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Impact of Biological Invasions on Ecosystem Services

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Chapter 10

Displacement and Local Extinction of Native and Endemic Species

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Abstract The observational evidence on non-native plants, mammals, reptiles, fish, mollusks earthworms, and insects as drivers of population declines or extinctions of native taxa suggests that non-native predators are far more likely to cause the extinction of native species than non-native competitors. Notable examples of such taxa include non-native vertebrates and mollusks as mainly predators and plants and insects as mainly competitors. The most vulnerable species are insular endemics, presumably because of the lack of coevolution between introduced pred-

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ator and native prey. Island-like situations contribute to severe impacts because the affected native taxa have nowhere to escape. The presence of dormant stages in plants makes it possible to escape unfavourable conditions over time and might contribute to the lack of clear evidence of native plant species driven to extinction by plant invaders. Overall, robust evidence has accumulated during the past few decades that non-native species are drivers of local and global extinctions of threatened, often endemic, native species.

Keywords Competition • Disease • Endemic species • Invasion debt • Island • Species extinction • Population decline • Predation • Vulnerable species

10.1 Introduction

Biodiversity, the variability among living organisms on Earth, represents the foundation of human well-being by providing different services to mankind (Millennium Ecosystem Assessment 2005), and extinction or deterioration of biodiversity puts the availability of many of these services at risk. The questions of whether, and if so, to what extent, non-native species are generally responsible for population declines or extinctions of native taxa has received increasing attention in the last couple of decades. A number of case studies had strongly implicated non-native species in extinctions of individual species (Bell 1978), or at specific locations (Fritts and Rodda 1998). These observations were followed by data-based analyses and evaluations of available data on causes of population declines and extinction, such as on threatened species in the USA (Wilcove et al. 1998) or species on the IUCN Red List (Gurevitch and Padilla 2004; Bellard et al. 2016). A number of these reports provided evidence implicating non-native species as a driver and a leading cause of native and endemic species extinctions (Blackburn et al. 2004; Clavero and García-Berthou 2005). Nevertheless, other authors have questioned these conclusions (Gurevitch and Padilla 2004; Sax and Gaines 2008).

A wide range of human activities are changing environments around the world, with deleterious effects on the species inhabiting these environments. Examples of these activities include agriculture and aquaculture, carbon emissions into the atmosphere leading to climate change, biological resource use, pollution, and residential and commercial development. These changes need to be taken into account when evaluating the role non-native species are thought to have in causing extinctions, because this role may be based to a large extent on circumstantial evidence. Species declines and extinctions are rarely associated with single driving processes (Bellard et al. 2016), and so it is possible that in many cases, native species declines and non-native species increases are coincidental, arising from simultaneous responses of native and non-native species to other anthropogenic disturbances. Direct causality is generally difficult to prove (Gurevitch and Padilla 2004), and the rigorous experiments that would allow the effects of multiple factors and their interactions to be

separated are logistically difficult and therefore largely nonexistent. Several recent authors have argued that the impacts of non-native species as drivers of extinction have been overestimated as a result (Gurevitch and Padilla 2004; Didham et al. 2007). Invasion debts, cumulative effects, or the decoupling of cause and effect by time lags, in combination with shifting baselines of the effect size over time, create further difficulties in evaluating the impacts of invasions (Essl et al. 2015).

Efforts to prevent, control, or mitigate the environmental impacts of these species soak up substantial financial and social resources from conservation organisations and concerned governments. In this chapter, the available evidence on non-native species as drivers of population declines, or extinctions of native taxa, is summarised. The analysis is focused on non-native plants, vertebrates, mollusks earthworms, and insects, but not examples of pollinators, pathogens, and pests to crops and forests, because these topics are presented in other chapters of this book (Fried et al. 2017; Kenis et al. 2017; Morales et al. 2017).

