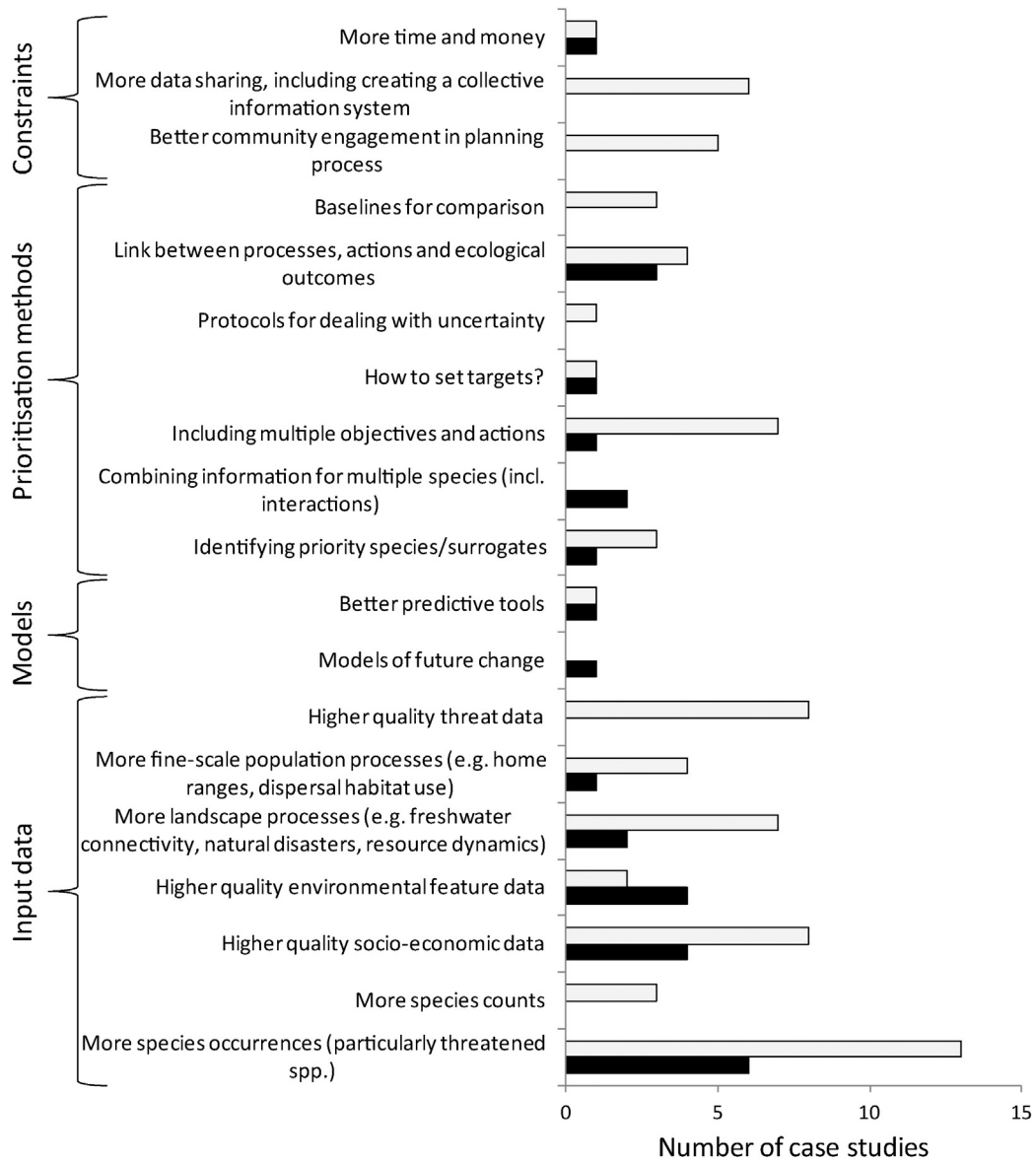
Text analysis suggested that only 10% of conservation planning research between 2006 and 2012 referred to SDMs (60 versus 581 prioritisations). Reviewing a sample of these articles in more detail revealed a slightly higher ratio of SDM- to non-SDM prioritisations (23% of 68 articles used SDMs). This 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  $345 \pm 169$  S.E. versus  $1214 \pm 865$  for SDM and non-SDM prioritisations, respectively) and had more spatially-explicit occurrence records per species compared to non-SDM prioritisations (mean of  $1499 \pm 1035$  S.E. versus  $128 \pm 19$  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
<i>Too expensive</i> 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)
<i>Time constraints</i> 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)
<i>Data biased: planning at a large scale</i> 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)
<i>Data insufficient: planning at a large scale</i> 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)
<i>Planning at a small scale</i> 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)
<i>Complex systems: interacting species</i> 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)
<i>Characteristics of target species</i> 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)
<i>SDMs too simplistic, need for population processes</i> Population modelling (using demography data) more important than distribution modelling	Integrated occurrence-mortality model	Faluccci et al. (2009), Franklin et al. (2014)	The Nature Conservancy (2010)
<i>Ecosystem rather than species approach</i> 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; <a href="http://californialcc.org/projects/decision-support-climate-change-adaptation-and-fire-management-strategies-risk-species">http://californialcc.org/projects/decision-support-climate-change-adaptation-and-fire-management-strategies-risk-species</a>	Jaguar National Action Plan (NAP); <a href="http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/plano-de-acao/1344-plano-de-acao-para-conservacao-da-onca-pintada.html">http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/plano-de-acao/1344-plano-de-acao-para-conservacao-da-onca-pintada.html</a>
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 JCU). 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: <a href="http://climate.calcommons.org/project/decision-support-climate-change-adaptation-and-fire-management-strategies-risk-species">http://climate.calcommons.org/project/decision-support-climate-change-adaptation-and-fire-management-strategies-risk-species</a>	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<sup>2</sup>: Avon Catchment Council, 2007) to global (Terribile et al., 2009). The average planning area for non-SDM prioritisations (mean = 15,078,456 km<sup>2</sup> ± 12,362,240 S.E.) was 62 times larger than for SDM prioritisations (mean = 239,364 km<sup>2</sup> ± 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; McMahan 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 using 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 (Akçakaya 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

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.04.023>.

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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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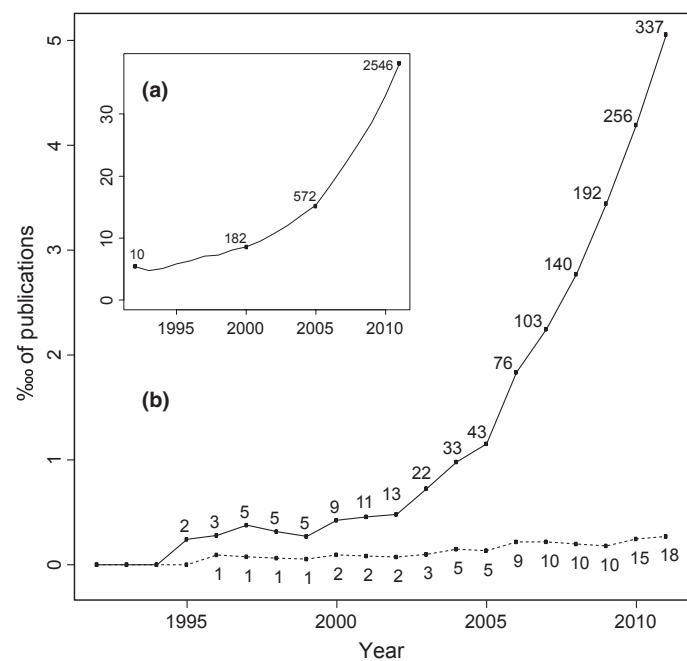
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relationships between species observations and environmental descriptors, although more mechanistic modelling approaches, and approaches involving expert opinion, also exist (Appendix S1). SDMs have the potential to play a critical role in supporting 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



**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 (%<sub>000</sub>) 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.

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.

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?

