THE LIVING PLANET

THE STATE OF THE WORLD'S WILDLIFE

Edited by **NORMAN MACLEAN**

The Living Planet

The State of the World's Wildlife

Since 1970, there has been an overall decline in wildlife populations in the order of 52%. Freshwater species populations have declined by 76%, species populations in Central and South America have declined by 83% and in the Indo-Pacific by 67%. These are often not complete extinctions, but large declines in the numbers of animals in each species, as well as habitat loss. This presents us with a tremendous opportunity, before it is too late to rescue many species. This book documents the present state of wildlife on a global scale, using a taxonomic approach, and serving as a one stop place for people involved in conservation to be able to find out what is in decline, and the success stories that have occurred to bring back species from the brink of extinction – primarily due to conservation management techniques – as models for what we might achieve in the future.

NORMAN MACLEAN is Emeritus Professor of Biology at the University of Southampton and a lifelong wildlife enthusiast. He has visited and studied wildlife in more than 50 countries around the world and has given numerous radio and TV interviews on the subject. He is the editor of *Silent Summer* (Cambridge, 2010), co-editor of *Austral Ark* (with Adam Stowe and Greg Holwell, Cambridge, 2015) and author of *A Less Green and Pleasant Land* (Cambridge, 2015).

Published online by Cambridge University Press

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CAMBRIDGE
UNIVERSITY PRESS

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Shaftesbury Road, Cambridge CB2 8EA, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314–321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi – 110025, India

103 Penang Road, #05–06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of Cambridge University Press & Assessment, a department of the University of Cambridge.

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www.cambridge.org
Information on this title: www.cambridge.org/9781108499828

DOI: 10.1017/9781108758826

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First published 2023

A catalogue record for this publication is available from the British Library.

Library of Congress Cataloging-in-Publication Data
Names: Maclean, Norman, 1932– author.
Title: The living planet : the state of the world's wildlife / edited by Norman Maclean, University of Southampton.
Description: First edition. | Cambridge, United Kingdom ; New York, NY, USA : Cambridge University Press, [2023] | Includes bibliographical references and index.
Identifiers: LCCN 2022044113 (print) | LCCN 2022044114 (ebook) | ISBN 9781108499828 (Hardback) | ISBN 9781108731652 (Paperback) | ISBN 9781108758826 (epub)
Subjects: LCSH: Wildlife conservation. | Wildlife reintroduction.
Classification: LCC QL82 .M325 2023 (print) | LCC QL82 (ebook) | DDC 333.95/4–dc23/eng/20221027
LC record available at https://lccn.loc.gov/2022044113
LC ebook record available at https://lccn.loc.gov/2022044114

ISBN 978-1-108-49982-8 Hardback
ISBN 978-1-108-73165-2 Paperback

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Published online by Cambridge University Press

FIFTEEN

Non-Marine Molluscs

ROBERT H. COWIE, BENOÎT FONTAINE
AND PHILIPPE BOUCHET

Summary

Non-marine molluscs stand out as the major animal group under the most severe threat. Among the 8664 mollusc species evaluated for the IUCN Red List (version 2019-1), 300 are considered Extinct out of a total 872 listed Extinct species. However, only ~10% of molluscs have been evaluated and other assessments of the number of extinct species are much higher, 3000 to over 5000, almost exclusively non-marine species. As for most other groups, threats faced by non-marine molluscs are habitat loss, probably the most important, but also impacts of introduced species, exploitation, generally of less concern, and climate change, likely to have serious effects into the future. Oceanic island species, often narrowly endemic, are especially threatened and constitute a high proportion of recorded extinctions. Anthropogenic activities have caused non-marine mollusc extinctions since prehistory, but threats have increased greatly over the last few centuries and will probably continue to increase. Most mollusc species for which a population trend has been evaluated by IUCN are stable or declining; those few that are increasing are primarily introduced and invasive. Most threatened are oceanic island snails, North American and other freshwater bivalves, and the diverse and highly endemic micro-snails of Southeast Asian limestone outcrops.

15.1 Introduction

The IUCN Red List is a rigorous vehicle for assessing the conservation status of plant and animal species. However, although all mammal and bird species and overall almost 70% of all vertebrates recognised by IUCN have been evaluated, only a tiny fraction of invertebrates has been evaluated (IUCN, 2019, Table 1a). As a measure of threat, the Red List is probably quite accurate for birds and mammals, but severely underassesses invertebrates. Non-marine molluscs (Figure 15.1) stand out as the major group under the most severe threat.

https://doi.org/10.1017/9781108758826.016 Published online by Cambridge University Press