10.2 Invasion-Caused Population Declines or Extinctions

10.2.1 *Searching for Patterns Across Taxa: Quantitative Evidence from Large Datasets*

Wilcove et al. (1998) were among the first to compile data on threats to a large number of threatened species for a large geographic area in the United States (USA). They identified non-native species as a major driver of threat. Subsequently, Gurevitch and Padilla (2004) focused on the causes of extinctions in the IUCN database, arguing that non-native species were implicated in only a small proportion of extinctions. However, their analysis was shown to be flawed, and greatly underestimated extinctions caused by non-native species, as pointed out by Clavero and García-Berthou (2005). These authors showed that of 680 extinct animal species, causes could be identified for 170 (25 %), of which 91 (54 %) included the effects of non-native species. Globally, non-native species were found to be the most frequent known cause of extinction for birds and the second most frequent for fish and mammals (Clavero and García-Berthou 2005). Revisiting this analysis using updated IUCN Red List data found similar results: non-native species are the second most common threat associated with plant, amphibian, reptile, bird, and mammals species that have gone completely extinct since 1500 AD, and the most common threat associated with extinctions in each of amphibians, reptiles, and mammals considered separately (Bellard et al. 2016). Non-natives had their lowest impact on plant species, where they were only the fourth ranked driver of extinction (Bellard et al. 2016). In a similar analysis of IUCN data for threatened species in Europe, 354 species (of 1872 threatened) were considered to be specifically affected by non-native species, and they represented the third most important cause of threat after dam construction and water management, and agricultural and forestry effluents (Genovesi et al. 2015). A recent global

meta-analysis of the ecological impacts of non-native species in inland waters revealed strong negative effects of invaders on native species abundances that were, however, not associated with a decrease in species diversity of invaded communities, suggesting a time lag between rapid abundance declines and local extinctions (Gallardo et al. 2015).

For birds, population declines for 68 of the 98 imperilled species in the USA (Wilcove et al. 1998) were attributed to non-natives. These impacts were mainly caused by non-native predators, which threatened 57 % of the 68 species; by non-native pathogens, affecting 34 % of the 68 species (all in Hawai'i); and by other non-native animals acting as competitors. Evidence for impacts of non-native plants is much weaker. Thus, less than 6 % of imperilled bird species were thought to be declining because of non-native plants as the only factor. However, if non-native plants exerted impacts, it was in the majority of cases in combination with habitat destruction (Wilcove et al. 1998). Evidence for damage to bird populations owing to non-native plants is correlative, and it is unknown whether the non-native plants have had a definitive causal role in the decline of any bird species (Gurevitch and Padilla 2004). Another analysis revealed that the number of non-native mammal species is positively correlated with the proportion of the endemic avifauna lost to extinction across islands worldwide (Blackburn et al. 2004).

Together, these data sets indicate that (i) most imperilled species face more than one threat, and (ii) it is difficult to disentangle proximate and ultimate causes of decline or interactions between different threats (Gurevitch and Padilla 2004). Overall, these studies provide consistent evidence that (iii) non-native species represent a major threat to rare and endemic native species that often leads to extinction. The mechanisms behind these processes are best illustrated by the examples of case studies that follow.

10.2.2 Case Studies of Non-native Plants: Past Population Declines of Native Species Suggest Future Extinctions

Numerous vegetation studies document the retreat of native species from invaded plant communities by competition with the invader (Brewer 2008). Only a few published cases, however, more or less clearly demonstrate the threat of particular plant invaders to specific conservation targets (some examples are listed in Table 10.1).

The paucity of hard evidence that non-native plants drive extinctions of native plant species may be caused by the interaction of mechanism and time. Plants interact primarily through competition, which is a slow and subtle process. Most non-native invasions have only occurred within the last few hundred years, and this may not be sufficient time for the full impacts of plant invasions to have played out, especially given the ability of plants to ride out difficult times in dormant stages. For example, the invasion of the South American native tree, *Cinchona pubescens*, into a formerly treeless environment in the Galápagos Islands decreased the diversity

Table 10.1 Selected studies investigating population displacement of native species caused by invasion