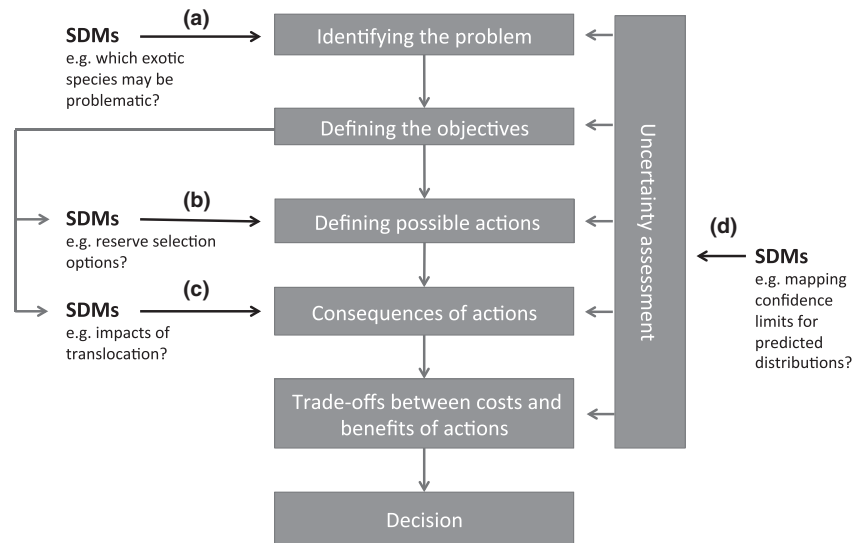
The potential of SDMs to guide conservation actions is best assessed by first considering the full decision-making process, a step rarely taken. Structured decision making (Gregory *et al.* 2012; Fig. 2) provides a rigorous framework for this process and is increasingly proposed to address environmental 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).

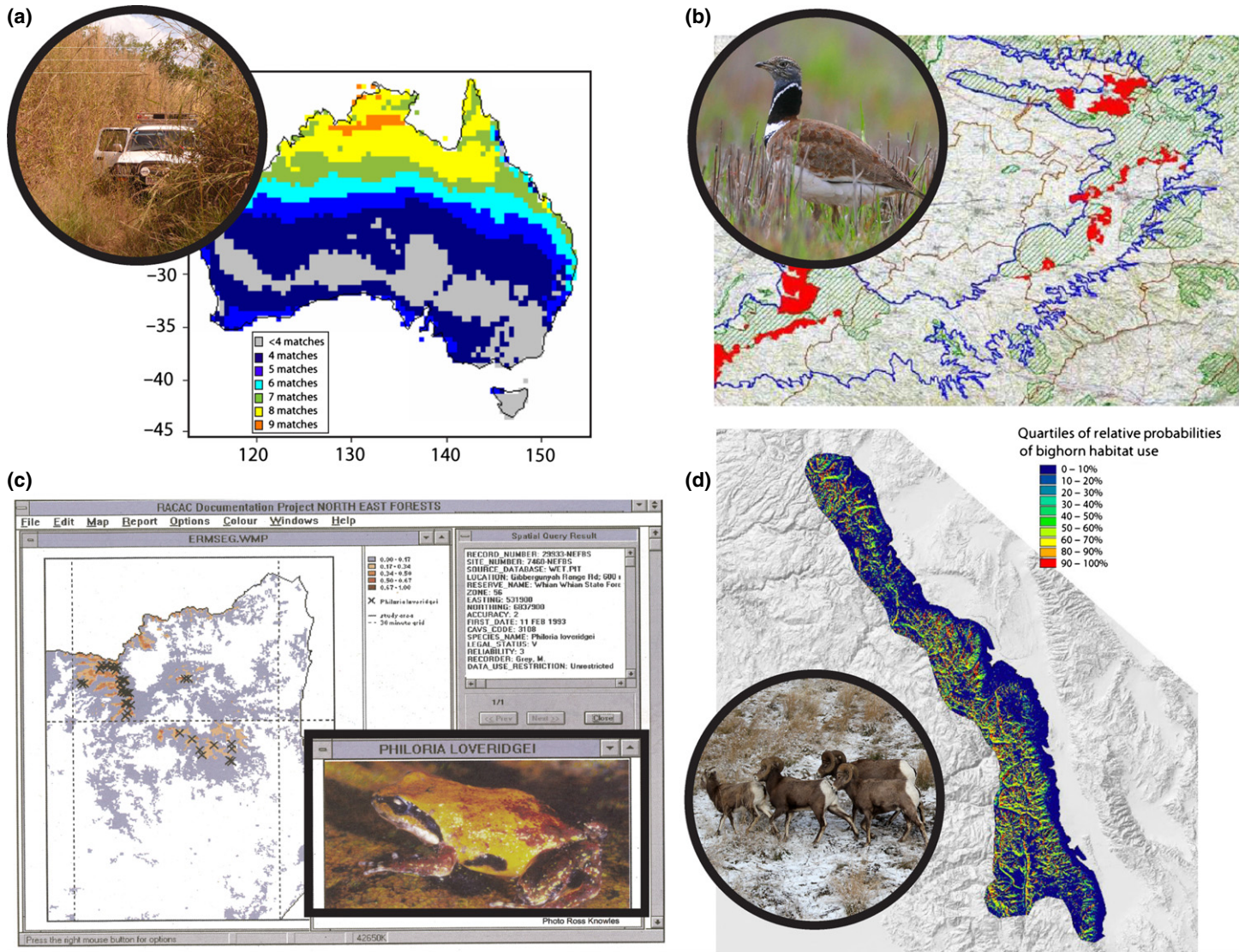
### Identifying and protecting critical habitats

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).

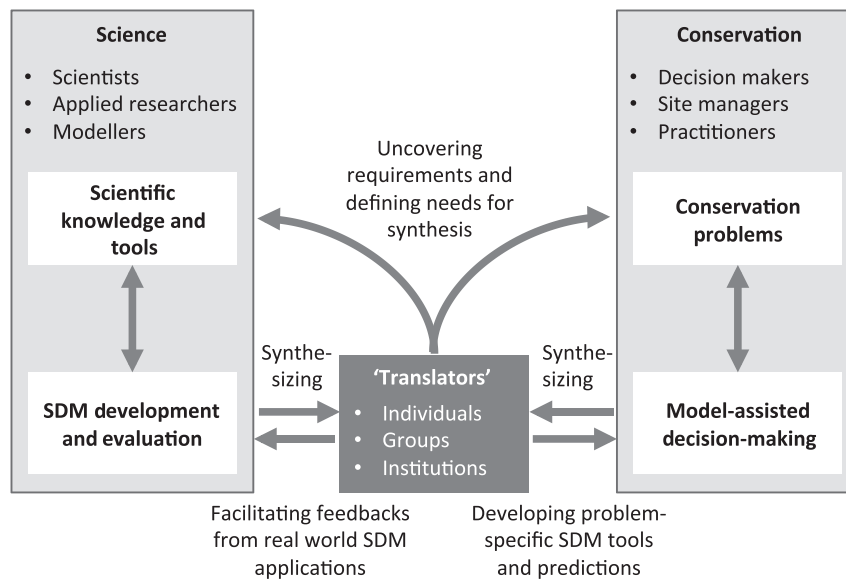
There are also cultural differences between researchers and decision makers arising from differences in sources of funding, career aspirations, temporal contingencies to solve problems, or differences in the philosophy of the evaluation of the work done (i.e. economic vs. peer-reviewed; Laurance *et 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, Nature-Print 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	<a href="http://www.ala.org.au/">http://www.ala.org.au/</a>	<a href="http://lifemapper.org/">http://lifemapper.org/</a>	<a href="http://www.niiss.org">www.niiss.org</a>	<a href="http://data.gbif.org/http://openmodeller.sourceforge.net/">http://data.gbif.org/http://openmodeller.sourceforge.net/</a>
9. Link to an official occurrence database	ALA	GBIF	NIISS	GBIF
10. Reference (if available)	–	Stockwell <i>et al.</i> 2006;	Graham <i>et al.</i> 2010;	Munoz <i>et al.</i> 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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# CAT NEWS

## Jaguar in Brazil







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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).

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](http://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<sup>2</sup> (~1 km<sup>2</sup>).

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

**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

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.

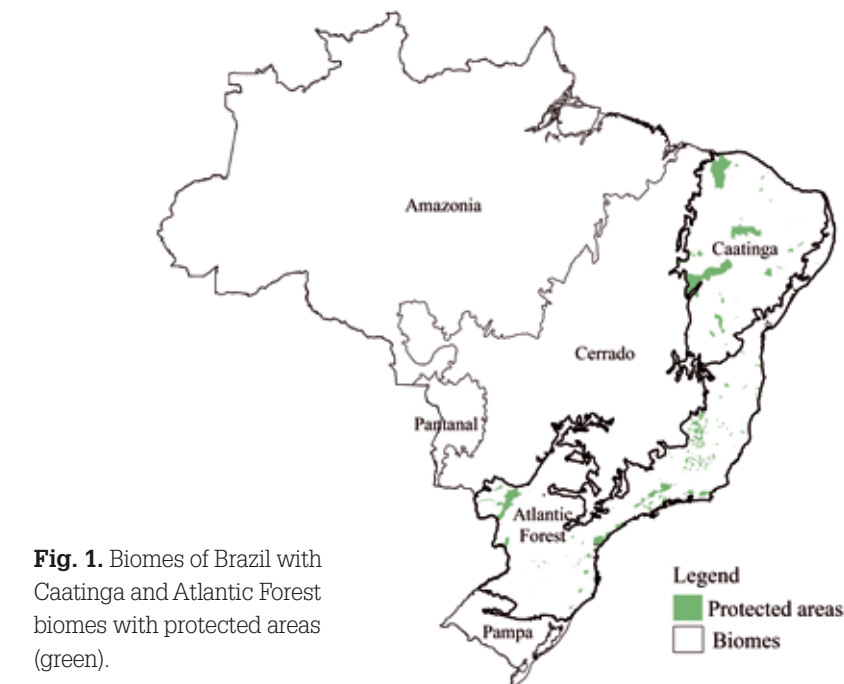
Models were evaluated by the AUC value, the omission error and by the binomial probability (Pearson 2007).