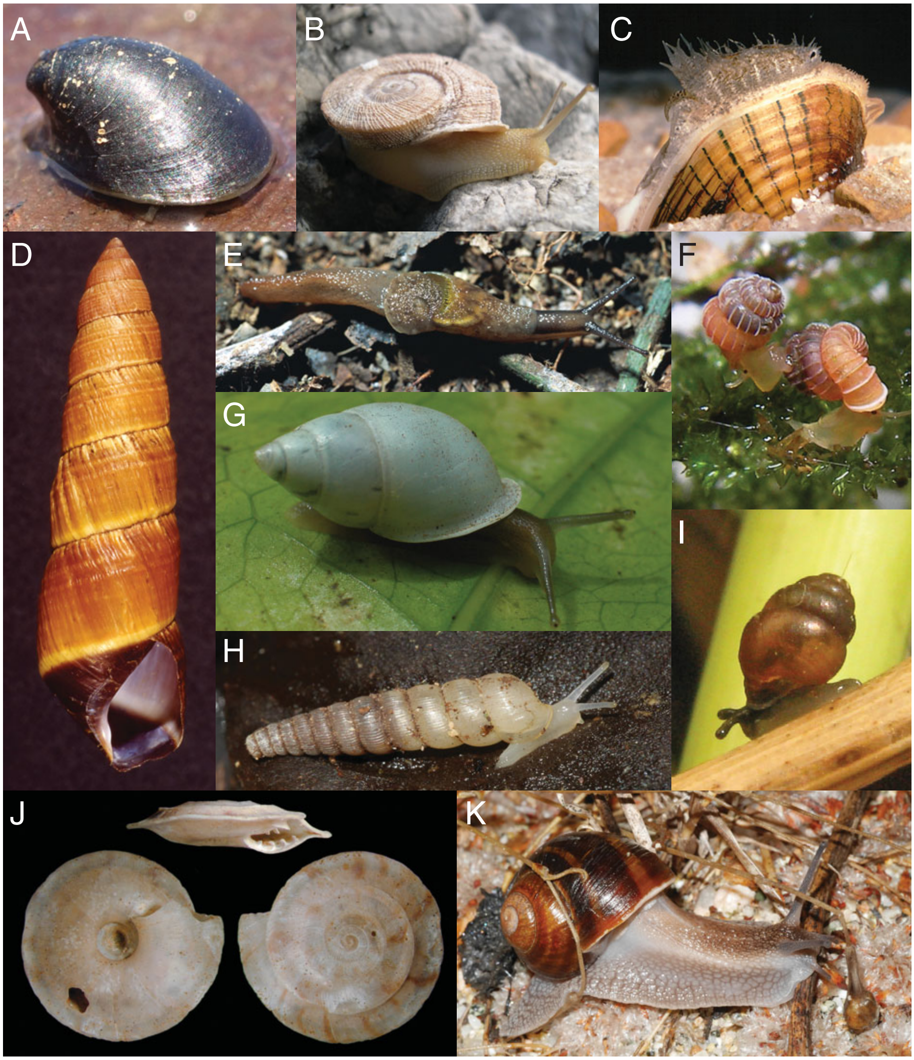

Figure 15.1 The diversity of non-marine molluscs: (A) *Ancylastrum cumingianus*, from Tasmania, listed as Critically Endangered by IUCN because of the impoundment of its freshwater habitat and predation by introduced fish (photo: K. Macfarlane), (B) *Iberus gualtieranus*, from southern Spain, listed as Endangered by IUCN as a result of habitat destruction and overexploitation (see text) (photo: Gualtieranus/Wikimedia Commons), (C) *Hamiota altilis*, a North American unionid bivalve, listed as Endangered by IUCN, displaying the lure it uses to attract a host fish (photo: W.R. Haag, US Forest Service), (D) *Carelia turricula*, from Hawaii, went extinct in the mid 20th century, listed as Extinct by IUCN (photo R.H. Cowie), (E) *Zonitarion* sp., an undescribed species, not listed by IUCN, from Gabon rainforest, illustrating the fact that we know nearly nothing about the conservation status of most tropical species from continental areas (photo: B. Fontaine), (F) *Plectostoma crassipupa*, a species from limestone hills in Malaysia, listed as Least Concern by IUCN (photo: Liew Thor-Seng), (G) *Partula hyalina* from the Austral Islands, to which it was introduced

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With the development of global taxonomic authority lists, the answers to the question 'How many mollusc species have been described?' are increasingly precise. As of 20 January 2020, MolluscaBase (www.molluscabase.org) had catalogued 74,942 valid described mollusc species, of which 48,704 were marine (estimated >98% complete, i.e. those not in MolluscaBase are described species not yet entered by the editors), 20,521 terrestrial (estimated ~70% complete) and 5884 freshwater (estimated ~80% complete). (The figure of 80,325 (IUCN 2019, table 1a) from MolluscaBase, as accessed by IUCN on 15 March 2019, mistakenly included fossils). The number of Recent described mollusc species is thus around 85,000. However, Recent Mollusca are far from fully inventoried globally, with a yearly increment of about 900 newly described species, with no sign of levelling; the real number of species is well in excess of 100,000, possibly even 150,000–200,000 (Bouchet, unpublished). A not negligible number of these newly described species are recently extinct, described based on specimens from the soil shell bank (e.g. Richling and Bouchet, 2013) or archaeological excavations (e.g. Haag, 2009).

Compared to other invertebrate groups, a relatively high number of mollusc species has been evaluated: 8664 species, just over 10% of the estimated 85,000 described species, with 2231 (26%) considered threatened (Box 15.1). Nonetheless, compared to mammals and birds, that only 10% of molluscan diversity has been evaluated is inevitably because of inadequate funding, not only for molluscs but for all invertebrates. Furthermore, and despite the fact that many of the evaluated mollusc species were chosen because they were judged sufficiently well known, a high proportion (25%) was evaluated as Data Deficient, compared to only 14.5% for all other non-molluscan species evaluated, and in stark contrast to mammals and birds, for which only 5.4% are listed as Data Deficient (Table 15.1). In terms of species listed as Extinct, molluscs stand out, with 300 of the 872 Extinct animal species. Combining this with those listed as Extinct in the Wild (14), Critically Endangered (Possibly Extinct) (141) and Critically Endangered (Possibly Extinct in the Wild) (1), gives a plausible upper estimate of 456 extinct mollusc species in the Red List (IUCN, 2019), i.e. 5.3% of those evaluated.

Of the mollusc species evaluated, only four marine species, all gastropods, are listed as Extinct, and only five cephalopods, four marine bivalves and 45 marine gastropods are listed in the threatened categories (Box 15.1), reflecting the general perception that marine

Figure 15.1 (*cont.*) by early Polynesian settlers from its native Tahiti, listed as Vulnerable by IUCN (photo: B. Fontaine), (H) *Pseudosubulina theoripkeni*, described from French Guiana in 2012 and found alive for the first time in 2018, but not listed by IUCN, another species illustrating how little we know about the conservation status of tropical continental species (photo: O. Gargominy), (I) *Vertigo moulinsiana*, from Europe, listed as Vulnerable by IUCN, is more widespread than previously thought (see text) (photo: O. Gargominy), (J) *Australdonta teaae*, from Rurutu, Austral Islands, was already extinct when described but not listed by IUCN, though listed by Cowie et al. (2017) (photo: O. Gargominy), (K) *Helix ceratina*, from Corsica, listed by IUCN (2019) as Critically Endangered but benefitting from habitat restoration (see text) (photo: O. Gargominy). Photos not to the same scale.

https://doi.org/10.1017/9781108758826.016 Published online by Cambridge University Press

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Box 15.1
IUCN Listings

Numbers of Mollusca in IUCN *Red List* categories[a] by ecosystem[b] (Red List version 2019-1, via 'advanced search').

Class	EX	EW	CR	EN	VU	NT	LR/CD	DD	LC	Total
Bivalvia										
Marine	0	0	0	0	4	0	4	15	6	29
Freshwater	32	0	72	62	50	55	0	155	312	738
Both	0	0	0	0	0	0	0	5	19	24
Total Bivalvia	**32**	**0**	**72**	**62**	**54**	**55**	**4**	**175**	**337**	**791**
Gastropoda										
Marine	4	0	5	13	27	29	0	152	488	718
Freshwater	74	3	263	228	416	165	0	922	823	2894
Terrestrial	190	11	317	252	517	431	0	558	1299	3575
Total Gastropoda	**268**	**14**	**585**	**493**	**960**	**625**	**0**	**1632**	**2610**	**7187**
Cephalopoda										
Marine	0	0	1	2	2	1	0	376	304	686
Total Cephalopoda	**0**	**0**	**1**	**2**	**2**	**1**	**0**	**376**	**304**	**686**
Total Mollusca	**300**	**14**	**658**	**557**	**1016**	**681**	**4**	**2183**	**3251**	**8664**

[a] EX – Extinct, EW – Extinct in the Wild, CR – Critically Endangered, EN –Endangered, VU – Vulnerable, NT – Near Threatened, LR/CD – Lower Risk: Conservation Dependent, LC – Least Concern, DD – Data Deficient

[b] A small number of gastropod species are categorised on the Red List as occurring in two and in some cases three ecosystems and are therefore counted more than once in Red List totals. We allocated them reasonably but somewhat arbitrarily to a single ecosystem for the purpose of this analysis.