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
Galápagos	<i>Cinchona pubescens</i> (Rubiaceae); South America	Plant: tree	<i>Pteridium arachnoideum</i> ,	Cover of most native species decreased by at least 50 %, cover of endemic herbaceous species reduced by 89 %; no species lost at the landscape scale	Increased shade and precipitation	Jäger et al. (2009)
			<i>Cyathea weatherbyana</i> *, <i>Miconia robinsoniana</i> *, <i>Pilea baurii</i> *			
Mauritius (Black River Gorges National Park)	<i>Psidium cattleianum</i> (Myrtaceae); South America	Plant: tree	<i>Ixora vaughanii</i> *, <i>Nervilia bicarinata</i> , <i>Chassalia capitata</i> *, understory flora critically threatened (IUCN criteria)	Two species that were presumed extinct and several critically threatened with extinction had recovered following the removal of non-native plants; no species lost	Competitive exclusion	Baider and Florens (2011)

(continued)

Table 10.1 (continued)

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
California, USA	<i>Ammophila arenaria</i> (Poaceae); Europe	Plant: grass	<i>Lupinus idestromii</i> (endangered)	Population models derived from field data projected that 2 of 3 study populations will decline toward extinction under ambient levels of consumption	Apparent competition: native species experienced high levels of pre-dispersal seed consumption by the native rodent <i>Peromyscus maniculatus</i> from the proximity to the non-native grass <i>Ammophila arenaria</i>	Dangremond et al. (2010)
Alberta, Canada	<i>Bromus inermis</i> , <i>Poa pratensis</i> (Poaceae); Eurasia	Plant: grass	<i>Anemone patens</i>	Long-term persistence of <i>A. patens</i> in habitats dominated by non-native grasses is unlikely	Decreased survival and reduced population growth of <i>A. patens</i> among non-native grasses	Williams and Crone (2006)

California, USA	<i>Aporrectodea trapezoides</i> (Lumbricidae); Holarctic	Invertebrate: earthworm	<i>Argilophilus marmoratus</i>	Displacement of the native species only occurs in disturbed habitats	Higher relative growth rates of non-native <i>Aporrectodea</i> in high-productivity conditions	Winsome et al. (2006)
Mediterranean Sea	<i>Brachidontes pharaonis</i> (Mytilidae); Indian Ocean, Red Sea	Invertebrate: mollusk	<i>Mytilaster minimus</i>	Displacement following change of habitat; no extinction	Habitat degradation caused an increase in abundance of the invader, displacing the native through increased propagule pressure	Rilov et al. (2004)
North America	<i>Dreissena polymorpha</i> (Dreissenidae); Europe	Invertebrate: mollusk	Freshwater unionid bivalves	Of the historic 281 species, 19 are known to be extinct, 21 are thought to be extinct, 77 are endangered, 43 are threatened, and 72 are of special concern	Competition, substrate (habitat) and water quality alteration	Ricciardi et al. (1998)
Pacific islands	<i>Euglandina rosea</i> (Spiraxidae); North America	Invertebrate: mollusk	Endemic snails*	More than 100 endemic species are considered to be extinct	Predation of native snails	Hadfield et al. (1993) and Régnier et al. (2009)

(continued)

Table 10.1 (continued)

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
California, USA; Mexico	<i>Cactoblastis cactorum</i> (Lepidoptera); South America	Invertebrate: insect	<i>Opuntia</i> spp.*	Some 80 <i>Opuntia</i> species endemic to Mexico and the USA are considered at risk; also cultivated and used wild species are considered vulnerable	Herbivory	Hoffman et al. (2000) and Stiling (2002)
Madeira	<i>Pieris rapae</i> (Lepidoptera); Europe	Invertebrate: insect	<i>Pieris brassicae</i> subsp. <i>wollastoni</i> *	Introduction led to the extinction of the native subspecies	Disease transmission	Kenis et al. (2009)
Europe (UK, Belgium)	<i>Harmonia axyridis</i> (Coleoptera); Asia	Invertebrate: insect	<i>Adalia bipunctata</i>	Declines of 30–44 % over 5 years after the arrival of <i>H. axyridis</i> led to displacement of the native species	Direct predation and resource competition	Roy et al. (2012)
New Zealand	<i>Vespa vulgaris</i> and <i>V. germanica</i> (Hymenoptera); Europe	Invertebrate: insect	Birds*, insects	Several common and widespread bird species have had significant declines in their abundance of the last 30 years; attributable to the impacts of a number of introduced species, but especially wasps	Foraging behaviour of birds affected; Predation of caterpillars;	Kenis et al. (2009)