### Results and Discussion

The SDM for Caatinga and Atlantic Forest biomes presented high predictive success and were highly statistically significant (AUC =  $0.880 \pm 0.027$ , omission error = 0.206,  $p < 0.001$ ; AUC =  $0.944 \pm 0.022$ , 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<sup>2</sup>) 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



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

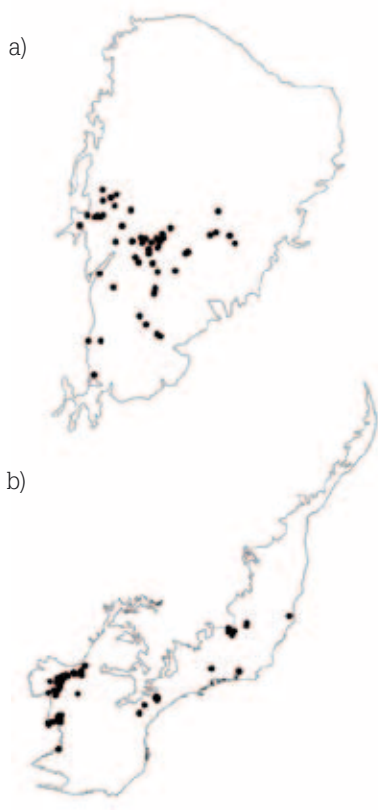
than 50% of its natural cover and greatly impacted and fragmented by human activities (Leal et al. 2005). Most of the protected areas found in this biome (Fig. 3) presented large areas as suitable for jaguar occurrence, such as Serra Branca Ecological Station (ES) and Serra da Capivara National Park (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<sup>2</sup>), 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<sup>2</sup>) predicted as suitable (27.44%) for jaguar occurrence encompassed the closed to

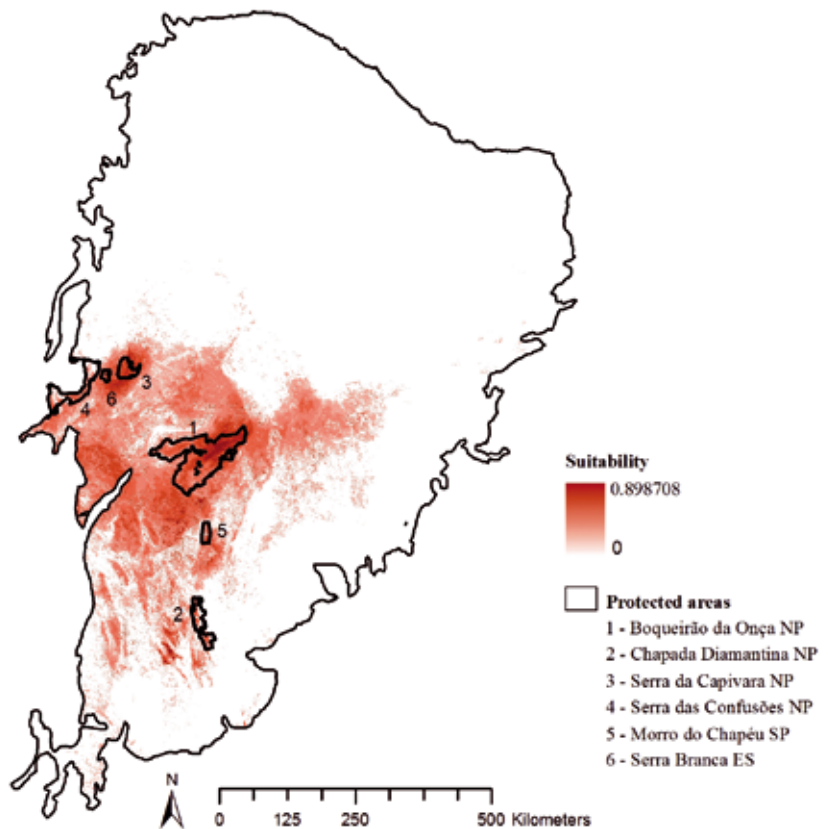
open (>15%) broadleaved evergreen or semi-deciduous forest (55.26%), while unsuitable areas encompassed mainly mosaic cropland (50-70%)/ vegetation (grassland/shrubland/forest) (20-50%).

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, Intervalles SP, Alto Ribeira Touristic SP and Xitué ES, Iguazu 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 over-prediction (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.

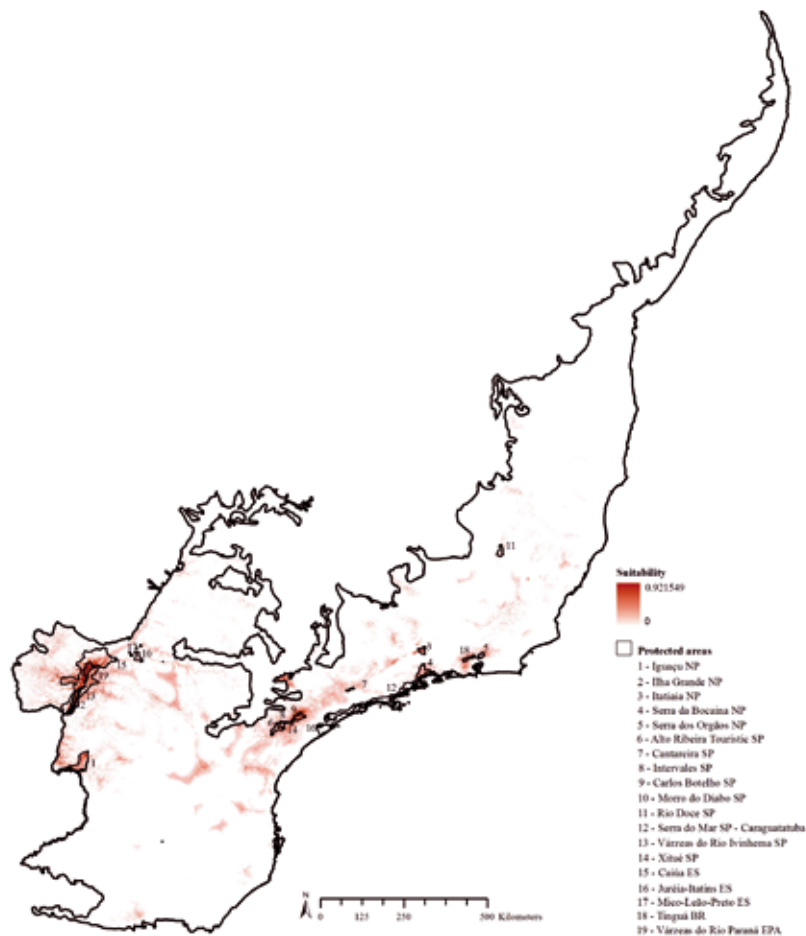


**Fig. 3.** Potential distribution model for jaguar in Caatinga biome with some protected areas highlighted.

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).

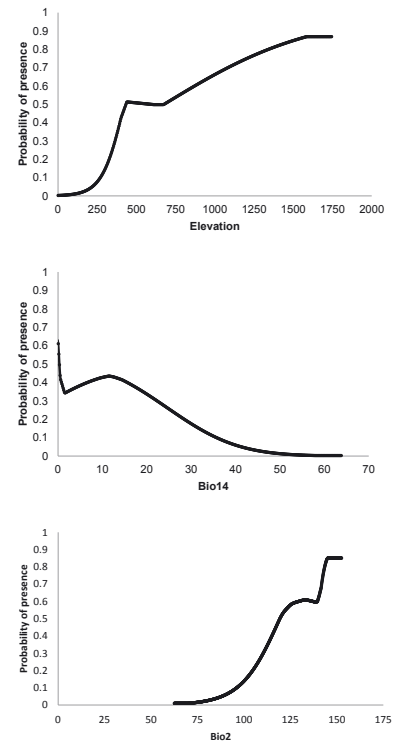
The SDM approach can improve our knowledge about cat species worldwide by 1) highlighting areas where the species might occur but confirmed observation is missing, 2) identifying gaps in data collection and guiding the sampling efforts, 3) identifying key areas for conservation efforts and potential 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).