IUCN has evaluated ~10% of described mollusc species, with the overwhelming majority being gastropods, and of which most are non-marine. Of those listed as Extinct (300) or Extinct in the Wild (14) only 4, all Extinct, are marine. Of those in the threatened categories (Critically Endangered, Endangered, Vulnerable), all but a few are non-marine. However, of all mollusc species evaluated 25% are Data Deficient, with the majority of these being non-marine, reflecting the lack of adequate knowledge for many species.

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Table 15.1 *Numbers of Mollusca, of mammals and birds and of all non-mollusc taxa in IUCN Red List categories (Red List version 2019-1)*

	EX	EW	CR	EN	VU	NT	LR/CD	DD	LC	Total
Mollusca	**300**	**14**	**658**	**557**	**1016**	**681**	**4**	**2183**	**3251**	**8664**
Mammals and birds	**237**	**7**	**426**	**960**	**1329**	**1363**	**0**	**911**	**11,685**	**16,918**
All non-mollusc taxa	**572**	**55**	**5256**	**8618**	**11,054**	**5506**	**204**	**13,032**	**45,551**	**89,848**

species are less threatened and have suffered lower extinction rates than non-marine species (e.g. McKinney, 1998). Although this view has been challenged on the grounds that knowledge of marine species is more limited than of non-marine species (e.g. Carlton et al., 1999), we suggest that knowledge of many, especially tropical, land snail species is at least as inadequate as knowledge of many marine mollusc species, and we do not think there is a demonstrated bias in recording marine versus non-marine mollusc extinction.

15.2 Timeframe for Listing Molluscs

The IUCN Red List was initiated in 1964. Molluscs were first included in 1983, when six species, all North American freshwater mussels (Unionida), were listed as Extinct out of 123 mollusc species evaluated (Figure 15.2). Following the realisation that an ill-conceived biological control programme begun in 1977 (Clarke et al., 1984) had caused the extinction of the entire fauna of partulid snails on the island of Moorea in French Polynesia (Murray et al., 1988) and that the extinction of Hawaiian species could be attributed in part to the same cause, initiated in the mid-1950s (Hadfield, 1986), more effort was put into evaluating molluscs for the Red List. In the 1986 Red List 53 species were listed as Extinct (45 Hawaiian land snails, 8 North American freshwater bivalves) out of 323 species evaluated. In 1988, 68 were listed as Extinct (four North American freshwater snails, the same 45 Hawaiian species, 7 *Partula* from Moorea and 12 North American bivalves) of 438 evaluated. The 1990 Red List added just one extinct species, *Parmacella gervaisi* from southern France, out of 513 species now evaluated. Following evaluation of many oceanic

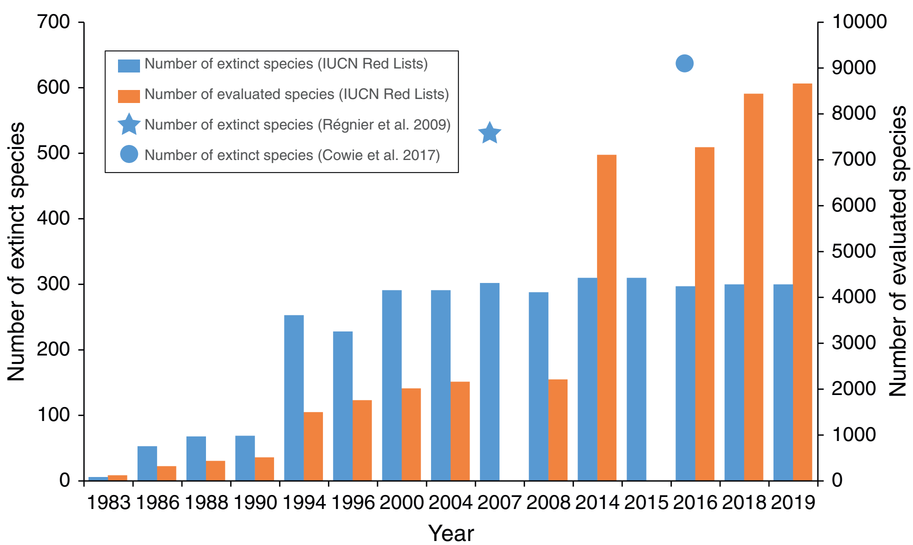

Figure 15.2 Numbers of mollusc species listed as Extinct by IUCN since the initiation of the Red List in 1964 to version 2019–1 (selected versions of the Red List only) with the total numbers of mollusc species evaluated, and estimates of actual known mollusc species extinctions (Régnier et al., 2009; Cowie et al., 2017).

https://doi.org/10.1017/9781108758826.016 Published online by Cambridge University Press

island species, notably from Hawaii and French Polynesia, the 1994 Red List included 253 extinct species out of 1501 evaluated. The 1996 Red List followed a new system of categories, with a number of species previously listed as Extinct recategorised as Not Evaluated, reducing the number listed as Extinct to 228 of 1760 evaluated.

In subsequent lists the number listed as Extinct increased to around 300 and has hovered there for the last two decades, despite the total number of species evaluated having almost quintupled (Figure 15.2). At the time of writing, 300 molluscs were listed as Extinct out of 8664 evaluated (IUCN, 2019).

15.3 Red List Extinctions Underestimate the Real Number

The Red List (IUCN, 2019) lists 872 species (750 animals, 122 plants) as Extinct, including 300 mollusc species. Molluscs, despite the small proportion that has been evaluated, thus represent 34% of all species extinctions and 40% of animal extinctions, as listed by IUCN. Based on bibliographic research and consultation with experts, Régnier et al. (2009) obtained, at that time, a more realistic assessment of the numbers of recorded mollusc extinctions, 533 species, far more than the number on the Red List, leading these authors to comment 'For mollusks [sic] (and all invertebrates) there is a disconnect between extinctions known to experts or published in the scientific literature and extinctions on the IUCN Red List, whereas for birds and mammals, the IUCN Red List is the scientific reference'. Following this approach, Cowie et al. (2017) listed 638 extinct species, 380 possibly extinct and 14 extinct in the wild, a total of 1032 species in these combined categories, and more than twice as many as IUCN listed in these categories. Even so, this approach only considers species with readily available information; it is therefore biased. To overcome this bias, Régnier et al. (2015a) developed an alternative approach using a random global sample of land snails. They found that, based on expert opinion and a probabilistic model, respectively, 10% and 12.5% of land snail species in the random sample should be classified as Extinct. When extrapolated to all non-marine mollusc species, this suggests that 3000–3750 are extinct, or even 5100 species (Cowie et al., 2017), an order of magnitude more, at least, than the IUCN number.