Christmas Islands, Australia	<i>Anoplolepis gracilipes</i> (Hymenoptera); Africa	Invertebrate: insect	<i>Gecarcoidea natalis</i> *	The yellow crazy ant has killed millions of red crabs, approximately a third of the population, with subsequent invasional meltdown and significant declines of other species	Direct predation, nuisance and habitat modification by seed predation and removal	O'Dowd et al. (2003)
Lake Victoria, Africa (Kenya, Uganda, Tanzania)	<i>Lates niloticus</i> (Latidae); tropical Africa	Vertebrate: fish	Endemic cichlids	Extinction of 200 or more of the approximately 500 species radiation of endemic cichlid fishes (<i>Haplochromis</i> spp.)	Predation	Aloo (2003)
Spain	<i>Gambusia holbrooki</i> (Poeciliidae); North America	Vertebrate: fish	<i>Aphanius iberus</i> (cyprinodontid fish)	Extirpation of many populations	Mostly through predation on juveniles and possibly competition. Habitat alteration (e.g., salinity) mediates the interaction	Alcaraz and Garcia-Berthou (2007)
Guam	<i>Boiga irregularis</i> (Colubridae); Australia	Vertebrate: reptile	Birds, bats, reptiles	Introduction led to the extinction of several bird species on Guam	Predation (incl. eggs); presence of alternate introduced prey	Fritts and Rodda (1998)

(continued)

Table 10.1 (continued)

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
Islands worldwide	<i>Felis catus</i> (Felidae)	Vertebrate: mammal	Birds, mammals, reptiles (48, 16 and 4 endemic, respectively)	Feral cats on islands are responsible for at least ~14 % of the modern bird, mammal, and reptile global extinctions and threaten ~8 % of critically endangered species in these groups	Predation; presence of introduced alternate prey (rodents and rabbits)	Medina et al. (2011)

Note that the overview is to illustrate the variety of mechanisms reported in various taxonomic groups rather than providing an exhaustive summary of known cases of extinctions and population declines caused by invasive species



Fig. 10.1 *Cinchona pubescens* invasion on the island of Santa Cruz, Galapagos. (Photograph by Heinke Jäger)

and the cover of most native species by at least 50 %, and of endemic herbs on average by 89 %, over 7 years (Fig. 10.1). However, the number of native, endemic, and non-native species in the study area remained constant: no plant species has been lost completely at the landscape scale (Jäger et al. 2009). Nevertheless, if the present 20 % cover of *C. pubescens* continues to grow, local extinctions are likely.

A range of studies suggest that, as with *C. pubescens*, plant invasions are generating situations where extinctions of native species are likely or inevitable given enough time, assuming that the trajectory of the invasion continues as it is. For example, meta-population models of Californian grasslands suggest that, even at low levels of invasion, the spread of European grasses may generate an extinction debt (Gilbert and Levine 2013). Although the time to extinction of the species that cannot persist with invasion in this system can be in terms of hundreds of years, these authors concluded that recent suggestions that plant invasions fail to drive native plant extinctions may be premature. In a similar vein, demographic models indicate that non-native grasses in Alberta, Canada, may cause slow declines in populations of the native *Anemone patens*, and that despite short-term coexistence, extinction risk in *Bromus inermis* grass patches is too high over a 50-year time period to make the survival of *A. patens* likely (Williams and Crone 2006).

The complexity of the interactions that may cause non-native plant species to drive out natives can be demonstrated in another coastal dune system in California.

Here, the endangered native plant *Lupinus tidestromii* experiences high levels of pre-dispersal seed consumption by the native rodent *Peromyscus maniculatus* as a result of the proximity of the non-native grass *Ammophila arenaria*. Population models projected that two of three study *Lupinus* populations will decline toward extinction under ambient levels of consumption (Dangremond et al. 2010). The phenomenon of consumer-mediated apparent competition posing a strong extinction threat to native plant species may be more frequent than realised if non-native plants can support large increases in consumer density, and hence consumption of native species and their seed. If this consumption occurs before seed dispersal, it can have strong population-level effects on native plants (see Dangremond et al. 2010 and references therein). Another mechanism that can eventually lead to population decline of a rare native species is hybridisation. For example, *Lantana depressa*, an endemic species in Florida, is hybridising with the non-native South American species, *Lantana camara*, and the hybrid offspring are competitively replacing the rare native (Schierenbeck 2011). Further evidence comes from Mauritius, where two plant species that were presumed extinct, several plant species that were critically endangered, and one endemic butterfly species, all recovered dramatically as a consequence of the removal of the non-native tree *Psidium cattleianum* (Baider and Florens 2011).