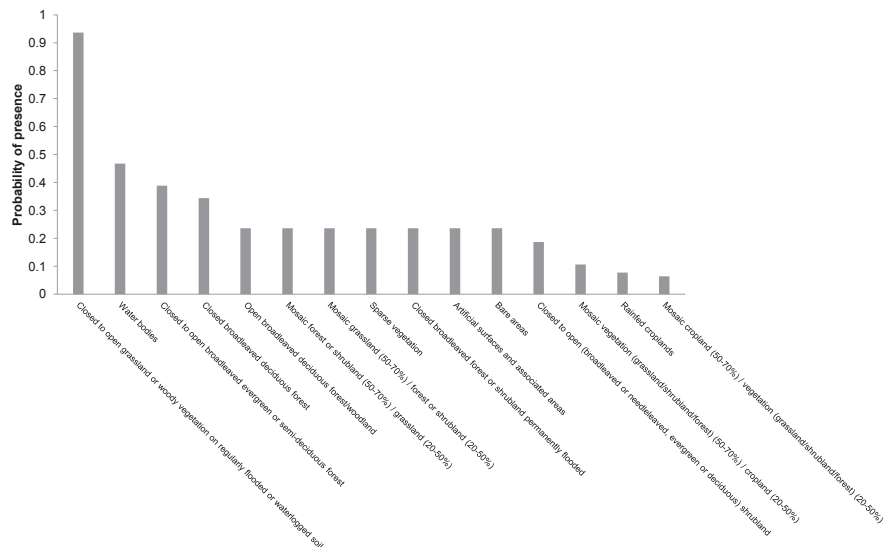
The assessment of conservation priorities for felids should consider the environmental suitability of landscape in a modeling framework. Suitability maps could be considered by stakeholders for defining priority areas for the establishment of new protected areas or corridors. However, conservation inferences 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



**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.

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. 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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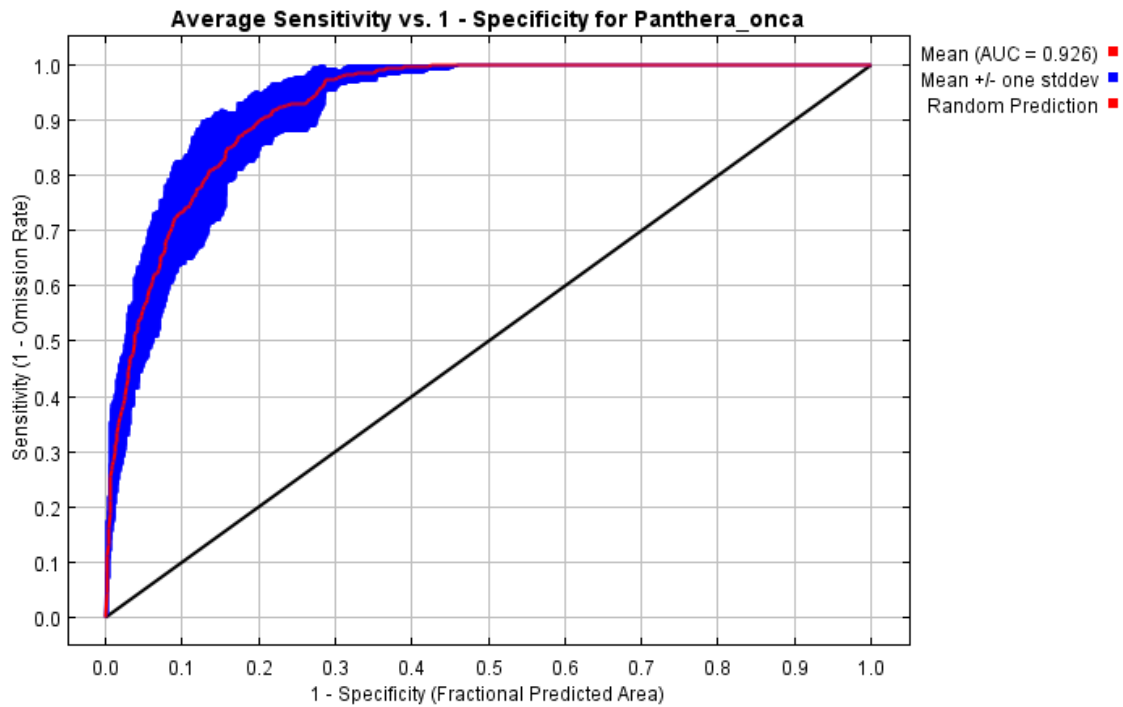
Supporting Online Material SOM available at [www.catsg.org/catnews](http://www.catsg.org/catnews)

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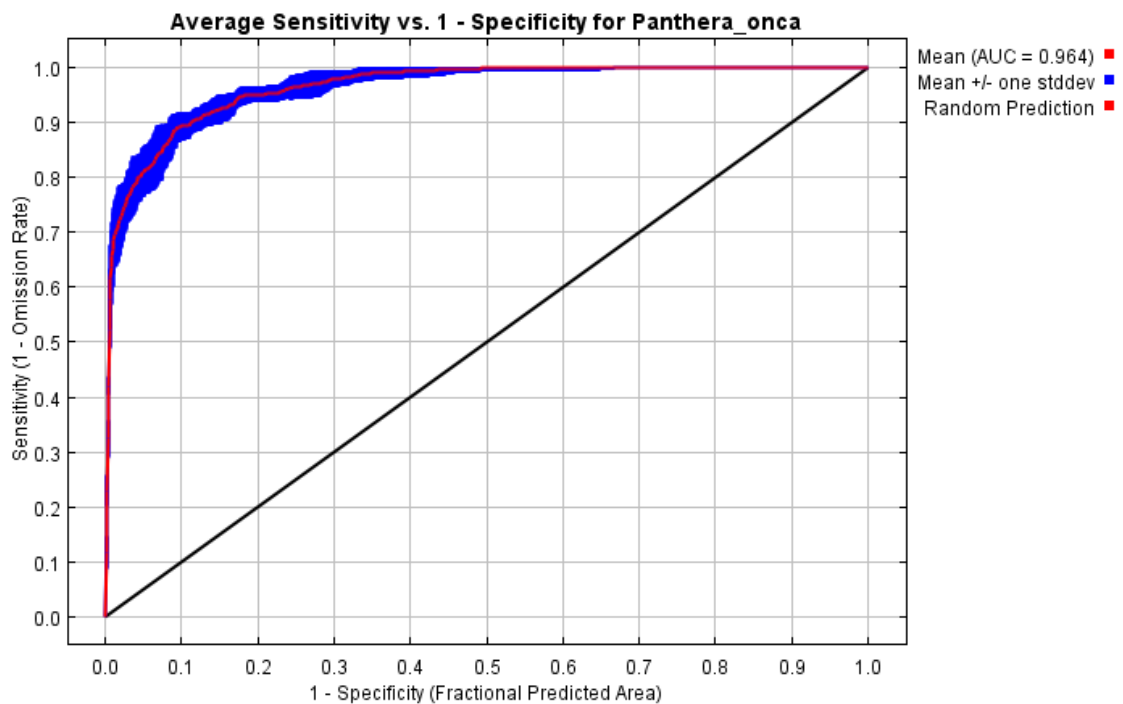
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Supporting Online Material SOM Figures 1 and 2.

a)



b)



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 exist 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://slink.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 ( $1 - \text{sensitivity}$ ) 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<sup>2</sup> to 4,311.0 km<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup>) 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<sup>2</sup>), 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].