15.4 Causes and Timeframe of Mollusc Extinctions

Although anthropogenic extinctions are best documented in the last two centuries, modern extinctions appear to have begun well before AD 1500, the starting point of the IUCN Red List. The following paragraphs outline some examples of non-marine mollusc extinctions and their causes over the course of time up to the present. Habitat loss is probably the most important threat, although interactions among the various causes may be complex.

15.4.1 Non-Anthropogenic Causes

There is a rich molluscan fossil record, the vast majority of species having gone extinct long before the advent of *Homo sapiens*. For others, in some cases known as 'subfossils' (e.g. Régnier et al, 2015b), the relative roles of climate, habitat change and anthropogenic

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impact are unknown. However, there are few Recent documented land snail extinctions for which anthropogenic impact is excluded, e.g. the land snail *Zonites santoriniensis*, endemic to Santorini in the Aegean Sea, which probably did not survive the cataclysmic eruption of the island in around 1500 BC (Riedel and Norris, 1987).

15.4.2 Habitat Loss

Loss of habitat is probably the main cause of extinction and continues to be a major threat, because of deforestation, cultivation, mineral extraction and urbanisation.

On Porto Santo, in the Madeiran archipelago, at least nine geomitrid land snail species are known only from empty shells. They are presumed to have gone extinct before the nineteenth century scientific exploration of the island (De Mattia et al., 2018), no doubt a result of massive deforestation that also impacted the land snails of Madeira itself (Goodfriend et al., 1994).

The freshwater mussel *Reginaia apalachicola* is known only from pre-Columbian archaeological sites dating from 650 to 1500 years BP in the Apalachicola basin of the southeastern USA. Its demise has been related to the clearing and settlement of the Apalachicola basin, but it is possible that although it became extinct before it was described, it may have persisted into the late nineteenth century and no other mussel extinctions were documented in North America until 1924 (Haag, 2009).

Oceanic islands, particularly Pacific islands, have seen more mollusc extinctions than any other geographical region (Chiba and Cowie, 2016). In the Hawaiian Islands, which supported a documented fauna of >750 land snail species, it has been estimated that 65–90% of the fauna has gone extinct (Lydeard et al., 2004). Some of these extinctions may have occurred before human discovery and settlement of the islands 1200–800 years ago, but most happened subsequently (Régnier et al, 2015b).

Elsewhere in the Pacific, similar scenarios have affected many land snail groups, and while some extinctions through habitat destruction took place following early colonisation of the islands, the rate of habitat loss and consequent land snail extinction increased markedly following European arrival (e.g. Neubert et al., 2009; Sartori et al., 2014). For example, in the Gambier Islands, deforestation began with the first arrival of Polynesian people around 1000 years ago and peaked in the seventeenth and eighteenth centuries, with total destruction of the native flora (Conte and Kirch, 2008). A few of the 46 known land snail species were yet extant in the 1840s–1860s, but no living specimens of any but the three still extant in 1997 have been collected since the nineteeth century; the remainder were described from shells collected from the shell bank of the soil (Richling and Bouchet, 2013). Habitat destruction and species loss will probably continue, especially on islands not yet so severely affected (e.g. Rundell, 2010).

Although the Pacific islands stand out, snails of other oceanic islands have suffered similarly. In the Atlantic, soon after St. Helena was discovered in 1502, habitat destruction began and continued through to the mid-twentieth century, when a goat eradication programme (ultimately unsuccessful; Campbell and Donlan, 2005) was undertaken and the need for wood fuel had declined. But by then the natural vegetation had disappeared

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from most of the island, and of the 20 endemic snail species, only one or perhaps two remained; predation by rats, introduced at least by the end of the sixteenth century, may also have played a part in their extinction (Ashmole and Ashmole, 2000).

Much the same train of events led to the demise of many of the land snails of Mauritius. First colonised in the seventeenth century, gradual expansion of deforestation resulted in ~80% loss of native vegetation by the end of the nineteenth century, with less than 2% remaining at the end of the twentieth century; of the 81 endemic land snail species only 36 remain (Griffiths and Florens, 2006). Predation, notably by introduced rats but possibly also toads, in remnant snail populations may have been the death knell for these species.

Even once habitat loss has been arrested, which in most parts of the world it has not, there may still be an extinction debt to pay; we have not seen the last of land snail extinctions caused by past habitat destruction (Otto et al., 2017).

While anthropogenic extinction of non-marine molluscs has taken place over centuries, many species are still threatened by recent and ongoing habitat loss. For example, the freshwater snail *Melanopsis parreyssii* was listed as Critically Endangered on the Red List in 2013. It was extremely narrowly endemic in Romania but had been introduced to Hungary and Bulgaria. However, by 2010 these introduced populations had vanished (Sîrbu et al., 2013). The Romanian locality was part of a system sustained by a geothermal aquifer that was a nature reserve and a Natura 2000 Site of Community Importance. Yet despite the ostensible protection, rapidly increasing development of the geothermal waters, especially for tourism, led to shrinking of the thermal lakes to the point at which only one tiny lake remained. By 2011 the spring serving it ceased activity (Sîrbu et al., 2013) and by 2015 it had become little more than a puddle supporting no molluscs except an invasive bivalve; *M. parreyssii* was therefore deemed extinct in the wild (Sîrbu and Benedek, 2016), although it remains Critically Endangered on the Red List (IUCN, 2019).

A species of *Powelliphanta* is another example of a species on the brink of extinction from loss of its entire habitat. First collected in 1996 on Mount Augustus, a peak in New Zealand's South Island and the site of a large open cast coal mine, it was not recognised as a possible new species until 2003, by which time much of its habitat had been destroyed, with the entire remaining 8.5 ha of ridge-top habitat under severe threat (Walker et al., 2008). The species was described as *Powelliphanta augusta* in 2008 (Walker et al., 2008). Following legal action (see Walker et al., 2008), all snails and eggs that could be found were brought into captivity, beginning in 2006. Soon thereafter, all but a tiny piece of snail habitat was destroyed (Walker et al., 2008). Many of the snails were transferred back to the wild at three sites with supposedly similar habitat, but they were invaded by weeds and the mortality rate in these populations meant they were unlikely to survive (Morris, 2010). The captive snails exhibit slower growth and higher hatchling mortality than in the original wild population, and tragically, a large proportion died following an electrical malfunction in their temperature-controlled facility (James et al., 2013).