Our fears about the impacts of non-native plant species mainly derive from predictions, from explicit or implicit models, about the likely outcomes of on-going invasions and their potential to generate extinction debts (Gilbert and Levine 2013), rather than from direct observations of extinctions. However, the fact that no species extinctions have yet been caused solely by competition with non-native plants (Sax and Gaines 2008) is not an excuse for complacency. As with climate change, the predictions of models based on well-established processes cause significant concern and should not be dismissed without equally good evidence to the contrary.

10.2.3 Case Studies of Non-native Animals: Robust Evidence for Native Species Extinctions and Declines

In general, examples of native species population declines caused by animal invaders, both invertebrates and vertebrates, reflect clearer population impacts than are documented for plants, and often lead to local and global extinctions of native species. This trend is likely to result from the impacts of non-native animals often acting through predation or disease, both of which are strong and rapid processes compared to competitive displacement. Examples of non-native animal species that have driven native population declines and extinctions are given in Table 10.1.

Vertebrates: Mammals, Reptiles, and Fish Vertebrate invasions have been responsible for some of the most serious ecological catastrophes in history, which correspond with some groups, mammals in particular, having the most severe environmental impacts of all invading organisms. For example, a review of feral

cats, *Felis catus*, on islands as drivers of native species extinctions (Medina et al. 2011) showed that impacts have been documented from at least 120 different islands on at least 175 vertebrate species (25 reptiles, 123 birds, and 27 mammals), many of which are listed as threatened by IUCN. Cat impacts were greatest on endemic species, particularly mammals, and were more severe if alternative non-native prey species, such as rodents and rabbits, were also introduced. Feral cats on islands are considered to be responsible for at least 33 global bird, mammal, and reptile extinctions recorded by the IUCN Red List (14 % of the 238 extinctions in total), and have contributed to the critically endangered status of 38 (8 %) of the 464 taxa within these groups. It is nonetheless important to keep in mind that these figures are conservative: the impact of cats on many, perhaps most, species has not been yet studied (Medina et al. 2011). The red fox, *Vulpes vulpes*, is another major predator responsible for species extinctions. Together with cats it is thought to have contributed to the disappearance of all but 2 of the 22 completely extinct marsupials and rodents in Australia.

A classic example of non-native mammal species driving native species to extinction is given by the avifauna of the New Zealand archipelago (Holdaway 1999). New Zealand had no native terrestrial mammal predators before around 800 years ago and the arrival of the Maori, who brought with them the Pacific rat, *Rattus exulans*. A wave of extinctions in the native avifauna followed this colonisation, with the species disappearing having characteristics that either made them attractive to human hunters (flightless, large-bodied species) or susceptible to Pacific rat predation (small-bodied, ground-dwelling, and ground-nesting species laying small eggs). A subsequent extinction wave followed the arrival of Europeans in the eighteenth century. They introduced additional non-native mammals, such as cats, stoats (*Mustela erminea*), and black and brown rats (*R. rattus* and *R. norvegicus*), which preyed upon species that had thus far survived by being too large to be susceptible to Pacific rats and too small to be of interest of humans (Holdaway 1999). A specific example of these impacts concerns the black rats that reached Big South Cape Island around 1964 (Bell 1978, cited in Courchamp et al. 2003). This island was, up to that point, free of non-native predatory mammals and was home to the last viable populations of four endemic vertebrate species that had formerly been widespread across New Zealand (South Island snipe, *Coenocorypha iredalei*; South Island saddleback, *Philesturnus carunculatus*; bush wren, *Xenicus longipes*; greater short-tailed bat, *Mystacina robusta*). Once local conservationists realised that rats had reached the island, attempts were made to catch and translocate individuals of these four species to other islands. Some of these translocation programs were, however, unsuccessful, and three of these species are now globally extinct as a result.