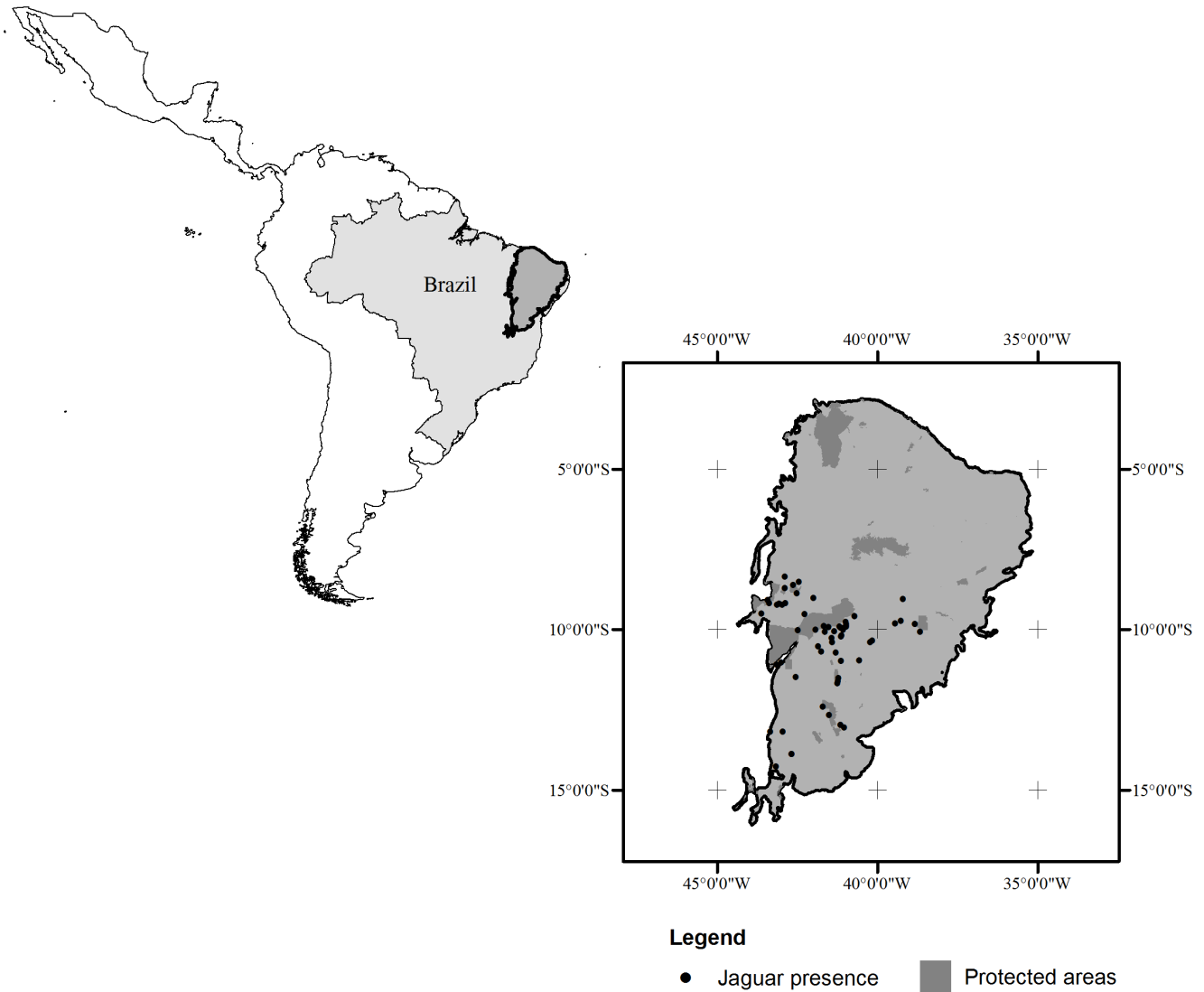
Models were generated using presence-only data (N = 62) (Table S1; Figure 1) and environmental variables (Table 1) at a spatial resolution of 0.0083 decimal degree (~1 km<sup>2</sup>). We selected functionally relevant variables for the species [38], avoiding the autocorrelation. We considered climatic 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 1.0E<sup>-5</sup> with 500 iterations 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

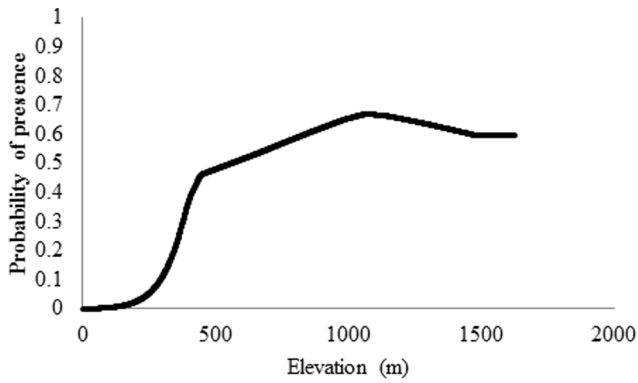


**Figure 1. Location of Caatinga biome in Brazil, protected areas in the Caatinga biome and the presence data used for modeling.**  
doi:10.1371/journal.pone.0092950.g001

**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 vector 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.**

doi:10.1371/journal.pone.0092950.g002

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 PJCUs. 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) PJCUs size; 2) connectivity, and; 3) jaguar population status [24]. For PJCUs 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<sup>2</sup> for males and 41 km<sup>2</sup> 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<sup>2</sup> of high suitability habitats. In this way, PJCUs ≥ 1,700 km<sup>2</sup> received three points. Areas smaller than 1,700 km<sup>2</sup> 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 PJCUs received one point for each possible connection. Considering the jaguar population status, we combined the PJCUs 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 ± 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 (≥ 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<sup>2</sup> (18.46% of the total biome). This area is composed mostly by closed to open shrubland (50.87%; 79,130 km<sup>2</sup>).

**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 vector 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)

doi:10.1371/journal.pone.0092950.t002

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

ID	Landscape cover Classes	Elevation (m)		Human Population Density (inhabitants/km <sup>2</sup> )		Distance from roads (km)		Distance from settlements (km)		
		Cost values	Classes	Cost values	Classes	Cost values	Classes	Cost values	Classes	
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. doi:10.1371/journal.pone.0092950.t003

**Table 4.** Priority Jaguar Conservation Units (PJCUs) identified in the Caatinga Biome.

PJCUs	Area (km <sup>2</sup> )	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
<b>Total</b>	<b>6,283.2</b>	<b>94.4 (68.52–120.1)</b>			

Total area, estimated population size and connectivity were used to prioritize the PJCUs.

NA = smaller estimated population is less than 1.0.

doi:10.1371/journal.pone.0092950.t004

We identified ten PJCUs (6,283.2 km<sup>2</sup>) 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<sup>2</sup>, encompassing 50.89% (~4,524.3 km<sup>2</sup>) of closed to open shrubland. The area also included 13.22% (~1,175 km<sup>2</sup>) of a mosaic with predominance of cropland, and less than 50% of grassland, shrubland or forest, and 11.61% (~1,032.5 km<sup>2</sup>) of an open (15–40%) broad-leaved 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<sup>2</sup> to 4,311.0 km<sup>2</sup>. 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

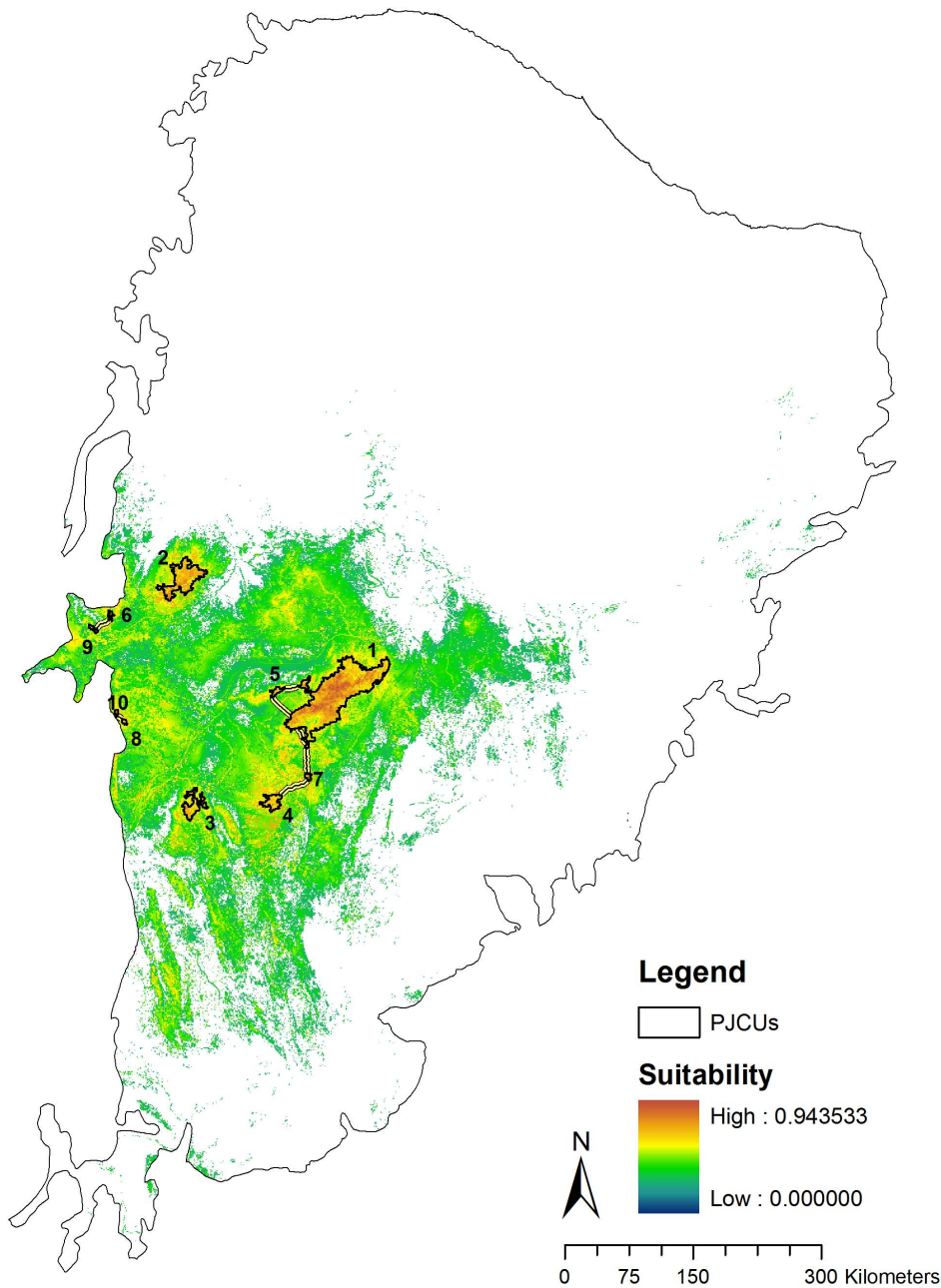
National Park previously described by Sanderson et al. [24]. Since this first report, further scientific studies in the field [25] [42] [43] and literature reviews [54] [55] have been performed, resulting in a higher number of jaguar point locations and better knowledge of the Caatinga’s fauna [56].