Limestone outcrops in Southeast Asia support extremely narrow endemic land snails, in some cases endemic to a single outcrop, with many undescribed. But they are under severe

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threat from mining of their habitat for cement production and for marble and road-surfacing materials (Schilthuizen et al., 2005). One species from Peninsular Malaysia was even named *Charopa lafargei* after the Lafarge cement company that was threatening its habitat, despite the company's stated positive biodiversity goals (Vermeulen and Marzuki, 2014). At the time of writing it remains extant (J.J. Vermeulen, personal communication).

Ancient oligotrophic lakes are another kind of 'island' that host highly endemic freshwater gastropod faunas that may vanish even before being documented. They are threatened by eutrophication and landfilling. For example, *Tchangmargarya ziyi* is a large (45 mm) recently described viviparid from Lake Babuhai in Yunnan, China, most of which has been filled for golf course construction, with the population probably now extinct (Zhang, 2017). Ancient lakes in the Balkans face severe reduction of habitat quality because of eutrophication and excessive water abstraction for agriculture. For example, 37% of the malacofauna of Lakes Prespa and Mriki Prespa is endemic to the lakes. Surveys conducted during 2003–2010 demonstrated a decline and potential loss of mollusc diversity, with all endemic species being of conservation concern (Albrecht et al., 2012); five are classified as Critically Endangered, although one of these (*Vinodolia lacustris*) was not found during the survey and could well be evaluated as Extinct.

Many reaches of large rivers, especially rapids, riffles and shoals that are key habitats for numerous freshwater molluscs are threatened everywhere by the construction of dams and by blasting to remove obstacles to navigation. Examples of extinct, probably extinct or extinct in the wild species from such habitats include *Helicostoa sinensis*, from the Yangtze (Wilke, 2019), *Melanoides agglutinans*, from the Congo (IUCN, 2019), and species of *Aylacostoma*, from the Paraná (Vogler et al., 2016; Cowie et al., 2017). *Helicostoa sinensis* (not listed by IUCN, 2019) and *Melanoides agglutinans* (Critically Endangered; IUCN, 2019) became Extinct without any conservation action. *Aylacostoma guaraniticum* and *A. stigmaticum* are Extinct (listed Extinct in the Wild; IUCN, 2019) and *A. chloroticum* and *A. brunneum* are Extinct in the Wild (the former so listed, the latter not listed; IUCN, 2019) and held in a captive breeding programme. Habitat loss from impoundment and channelisation of streams and rivers has been considered the main cause of the extinction of many species of North American mussels, although the ongoing decline may also be due to other, enigmatic causes (Haag, 2009, 2019). With so many such construction projects worldwide, this is a serious conservation issue.

Many more examples of decline and extinction of non-marine molluscs resulting from habitat loss could be provided, and as vast tracts of the Earth continue to be altered, often irreversibly, it is difficult to imagine that such trends will slow. Many species will no doubt not be described or even discovered prior to their demise.

15.4.3 Impacts of Introduced Species

It is generally difficult to demonstrate definitively that an invasive species has caused the extinction of another species. For example, following the zebra mussel (*Dreissena polymorpha*) invasion of North America beginning around 1985, many native freshwater mussels (Unionida) were considered doomed (Ricciardi et al., 1998). At localities with

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high zebra mussel densities, native mussel populations were being extirpated and some species were in steep decline or becoming regionally extinct. Over 60 species were thought to be in danger of global extinction from the combined effects of zebra mussels and habitat degradation (Ricciardi et al., 1998). However, a decade later, Strayer and Malcom (2007), focusing on four species, showed that although they had declined steeply following zebra mussel invasion, by 2000–2004 their populations had stabilised at 4–22% of their pre-invasion densities, offering hope that they could co-exist with the invaders, albeit at much lower densities. Another species of *Dreissena*, the Quagga mussel (*D. bugensis*), had been introduced at around the same time. It also became widespread in North America, but less is known about it and its distribution seems not to have expanded as comprehensively as that of *D. polymorpha*; it seems less likely to affect native unionids (Karatayev et al., 2015). Another mussel, *Limnoperna fortunei*, is having similar impacts in South America (Darrigran et al., 2012), but no extinctions have been attributed to it.

In contrast, the prime example of an invasive species causing extinction of mollusc species is the introduction of the predatory snail *Euglandina rosea* (in fact a species complex; Meyer et al., 2017) to the islands of the Pacific, notably to the Hawaiian Islands and the Society Islands of French Polynesia, but also elsewhere (e.g. Cowie and Cook, 2001), in poorly considered efforts to control the invasive giant African snail, *Achatina fulica* (Hadfield, 1986; Murray et al., 1988). The clearest evidence of direct impact was that as *E. rosea* spread across the island of Moorea, the endemic *Partula* tree snail species vanished in its wake (though a few remnant populations were subsequently discovered and represent most of the major genetic lineages; Haponski et al., 2019); it did not control *A. fulica* (Murray et al., 1988; Chiba and Cowie, 2016). On the other islands of the Society group the same story played out, with the exception of a few remnant populations surviving on Tahiti in addition to those on Moorea (Coote and Loève, 2003; Gerlach, 2016). As currently recognised (Gerlach, 2016), of 18 Moorean and Tahitian species, 6 are Extinct, 5 are Extinct in the Wild, 4 are represented by remnant wild individuals and 3 by both captive and remnant wild individuals (Haponski et al., 2019). Taxonomic revision of these partulid species is sorely needed to resolve the discord between the traditional morphological taxonomy (Gerlach, 2016) and molecular (including phylogenomic) data (Haponski et al., 2019).

In Hawaii, the combination of *E. rosea* and invasive rats, following on from habitat destruction, caused the decline of endemic achatinelline tree snails (Hadfield, 1986). Another introduced predatory snail, *Oxychilus alliarius*, may yet impact endemic Hawaiian species, notably the single species in the monotypic helicarionid genus *Kaala* (Curry et al., 2016), and potentially other oceanic island species (Curry et al., 2019). Rats have been widely implicated in land snail extinction in the Pacific (Chiba and Cowie, 2016). The invasive predatory flatworm *Platydemus manokwari* has caused the extinction of endemic Pacific island snails, notably in the Ogasawara Islands (Chiba and Cowie, 2016). Competition between invasive and native snails may also be important, but few definitive instances have been documented (e.g. Riley and Dybdahl, 2015).

The impacts of invasive species are often inextricably linked to those of habitat loss, as invasive species such as ungulates (especially goats) and rats, may drastically alter habitat,

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rendering it unsuitable for native animal species, and habitat alteration may facilitate the spread of additional invasive species. As such, invasive species can be at least the partial cause of extinction, acting in concert or consecutively with habitat alteration. But, with some clear exceptions, it is difficult to say that invasive species, per se, have been the cause of specific mollusc extinctions.

