Article

Species extinction: Frequency and biogeography

John C. Briggs
Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97333, USA
Present address: 2320 Guerneville Rd., Santa Rosa, CA 95403, USA
E-mail: clingfishes@yahoo.com

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Abstract
Documented extinctions, that have taken place among surrogate taxa during the past 500 years, provide useful information about the extent of recent faunal extinctions and their geographic locations. Species extinctions among terrestrial vertebrates (birds and mammals) and invertebrates (insects and molluscs) have generally taken place in space-restricted habitats, primarily oceanic islands. An extinction pathway leads from the high diversity tropics to less diverse, peripheral habitats that function as extinction traps. The pace along the extinction pathway is gradual and its function is similar to a pathway which has been observed in the marine environment. Overall, the low incidence of recent extinctions appears to be a continuation of the minimal rates that were characteristic of the Pleistocene epoch. Thousands of species, represented by small populations on the pathways to extinction, can still be rescued if there is sufficient interest in doing so.

Keywords extinction pathways; extinction traps; global extinctions; vertebrates; invertebrates.

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1 Introduction

Previous estimates of global species extinction have been largely based on terrestrial vertebrates and higher (angiosperm) plants. It is time we make the effort to learn more about the animal species that comprise the great majority in the terrestrial world. The insects and the molluscs have been relatively neglected, and we need to know how they have fared under human influence. The insects, by themselves, have invaded almost every possible niche and have discovered almost every way to make a living. They may be said to control the living world above the level of the sea and their fate is our fate. There is fear that insects may be undergoing a mass extinction (Fonseca, 2009) but there is no evidence in the form of documented extinctions. Life in the marine environment has apparently suffered very little extinction following the beginning of the Pleistocene. In comparison, the precarious state of numerous small populations on land and in the sea indicates a looming extinction debt. This debt constitutes the world's true biodiversity problem.

2 Terrestrial Environment

2.1 Insects

More than one half of all described species of multicellular organisms are insects (Mayhew, 2007) and there have been many estimates of the total number of insect species ranging from two million to ten million or more. A recent estimate by an entomologist is about 3.4 million species (Dunn, 2005). In the terrestrial environment, about 90% of all species are insects. Published estimates of global biodiversity loss for the past 35 years have been based entirely or primarily on theoretical extinctions among terrestrial vertebrate animals and higher plants. Considering the overwhelming species diversity of insects, it seems odd that little attention has been paid to their effect on global biodiversity. Apparently, the sheer number of insect species, and the fact that most of them are still undescribed, has discouraged estimates of their global extinction rate. Yet, certain groups of insects are well known and provide data that can be used to give an approximation of biodiversity loss in insects as a whole.

Thanks to the interests of professional and amateur entomologists, the species of butterflies, tiger beetles, and the dragonflies plus damselflies (Odonata) are well known. The world total of butterfly species is about 17,280 (Shields, 1989). Although three species are often listed as extinct (two in South Africa and one in the USA), the records are doubtful. Ehrlich (1995) found that there was no documented extinction of a continental butterfly species anywhere in the world. Although island butterfly species are numerous, there is only one documented extinction, a species that was endemic to the Island of Mauritius (IUCN, 2011).There are about 2,300 species of tiger beetles (Pearson, 2001) and, although several are listed as endangered, none has become extinct. For the Odonata, a random sample of 1,500 of the 5,680 described species was assessed (Clausnitzer et al., 2009). Ten percent of the sample was considered to be threatened but none of them had become extinct. In fact, there are only two documented extinctions, one from Maui in the Hawaiian Islands and the other from St. Helena, an island in the South Atlantic.

It has been observed that biodiversity is often too complex to measure directly, so conservation planning must rely on surrogates to estimate the biodiversity of given areas. Published studies, testing the ability of surrogate taxa to capture the richness of other (target) taxa, have been reviewed (Lewandowski et al., 2010). It was found that the most effective surrogates tended to have large numbers of habitat specialists spread over extensive environmental gradients (e.g., plants, birds, and mammals). The three insect orders meet those criteria and should provide a suitable surrogate for all insects. If the extent of extinction (three species out of 25,260) is indicative, the extinction rate has been exceedingly low. According to the IUCN Red List, the total number of documented extinctions for all insects over the past 500 years is 66, and 38 of these losses took place on the Hawaiian Islands. These numbers are also small relative to the estimated 3.4 million species. Compared to the species extinctions recorded for the terrestrial vertebrates, the lack of extinctions among the insect groups is astonishing. Records for the birds and mammals for the past 500 years, based on evidence in the IUCN Red List and the CREO List at the American Museum of Natural History, indicate losses of 128 bird species and 61 mammals; in each case about 95% of the extinctions occurred on oceanic islands (Loehle and Eschenbach, 2012). In their analysis, the authors considered Australia (a physiographic continent) to have functioned as a biogeographic island, due to its separation from other parts of the world during the latter half of the Cenozoic. If insect extinctions had occurred at the same rate as the birds over the same time, we would expect the loss of about 44,000 species (Dunn, 2005). Such an enormous loss of insect species would surely have been detected. As in the case of the vertebrates, the majority of the insect extinctions apparently took place on oceanic islands.

2.2 Molluscs

In comparison to the relatively few extinctions among the insects and vertebrates, a large number, more than half of all recorded species extinctions over the past few centuries, has taken place among the Mollusca. The number of living molluscan species has been estimated at 200,000 (Lydeard et al., 2004). The most recent analysis (Régnier et al., 2009) identified 566 extinct molluscs; about 400 of them were from oceanic islands representing 71% of the total. The extinct island species were terrestrial, mostly from Hawaii, French Polynesia, and the Mascarene Islands. About one-third of the island extinctions were caused by the human introduction of the predatory snail *Euglandina rosea*. The IUCN Red List identified 842 animal and plant species as having gone extinct in the past 500 years; 746 of the total were animals. It seems incredible that the great majority should be molluscs, almost all of them terrestrial and freshwater. Only 4 of the 55,000 marine molluscs were considered to be extinct.