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





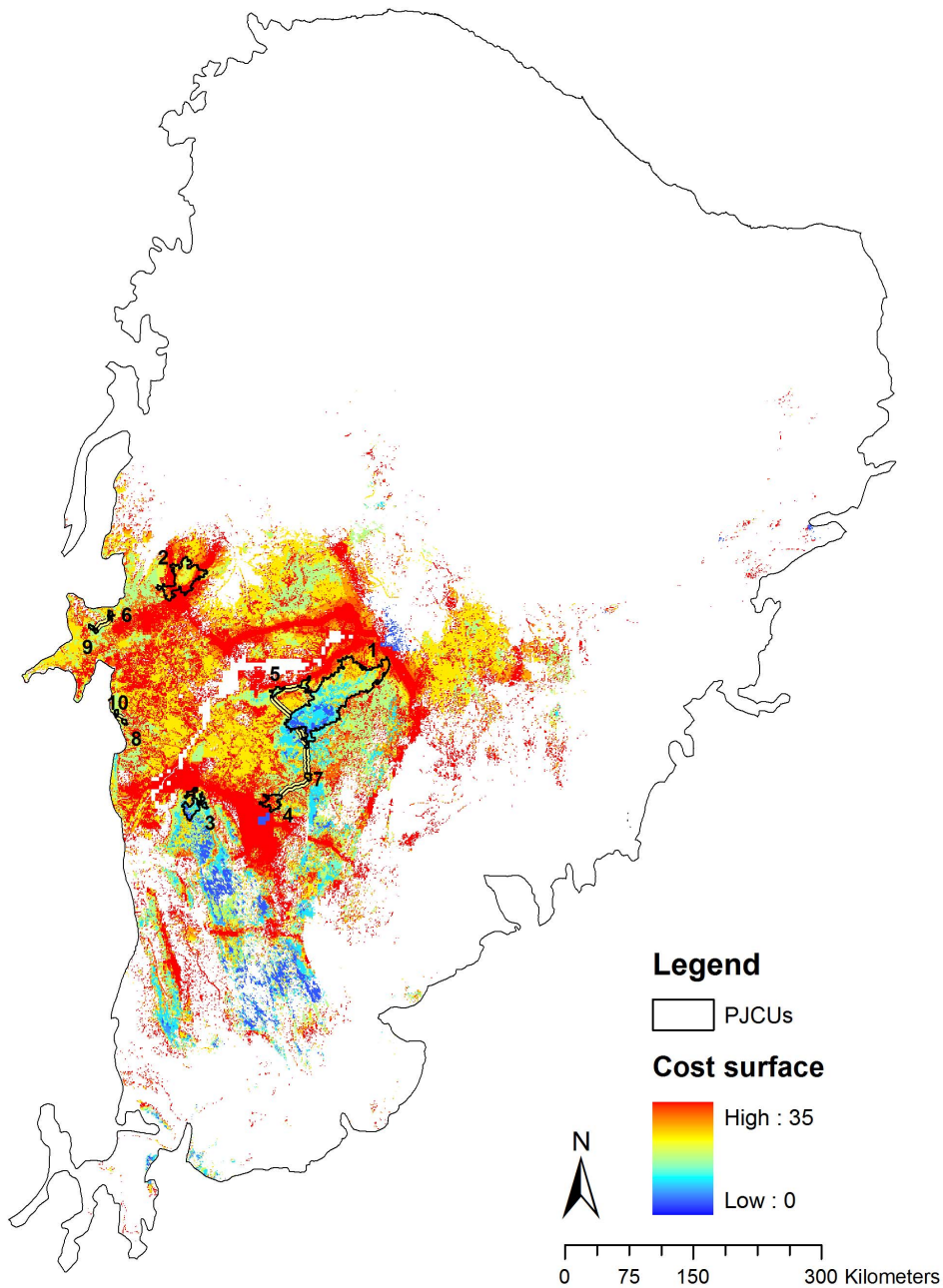
**Figure 3. Jaguar distribution model and the Priority Jaguar Conservation Units (PJCUs) with high suitability areas (equal to or higher than the median suitability value of 0.595) (in detail).**

doi:10.1371/journal.pone.0092950.g003

connection of Caatinga's jaguar populations would be with the Cerrado biome through the western PJCUs' (# 6, 8, 9 and 10). The PJCUs 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 PJCUs 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 PJCUs # 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 PJCUs is completely isolated corroborating a recent study that showed signs of reduced gene flow between jaguars from Serra da Capivara National Park (PJCUs #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.**  
doi:10.1371/journal.pone.0092950.g005

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 PJCUs # 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, PJCUs # 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 PJCUs # 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.

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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 PJCUs # 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  $0.860 \pm 0.0268$ ; 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 ecoregion (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<sup>2</sup> 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).

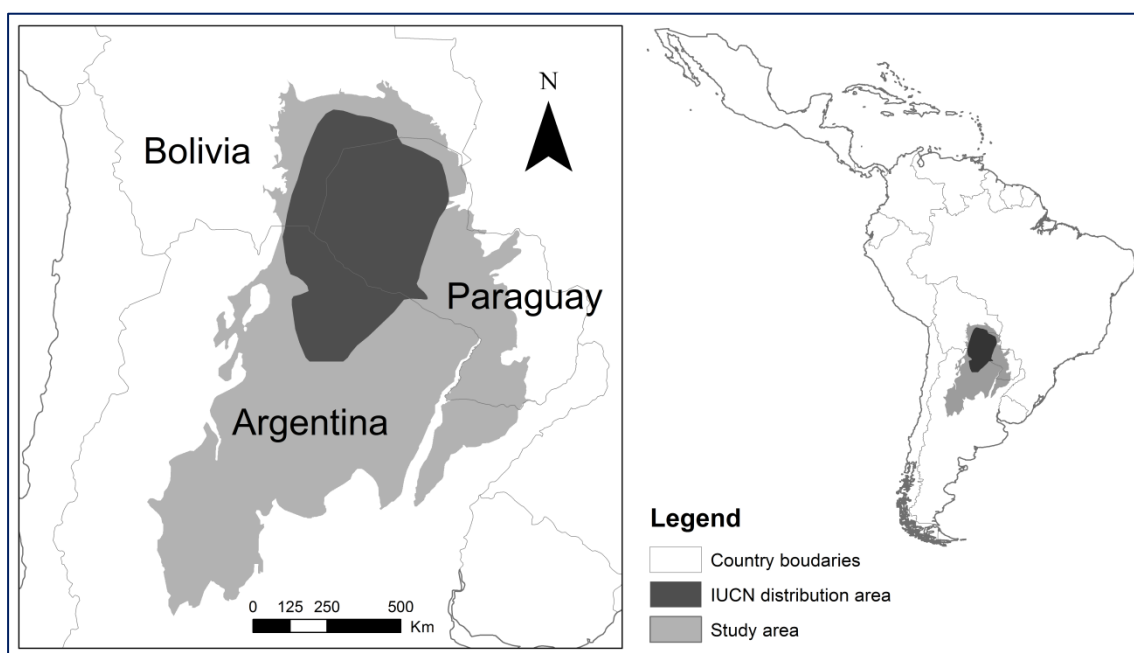


Fig 1. Map of the study area for the Chacoan peccary distribution model.