15.4.4 Exploitation and Collecting

Numerous non-marine mollusc species are exploited for human consumption. In Europe, and especially in Mediterranean countries, various larger species of land snails are eaten, most notably *Helix pomatia*, *Helix lucorum* and *Cornu aspersum*, which used to be collected in the wild but are now increasingly farmed. Despite local declines in *Helix pomatia* abundance, whether this is a conservation issue is unknown. Various other species are eaten around the Mediterranean (Yildirim et al., 2004) but few seem to have attracted concern, for instance *Iberus gualtieranus* (Figure 15.1b), a species from southern Spain, which is listed as Endangered in part because of to indiscriminate and uncontrolled collecting, as it has great gastronomic appeal. In New Caledonia, the endemic 'bulimes' (genus *Placostylus*) have regressed everywhere because of habitat loss (Neubert et al., 2009), but they remain common on the Isle of Pines, where they are harvested for the gourmet trade, necessitating regulations that prohibit export from the island. In Asia, various species of Ampullariidae, Viviparidae and Pachychilidae are eaten, as are a number of clams and mussels (e.g. Köhler et al., 2012), and Achatinidae are eaten in West Africa (e.g. Nyoagbe et al., 2016); but none of these species has attracted great concern.

A few land snails are used for medicinal and religious purposes (Cowie and Robinson, 2003; Neto et al., 2012) but there is no evidence that these usages have led to their decline and certainly not extinction.

In the nineteenth century, freshwater mussels (Unionida) were commercially harvested for their pearls, notably in the USA and Europe; overharvesting led to their decline and the fishery was largely abandoned (Anthony and Downing, 2001). However, soon thereafter, the demand for freshwater mussel shells for making buttons burgeoned, causing further declines and adding to the already serious and increasing threats from habitat degradation; but this industry essentially died out with the advent of plastics (Anthony and Downing, 2001), although it persists in other parts of the world (Beasley, 2001). However, the discovery in Japan that mussel shell material could act as nuclei for cultured pearl production, resulted in a further phase of exploitation in the USA for export, although as mussel stocks declined, so the industry began to wane (Anthony and Downing, 2001). Although overexploitation caused severe declines of some species, habitat degradation has been considered the primary cause of mussel extinction (Haag, 2009, 2019).

The shell-collecting hobby and associated trade focuses more on marine than non-marine species. However, among non-marine species there are a few notable instances in which shell collecting and ornamental use may have been at least partially responsible for the decline and perhaps extinction of certain species. For example, collecting of snails by late nineteenth- and early twentieth-century shell collectors quite possibly had an

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important impact on some of the larger and more colourful Hawaiian species (Hadfield, 1986). Partulids, achatinellines and other species have been used in the Pacific islands to make necklaces and other ornaments. For example, *Cyclomorpha flava* was heavily collected for this purpose on the island of Anaa (Tuamotu archipelago), possibly impacting its populations (Fontaine, personal observations). The collection of ~10,000 shells of the partulid *Eua zebrina* that were used to make the chandeliers in the lobby of American Samoa's then main hotel (Cowie and Cook, 2001) must have significantly reduced some of its populations. While collection and trade of shells of non-marine species is much more limited than of marine species, it nonetheless may lead to endangerment. However, the Convention on International Trade in Endangered Species (CITES) lists only three non-marine gastropod taxa: the genus *Achatinella*, with 39 species listed as either Extinct (15) or Critically Endangered (24) by IUCN (2019), the genus *Polymita*, with no species evaluated, and *Papustyla pulcherrima*, listed as Near Threatened.

Overall, therefore, exploitation and collecting have not been major causes of non-marine mollusc extinction.

15.4.5 Climate Change

Land snails may be especially susceptible to the ramifications of anthropogenic climate change (Nicolai and Ansart, 2017), but there is as yet no instance of extinction of a mollusc species that can be definitely attributed to such change. However, continued warming will probably have more serious effects in the future.

Rhachistia aldabrae, an endemic cerastid from Aldabra Atoll, was widespread and abundant in the 1970s, but was thought to have gone extinct by the late 1990s as a result of declining rainfall, and was therefore placed on the Red List as Extinct. This is the only instance of a mollusc reported as having gone extinct because of climate change. However, although in 2014 an adult and a few juveniles were located, it seems likely that with ongoing climate change it may yet succumb. It is now listed as Critically Endangered (IUCN, 2019).

Pearce and Paustian (2013) undertook extensive elevational surveys in Pennsylvania, USA, to assess whether, with climate warming, species forced ever upward would eventually be unable to retreat further. Of the 69 species recorded, 5 appeared especially susceptible. Such susceptibility is of particular concern on oceanic islands. On many Pacific islands, habitat destruction and establishment of invasive species at lower elevations has resulted in most of the remaining endemic land snails being confined to higher elevations (e.g. Régnier et al., 2015b), either because their lower elevation populations were extirpated or because they are evolutionarily adapted to the lower temperatures at these higher elevations and historically only ever occurred there (e.g. *Nesoropupa* spp. on Tahiti; Gargominy, 2008). A similar situation obtains in the Azores (Cameron et al., 2012). As such, with limited opportunity to move to higher elevations as the climate warms, these species face extinction.

There have also been several studies on the negative impact of climate change on freshwater mussels (e.g. Hastie et al., 2003).

Climate change has many complex and inter-related ramifications and while it may directly lead to extinction of non-marine molluscs as the climate exceeds their

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physiological tolerances, habitat change and the facilitation of invasive species resulting from climate change may also do so to the extent that the proximate cause of extinction may be the result of broader environmental change.

15.5 IUCN Species Trajectories

While the statistics regarding extinction of molluscs are depressing, the explicit goal of the Red List is not to assess extinction but to assess relative extinction risk, thereby focusing attention on conservation needs. Thus for each species, IUCN now evaluates (if there are adequate data) whether it is declining, stable or increasing, based on the IUCN Red List Categories and Criteria (IUCN, 2012), which generally means that trends are determined over 10 years or three generations, whichever is longer, up to 100 years.

Of the 7678 non-extinct gastropods in the Red List (Box 15.1), trajectories have been evaluated for 6578 (Table 15.2). However, among these, the trajectories of a high proportion of both gastropods (72%) and bivalves (65%) were evaluated as 'unknown'. Among the remainder, bivalves appeared to be declining more than gastropods; only 37% of these bivalves were stable, while 75% of the gastropods were stable. Very few were evaluated as increasing: 6 of 238 bivalves (2.5%) and 35 of 1,647 gastropods (2.1%).