These repeated examples of the temporal coincidence between non-native mammal species arrival and the extinction of bird species with traits that make them susceptible to predation strongly suggest cause and effect (Holdaway 1999). Further examples of massive extinction events following vertebrate biological invasions concern a fish and a snake. The former refers to the invasion of Lake Victoria in Africa by the Nile perch, *Lates niloticus*, in the 1950s, which was followed by the

extinction or near-extinction of several hundred endemic cichlid fishes. However, fishery overexploitation, eutrophication, and invasion by the water hyacinth, *Eichhornia crassipes*, have also been related to the decline of native fishes (Aloo 2003). No such ambiguity surrounds the other example, which relates to the invasion of the brown tree snake, *Boiga irregularis*, following its accidental introduction to Guam in the 1950s. This invasion induced a cascade of extinctions that may be unprecedented in terms of taxonomic scope and severity. The most affected taxa were birds, bats, and reptiles, and by 1990, Guam harboured only three native vertebrates, all of which were small lizards. A few other species persisted on small, offshore islands not reached by the snake. An important factor in this invasion was the presence of alternate introduced prey, such as the curious skink, rats, and mice, that contributed to maintaining the populations of the invader at high levels while it was driving the native prey species to extinction (Fritts and Rodda 1998).

Invertebrates: Earthworms, Mollusks and Insects As for non-native plants, the presence of non-native invertebrates often goes hand in hand with other anthropogenic impacts, making it hard to draw clear conclusions about the effects of non-natives in suppressing native species populations. For example, the displacement of native earthworms in California by the non-native Holarctic earthworm, *Aporrectodea trapezoides*, only happens in disturbed habitats (Didham et al. 2007). Similarly, habitat change and sedimentation in the Mediterranean Sea allowed an increase in the abundance of a non-native mollusk *Brachidontes pharaonis*, and local displacement, without extinction, of a native species (Rilov et al. 2004). Even the devastating impact of the invasion of *Dreissena polymorpha* in North America that resulted in the presumed extinction of around 40 native freshwater unionid bivalves cannot be unequivocally attributed to this invasion alone but to habitat destruction and deterioration as well (Ricciardi et al. 1998).

Biocontrol agents have been deliberately released with unintended consequences for native species. Among mollusks the predatory rosy wolfsnail, *Euglandina rosea*, was introduced as a biocontrol agent against the giant African landsnail, *Achatina fulica*, to many Pacific islands, and it is estimated one-third of native mollusk extinctions on oceanic islands may have been caused by the introduction of *E. rosea* (Régnier et al. 2009). Similarly, the cactus moth, *Cactoblastis cactorum*, native to South America and a successful biocontrol agent against *Opuntia* in many places around the world, has been introduced accidentally to southeast USA where it is a serious threat to endemic *Opuntia* species (Myers and Cory 2017). There is also convincing evidence for the substantial decline of native ladybird species as a consequence of the introduction of the harlequin ladybird, *Harmonia axyridis*, in Europe (Myers and Cory 2017), but again, there is no evidence of extinctions as yet (Fig. 10.2).

Examples of insects driving population declines include the North American non-native wasp, *Vespula pensylvanica*, that by direct predation and exploitative competition make several Hawaiian native bee and wasp species, including endemics, avoid floral resources occupied by the invader and become absent from areas near its colonies. The European *Vespula germanica* and *V. vulgaris*, introduced to

Fig. 10.2 Introduced *Harmonia axyridis* is displacing native ladybird species in Europe. (Photograph by Wolfgang Rabitsch)



New Zealand, prey on other arthropods, specifically butterflies, but also negatively affect endemic bird foraging behaviour (Table 10.1). Both cases point to the vulnerability of native island biota to ecological disruption caused by continental species. Ants provide multiple lines of evidence for competitive displacements of native species on all continents as well as many islands (Holway et al. 2002). The yellow crazy ant, *Anoplolepis gracilipes*, has decimated the population of native red crab on Christmas Island (O'Dowd et al. 2003). The Argentine ant, *Linepithema humile*; the red imported fire ant, *Solenopsis invicta*; the bigheaded ant, *Pheidole megacephala*; and several other non-native ant species have displaced native ant species and reduced diversity almost everywhere they have become established, yet no extinction of native species has been reported so far. The extinction of the endemic Madeiran large white butterfly, *Pieris brassicae* subsp. *wollastoni*, is considered to have been caused by the introduction of, and disease transmission by, the related *Pieris rapae* (Kenis et al. 2009).