### 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).

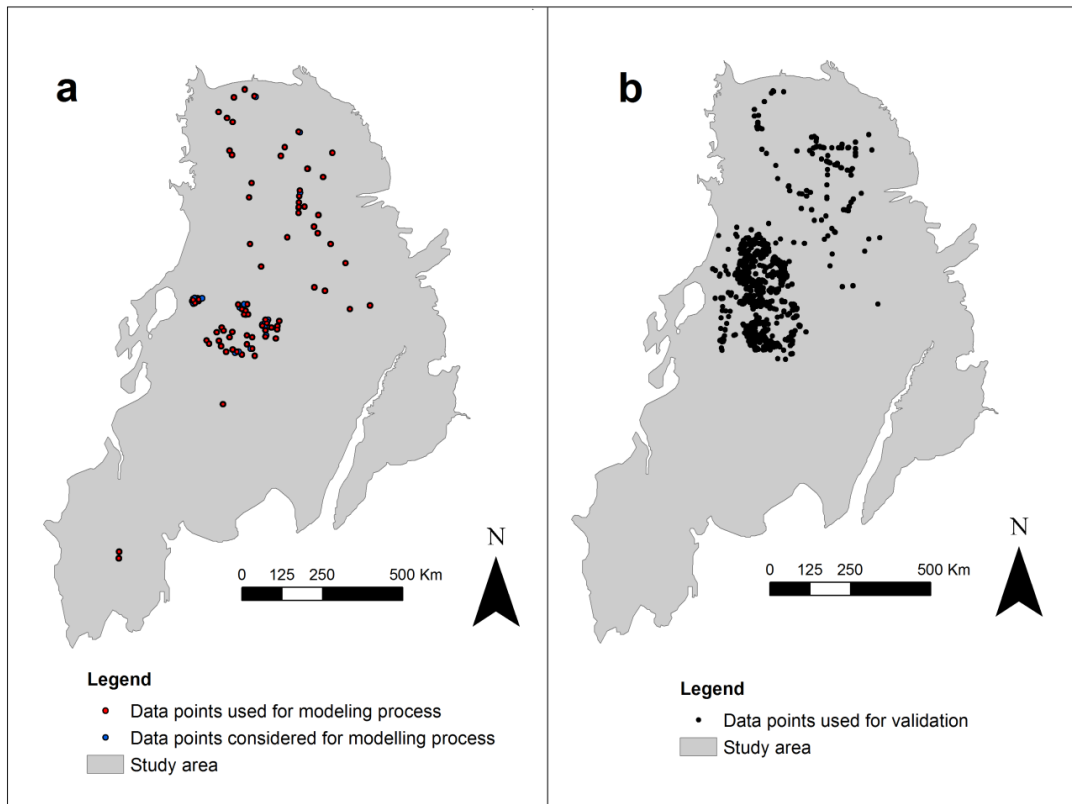


Fig 2. Chacoan peccary presence records considered (N=177) and used (N=87) for modeling (a) and presence points used for model validation (N=990) (b).

### 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<sup>2</sup>).

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)

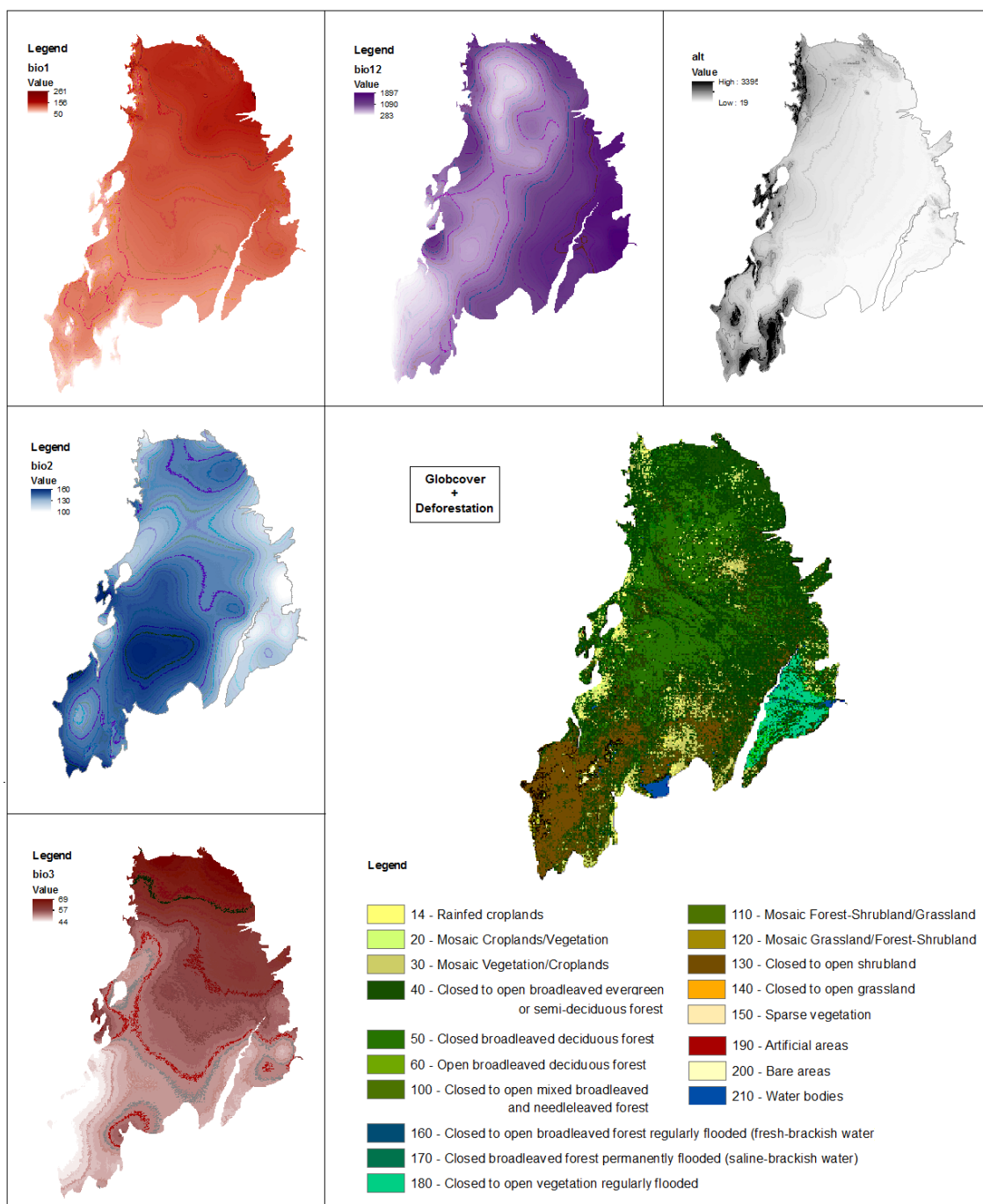


Fig 3. Environmental variables used in the Chacoan peccary model.

## 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 ( $0.25 \leq \text{values} \leq 0.50$ ) and high suitability ( $0.50 \leq \text{values} \leq 1$ ) 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 ( $0.860 \pm 0.0268$ ) 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% ( $\sim 497,577.34 \text{ Km}^2$ ) 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).