Reliance on the '10-year rule' (Fox et al., 2019) to assess trends of invertebrates has, however, received criticism, with 10 years considered too short to detect a real trend. Few mollusc species are monitored with sufficient frequency, which is a factor in the high proportion with 'unknown' trends. The number for which a trend could be evaluated may be highly biased.

Notwithstanding this criticism, among all 41 increasing species, the range of 27 at least has expanded because of anthropogenic introductions (Table 15.3). All but two of these

Table 15.2 *Population trends of those bivalve and gastropod species evaluated, by ecosystem*[a]*, based on Red List evaluations (Red List version 2019–1)*

	Unknown	Stable	Decreasing	Increasing	Total
Bivalvia					
Marine	18	1	0	0	19
Freshwater	417	86	145	6	654
Total Bivalvia	**435**	**87**	**145**	**6**	**673**
Gastropoda					
Marine	532	45	15	0	592
Freshwater	2254	195	168	17	2634
Terrestrial	1472	999	190	18	2679
Total Gastropoda	**4258**	**1239**	**373**	**35**	**5905**
Total	**4695**	**1326**	**519**	**41**	**6578**

[a] A small number of gastropod species are categorised on the Red List as occurring in two and in some cases three ecosystems and are therefore counted more than once in Red List totals. We have allocated them reasonably but somewhat arbitrarily to a single ecosystem only for the purpose of this analysis.

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Table 15.3 *Species of bivalves and gastropods evaluated as increasing, and whether introduced or invasive as reported in their Red List (IUCN, 2019) species accounts*

Species	Category	Habitat	Introduced/invasive
Bivalvia			
Dreissena polymorpha	LC	Freshwater	'Invasive'
Elliptio complanata	LC	Freshwater	Not known as introduced, 'stable'
Dreissena bugensis	LC	Freshwater	'Invasive'
Corbicula fluminea	LC	Freshwater	'One of the worst invaders of aquatic ecosystems'
Corbicula fluminalis	LC	Freshwater	'Introduced'
Limnoperna fortunei	LC	Freshwater	'Introduced'
Gastropoda			
Monacha fruticola	LC	Terrestrial	'Introduced'
Tandonia serbica	LC	Terrestrial	'Probably introduced'
Xerocrassa molinae	NT	Terrestrial	Not known as introduced
Pachnodus silhouettanus	NT	Terrestrial	Not known as introduced
Gyraulus chinensis	LC	Freshwater	'Introduced'
Brephulopsis cylindrica	LC	Terrestrial	'Widespread alien species'
Haitia acuta	LC	Freshwater	'Widely introduced'
Deroceras sturanyi	LC	Freshwater	'Very widely spread through introduction'
Cipangopaludina chinensis	LC	Freshwater	'Introduced widely in North America'
Oxychilus cellarius	LC	Terrestrial	'Introduced to many parts of the world'
Oxychilus draparnaudi	LC	Terrestrial	'Introduced to many parts of the world'
Xerocrassa meda	LC	Terrestrial	'Introduced'
Pomacea canaliculata	LC	Terrestrial	'One of the worst invaders'
Pseudosuccinea columella	LC	Freshwater	'Highly invasive'
Trochulus clandestinus	LC	Terrestrial	Not known as introduced
Ferrissia dohrnianus	LC	Freshwater	Not known as introduced
Chilostoma sphaeriostoma	LC	Terrestrial	'Expanded its range. . .possibly due to. . .human activities'
Discus macclintocki	LC	Terrestrial	Not known as introduced 'stable'
Biomphalaria choanomphala	LC	Freshwater	Not known as introduced
Biomphalaria pfeifferi	LC	Freshwater	'An invasive species'
Oxychilus alliarius	LC	Terrestrial	'Introduced. . .often invasive'
Tandonia kusceri	LC	Terrestrial	'Introduced'
Arion hortensis	LC	Terrestrial	'Outside Europe all records are likely to be introductions'

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Table 15.3 (*cont.*)

Species	Category	Habitat	Introduced/invasive
Gyraulus convexiusculus	LC	Freshwater	'Introduced'
Viviparus acerosus	LC	Freshwater	Not known as introduced
Trochoidea caroni	LC	Terrestrial	Not known as introduced
Gyraulus rossmaessleri	LC	Freshwater	Not known as introduced
Biomphalaria alexandrina	LC	Freshwater	Not known as introduced but 'a pest'
Charpentieria itala	LC	Terrestrial	'Introduced'
Deroceras invadens	LC	Terrestrial	'Invasive'
Bulinus liratus	LC	Freshwater	Not known as introduced
Tarebia granifera	LC	Freshwater	'Very widely introduced'
Ferrissia fragilis	LC	Freshwater	'Wide introduced distribution'
Bellamya constricta	LC	Freshwater	Not known as introduced
Melanoides tuberculata	LC	Freshwater	'Introduced'

increasing species are evaluated as Least Concern. The two others, *Xerocrassa molinae* and *Pachnodus silhouettanus*, are listed as Not Threatened, the former exhibiting a slight increase perhaps because the islands on which it lives are protected, and the latter increasing by actively colonising abandoned coconut plantations. The majority of these increasing species are introduced, often invasive, species. Also, two species, the bivalve *Elliptio complanata* and the gastropod *Discus macclintocki*, are indicated in the assessment text as stable but categorised as increasing. Thus only 15 (or perhaps 13) species are increasing naturally or in one case because of conservation action, a tiny fraction of the total of 1885 species for which a trajectory could be determined. But at least if species that were evaluated as stable really are stable over the long term then their conservation status is good.

15.6 Global Status

Although this chapter focuses heavily on mollusc extinction, noting that this is particularly severe on oceanic islands, it is becoming clear that much greater numbers of non-marine molluscs, though not yet extinct, are under considerable threat. For example, the European Red List of terrestrial molluscs (Neubert et al., 2019) considers 2469 species as native in Europe, but only five of these as Extinct, apparently in marked contrast to the picture painted above. However, 19.5% of the species are Critically Endangered, Endangered or Vulnerable. Adding the Near Threatened species, increases those at risk to 33.5%, and hypothesising that the Data Deficient species may also be threatened, gives a maximum of 43.6%, almost half the terrestrial malacofauna of Europe. Extrapolating to the rest of the world, suggests that over 9000 terrestrial mollusc species are at risk. The situation for freshwater species is probably worse. For example, in 2011, of 624 African species, although only 14 were considered Extinct, 57% were evaluated as being in one of the threatened categories or as Data Deficient (Seddon et al., 2011).

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Arguably then, although the likely number of recent mollusc extinctions is great, especially on oceanic islands, the overall global picture is even worse because close to half of all extant mollusc species are probably under some level of threat. Given the enormous and ongoing habitat loss in tropical continental regions, this scenario may not be exaggerated.