10.3 What Makes a Native Species Vulnerable to Population Decline and Extinction Resulting from Invasion?

Several principles have been put forward to explain differences in the vulnerability of particular taxonomic groups to population declines or extinctions caused by invasions, illustrated in these examples.

(i) Non-native predators and pathogens are far more likely than non-native competitors to cause the extinction of native species (Gurevitch and Padilla 2004). (ii) The most vulnerable species are island endemics; among hypotheses to account for the severity of extinction events on islands is the lack of coevolution between introduced predator and prey (Duncan et al. 2013). (iii) Presence of alternative non-native prey of the non-native predator increases the probability that it will drive the native prey to extinction (Fritts and Rodda 1998). The case studies summarised in

Table 10.1 further illustrate that island-like situations, be they oceanic islands or freshwater lakes, contribute to severe impacts because the affected native taxa have nowhere to escape. Islands with refuges tend to suffer lower levels of loss (Duncan et al. 2013).

One principal difference among plants and insects on one hand, and vertebrates on the other, related to the opportunity to escape from the immediate impact of the invader, is the presence of dormant stages in the former, such as seeds or pupae, which make it possible to escape not only in space but also in time, by waiting for more favourable conditions. Another explanation for the obviously less severe impacts, in terms of extinctions, on plants compared to vertebrates was suggested by Sax and Gaines (2008). For birds on islands, these authors suggest that the colonization-based saturation point has been reached, meaning that new species cannot be added unless existing species are removed. For plants, there is no evidence of extinction-based saturation on islands; this assumption is supported by the great numbers of plants that have become naturalized on islands worldwide (Sax and Gaines 2008) although relatively few native species have become extinct. Nevertheless, there is no robust evidence for colonization-based saturation in birds either, and we think that other explanations for the different levels of extinction between birds and plants on islands (e.g., the different interaction mechanisms at play) are more likely.

10.4 Conclusions

This review provides robust evidence accumulated over the past decade that non-native species cause local and global extinctions. Nevertheless, the impacts are not felt equally by all taxa, and direct evidence of native species extinctions as the result of invasion is still largely lacking for plants, and to some extent also for insects. We still need better data to allow us to separate unequivocally the cases of proven direct effects of invading non-native species on population declines and extinctions of native taxa from those where both the invading non-native and affected native species are passengers of the environmental change, such as habitat degradation (Gurevitch and Padilla 2004). Although many (if not most) extinctions can be attributed to multiple causes, among which non-native species are one of the contributing factors (and sometimes might be “the final nail in the coffin”), substantial datasets coincide in showing that non-native species do have an important role in these processes (Bellard et al. 2016).

One strong signal that has been already noticed by Gurevitch and Padilla (2004) is that a few non-native species have been known to cause a disproportionately large share of documented extinctions (Table 10.1). Prominent examples include cats, the brown tree snake, a few widespread rat species, predatory snails and fishes, and possibly also annual Mediterranean grasses. In general, however, non-native plant and insect impacts are expressed in terms of local displacement of native species and community changes, rather than in species extinctions. Interestingly, these

'superinvaders' that drive native biota to extinction comprise relatively few species (compared to the large number of introduced species worldwide) but recruit from diverse functional groups. Our review nevertheless indicates that despite some scepticism about the importance of non-native species for extinctions (Gurevitch and Padilla 2004; Sax and Gaines 2008), evidence has accumulated that makes it impossible to dismiss the impacts of non-native species, and in particular vertebrate animals, as drivers of native population declines and extinctions.

Although much still needs to be learned about the functionalities and interdependencies between biodiversity in all its expressions, it is evident that the increasing loss of native species can have cascading effects on interspecific species interactions and thus on regulating services. Because non-native species contribute to this loss, any attempts to reduce their impact means safeguarding ecosystem services provided for future generations.

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