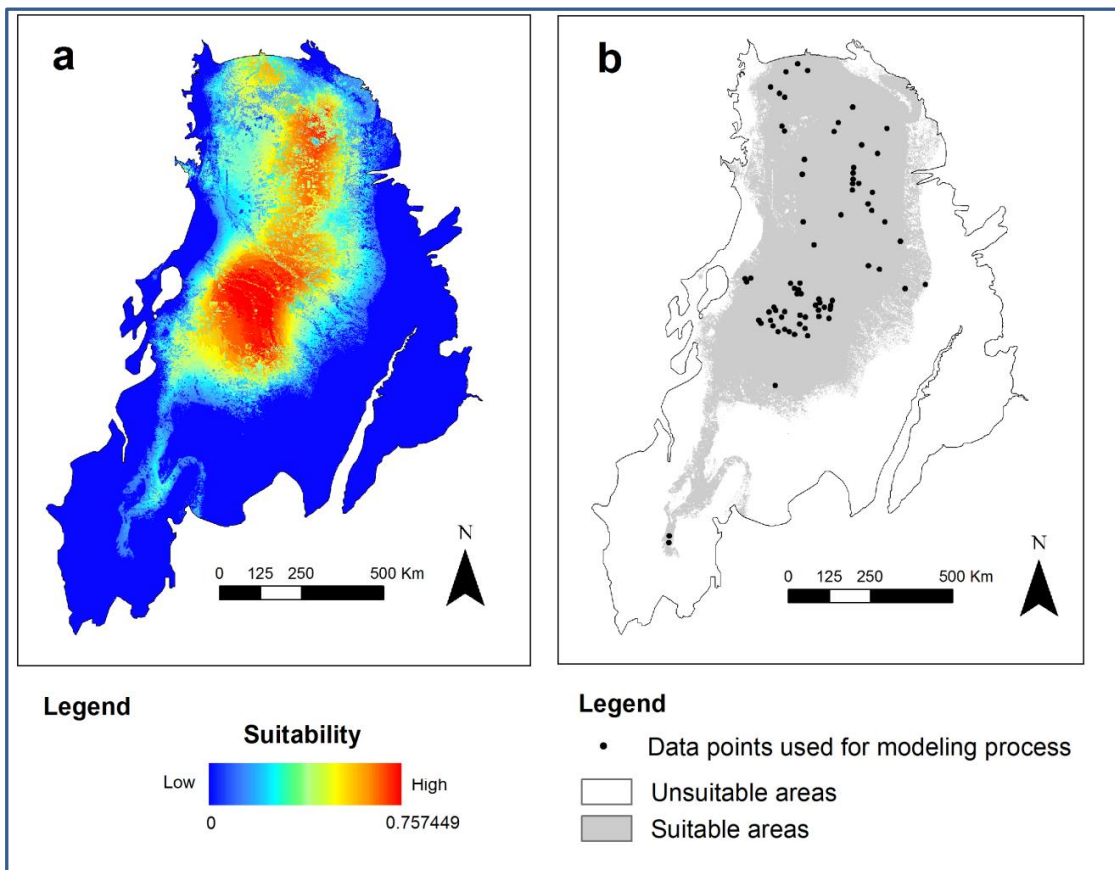


Fig 4. Predictive distribution model of Chacoan peccary. (a) Maxent average model shows the continuous suitability of the Chaco for the species. (b) Categorical suitable and unsuitable areas.

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.

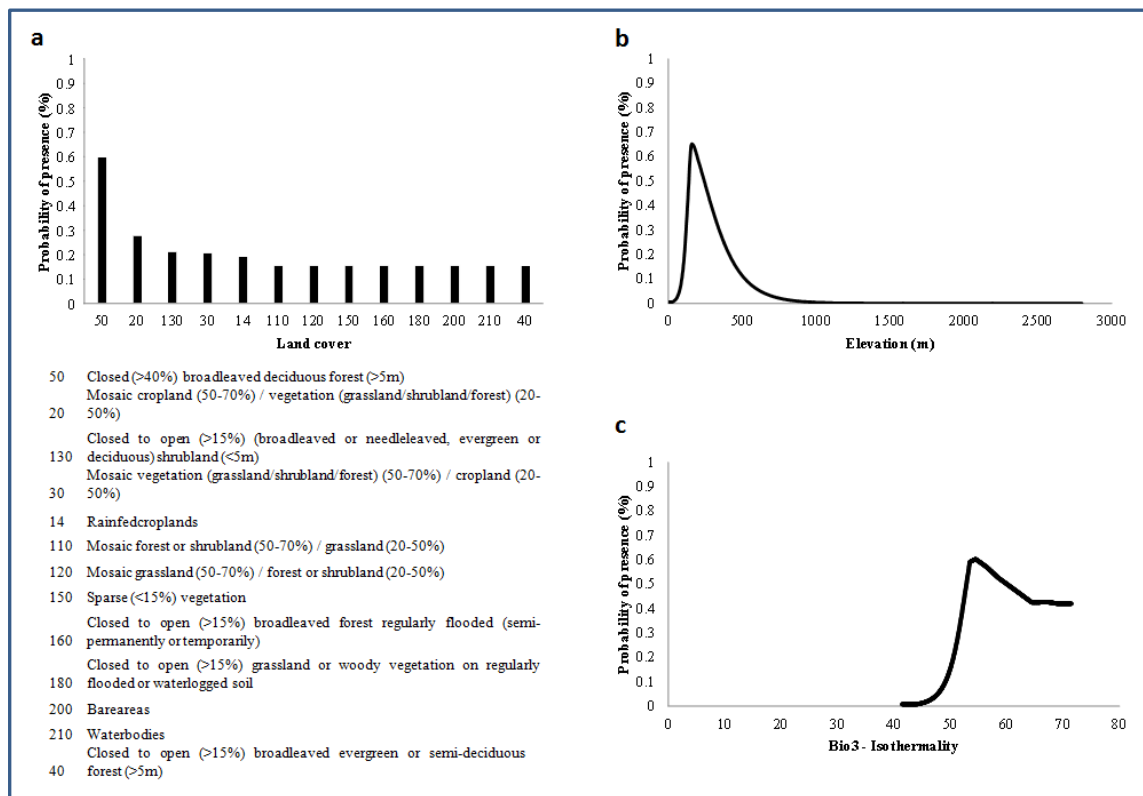


Fig 5. Response curves of probability of presence (%) according to Land Cover (a), Elevation (b) and Bio 3 – Isothermality (c).

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.

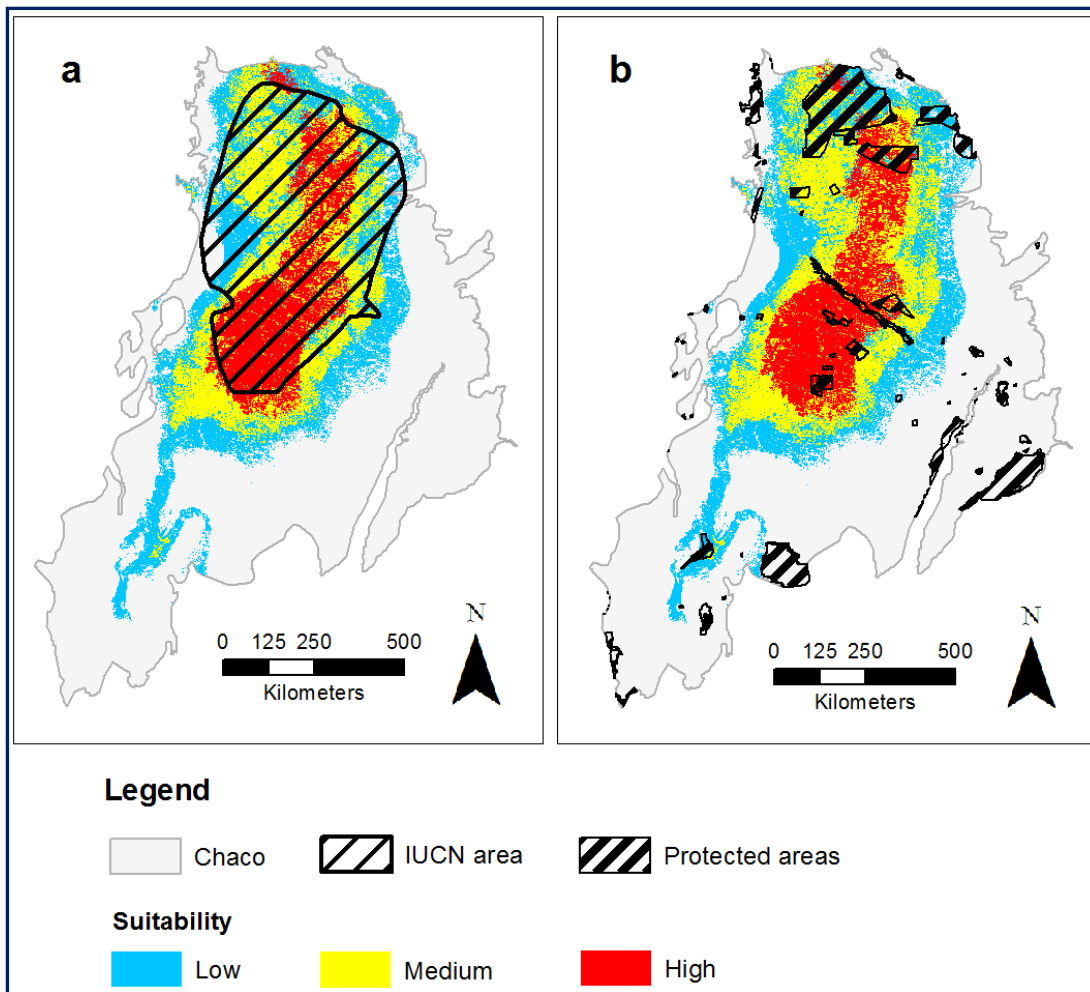


Fig 6. Suitable areas for the Chacoan peccary showing low suitability in blue (probability of presence from 0.0975 to 0.25), medium suitability in yellow (probability of presence from 0.25 to 0.50) and high suitability in red (probability of presence from 0.50 to 0.76), overlain with IUCN distribution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

<b>Argentina</b>				<b>Bolivia</b>		
Suitability	Total area (km <sup>2</sup> )	Protected (km <sup>2</sup> )	%	Total area (km <sup>2</sup> )	Protected (km <sup>2</sup> )	%
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
<b>Paraguay</b>				<b>All countries</b>		
Suitability	Total area (km <sup>2</sup> )	Protected (km <sup>2</sup> )	%	Total area (km <sup>2</sup> )	Protected (km <sup>2</sup> )	%
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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