15.7 Notable Conservation Efforts

Despite all the threats faced and extinctions suffered by non-marine molluscs, committed people have undertaken diverse projects to protect and save many threatened species. These projects include efforts to breed threatened species in captivity for introduction to the wild once, optimistically, threats are ameliorated, habitat protection to support populations of endangered species, inventory surveys to locate populations of threatened species and to identify hotspots of threatened diversity, and surveys to locate as yet undescribed species before they vanish.

Numerous projects have been undertaken by or under the aegis of the IUCN Mollusc Specialist Group. Particularly notable is the captive breeding and currently ongoing release programme for Society Island partulids (Coote et al., 2019). Other captive breeding programmes include those in Hawaii for achatinelline tree snails (e.g. Sischo et al., 2016), in Bermuda for *Poecilozonites* spp. (Outerbridge et al., 2019) and in the Ogasawara Islands of Japan primarily for *Mandarina* spp. (Mori et al., 2020), as well as for endangered bivalves in both North America (e.g. Neves, 2004) and Europe (e.g. Kyle et al., 2017).

Major efforts have continued to be made by IUCN to evaluate additional mollusc species in key regions including eastern Mediterranean freshwater species, European terrestrial molluscs and Pacific island land snails, among others referenced by Cowie et al. (2017), as well as the freshwater molluscs of Madagascar (Van Damme et al., 2018). Other concerted surveys have been undertaken over large regions, e.g. eastern and southern Africa (Seddon et al., 2005), and more narrowly focused but intensive surveys of highly endangered and locally endemic groups that have already suffered catastrophic extinction, e.g. Hawaiian Amastridae (Régnier et al., 2015b), have also been undertaken, in some cases rediscovering species previously considered extinct.

One of the few mollusc-specific conservation success stories is that of the endemic Corsican land snail *Helix ceratina* (Figure 15.1k). When rediscovered in 1994, it had not been seen since the 1910s and was confined to less than 7 ha of habitat in the suburbs of Ajaccio, squeezed between the airport, a large car park and beach access paths (Bouchet et al., 1997). It became the object of the first-ever ‘Arrêté préfectoral de Biotope’ project undertaken in France specifically for an invertebrate. Habitat was restored, including closure and restoration of the 2 ha car park to its natural state. This was accompanied by outreach promoting the value of *H. ceratina*, not so much for its scientific or ecological importance, but more for the heritage and cultural value of this narrow-range endemic.

Because many of the threats faced by non-marine molluscs (and many other species) are related to habitat degradation and loss, significant international efforts have been made to

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preserve and restore key habitats. For example, the European Union's 'Habitats Directive' aims to preserve habitats in order to conserve a large number of species listed in its Annexes, particularly Annex II, which lists 29 gastropod and 4 bivalve species. Among these are four species of wetland land snails in the genus *Vertigo*. As a result, there was a burgeoning of research on *Vertigo* spp. within the framework of the Habitats Directive. In England, when a population of *V. moulinsiana* was discovered in the path of a major road development, an entire segment of habitat, with snails, was moved to a location away from the road's path and additional habitat was created (Stebbings and Killeen, 1998). The project failed, but at least prompted additional surveys that revealed that the species was more widespread than previously thought (Williams, 2006). The Habitats Directive has, however, been criticised because of its highly vertebrate bias and because it is not adequately focused on rare and threatened species (Fontaine et al., 2007a).

Freshwater molluscs suffer from pollution and other impacts on water quality (e.g. Pérez-Quintero, 2011). Improving water quality may therefore improve the conservation status of threatened species. The problem of water quality has spawned national and regional policies and efforts that have reduced pollution, for example in Europe (e.g. bij de Vaate et al., 2006) and North America (Bogan, 2006). However, there seems to have been little effort to assess any direct effect of such improvement on threatened molluscs, and, indeed, repopulation (to the extent recorded) of improved habitat may involve primarily non-native species, thereby negatively affecting remnant native species (e.g. bij de Vaate et al., 2006) or species that are not threatened (Locy et al., 2002). In North America, filter/suspension feeding bivalves have been promoted for their ability to improve water quality, which in turn could focus attention on conservation and enhancement of those species chosen to implement such efforts (Kreeger et al., 2018), although these efforts are unlikely to focus on seriously threatened species.

Finally, the incorporation of molecular genetics in conservation has advanced more sophisticated efforts to, for instance, identify cryptic molluscan species via integrated taxonomic approaches (e.g. Collado et al., 2019), delineate evolutionary significant units or lineages within molluscan species (e.g. Buckley et al., 2014) and assess and avoid inbreeding in captive breeding programmes for molluscs (Price & Hadfield, 2014).

15.8 Conclusion

In 1983, 123 mollusc species were evaluated for the IUCN Red List, 6 of them deemed Extinct. By 2019, 300 of 8664 species evaluated were deemed Extinct (IUCN, 2019), although more realistic estimates of the number of extinctions are much higher (Régnier et al., 2009, 2015a, b; Cowie et al., 2017). Molluscs face diverse threats but because most are not 'charismatic', efforts to stem the rate of extinction and ameliorate the threats face an uphill battle. Nonetheless, small groups of dedicated people are doing everything they can to aid this effort, as attested to by the many articles from all over the world published in *Tentacle*, the IUCN Mollusc Specialist Group newsletter (www.hawaii.edu/cowielab/Tentacle.htm).

Often, when considering the daunting task of invertebrate conservation, vertebrate specialists will invoke the 'umbrella species' concept, suggesting that if we conserve the

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charismatic megafauna, then the invertebrates in the same habitats will also be conserved, almost by default. But conservation strategies for often narrowly endemic invertebrates, notably many of the threatened mollusc species discussed here, cannot be the same as those for wide-ranging vertebrates (Fontaine et al., 2007b), especially as many species are facing highly specific threats, e.g. predation by an introduced snail predator or elimination of a specific limestone outcrop.

There are more recorded extinctions among non-marine molluscs than in any other animal group; those that remain face a diversity of ongoing threats. Efforts to save some of the most threatened species continue, but their long-term chances of success may be slim. We are in a race against time. We need to continue to describe species before they vanish and place them on the conservation radar screen before they go extinct. We need to augment single-species approaches with broader conservation initiatives, identifying key habitats, regions, ecosystems and hotspots. Conservation-related research should be promoted in neglected regions of the world and should include generation of more basic knowledge of life history, habitat preferences, etc. Finally, if mollusc conservation is to surmount the huge barriers it faces, we must advocate, advocate, advocate.

Acknowledgements

We thank Eike Neubert and Gonzalo Giribet for reviews of drafts of the manuscript and Reuben Clements, Olivier Gargominy, Wendell Haag, Kevin Macfarlane and Liew Thor-Seng for providing photos in Figure 15.1. Publication number 11584 of the University of Hawaii School of Ocean and Earth Science and Technology.

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