3 Discussion

The foregoing data reveal some striking comparisons. In regard to the terrestrial environment, the 3.4 million insects comprise 90% of the biodiversity and, indications of their loss of species over the years, should allow a good estimate of overall biodiversity decline. But, utilizing the three best known insect groups as surrogates revealed only three extinctions for the past 500 years. What is there about the biology of insects that makes them so resistant to extinction? In contrast, we have the molluscs, with about 62,000 terrestrial and freshwater species (Lydeard et al., 2004), that have endured the loss of566 species (Régnier et al., 2009) which amounts to almost three quarters of all animal extinctions recorded on the IUCN Red List. Why have the molluscs been so vulnerable?

The three extinctions in the insect surrogate groups occurred on oceanic islands, and we may recall that 38 of the 66 extinctions recorded for all insects occurred on the Hawaiian Islands. About 400 of the 566 mollusc extinctions occurred on islands and of the 6,000 freshwater species, 140 have become extinct. As noted, only four marine mollusc extinctions have been recorded. The island and freshwater extinctions are comparable because they took place in space-restricted habitats. Therefore, if these data on the major invertebrate groups are considered together with the terrestrial vertebrate extinctions, it may be concluded that the great majority of all land and freshwater extinctions have taken place among species with small populations in small spaces, primarily oceanic islands. This suggests that such places function as extinction traps in which the occupants are highly vulnerable. Although one may find an occasional example of escape from such a restricted habitat, it is a rare occurrence. This leads to the conclusion that continental extinctions during the past 500 years have seldom taken place, excepting a few freshwater locations.

4 Marine Environment

Extinctions that have taken place in the marine environment during the past five centuries are far fewer than those that have occurred on land. The total marine species diversity has been estimated at 2.21 million eukaryotic species (Mora et al., 2011). An article by Dulvy et al. (2009) on Holocene extinctions in the sea has provided a useful history. A total of 20 marine extinctions have been recorded from the beginning of the Holocene about 12,000 years ago. The 20 extinctions include 4 mammals, 8 birds, 4 molluscs, 3 fishes, and 1 alga. One of the three fish species, the New Zealand grayling, is here excluded because it was primarily a freshwater species. Some have suggested that marine losses may actually have been substantial because so many species are still unknown that their extinctions may have escaped notice. In this regard, Reaka-Kudla (1997) estimated the number of coral reef species at 950,000, meaning that only about 10% of them have been described, and implying that numerous extinctions could have been missed. But, many coral reefs have been closely monitored in recent years, so the disappearance of familiar species should have been noted.

Of all the reef denizens, the fishes are the best known. In places such as the Florida Keys or Hawaii, any extinctions occurring during the past 50 years would have been recorded. As noted, only two marine fishes were known to have become extinct, the Galapagos damselfish and the Mauritius green wrasse (Dulvy et al., 2009). However, the latter species has been taxonomically confused and is actually the adult male (terminal phase) of *Anampses caeruleopunctatus*, a species that is common and widespread throughout the Indo-West Pacific (Russell and Craig, 2013). This leaves only one marine fish species documented to be extinct, and reduces the total known marine extinctions to 18.

Many shallow water marine species occur as small populations around isolated islands and archipelagos. Some of them represent remainders of once large and widely dispersed species. An example is the gastropod species *Strombus vomer* which had a continuous western Pacific distribution in the Pliocene (Abbott, 1960). This species now exists as small populations scattered across parts of its former range (Marshall and Crosby, 1998). The breakup of one central species into small, relict populations appears to indicate a progression toward extinction. Other examples, found among distribution patterns of Indo-Pacific reef fishes and mollusks suggest a possible sequence. In the Coral Triangle, new species evolving in the central area, often appear to displace their older relatives. This apparent, competitive displacement usually results in the new species expanding its range within the Triangle and beyond, while the older relative is relegated to peripheral locations. Most often, the older relative becomes split into relict populations that continue to exist to the north and south of the Triangle (antiequatorial positions)(Briggs, 1999).

Fricke (1983) has shown that the fish species *Diplogrammus xenicus* (Callionymidae) exists as two populations, apparently having been displaced by its close relative *D. goramensis* (Fig. 1). Another example is the gastropod mollusk *Mitra chinensis* (Mitridae); its relict populations are separated by its relative *M. triplicate* (Cernohorsky, 1976) (Fig. 2). In their analysis of the fish genus *Istiblennius* (Blenniidae), Springer & Williams (1994) found that *I. bellus, I. zebra*, and *I. muelleri* constituted a monophyletic triad. This unusual east-west pattern (Fig. 3) suggests that *I. muelleri* is the dominant species having replaced *I. bellus.* The Hawaiian Islands may have originally invaded by *I. bellus* which subsequently speciated in that isolated habitat. These examples of apparent competitive replacement provide snapshots of the start of a historical process that may take millions of years to finish. Extinction would be expected to occur as the disjunct populations grow smaller and eventually disappear. Thus, many of these relict populations, some of which may have speciated in isolation, appear to be on the verge of extinction but still manage to hang on.

The larger and more immediate part of the marine extinction threat consists of a thousand or more small populations of fishes and invertebrates that are the collapsed remnants of species that have been overfished (Briggs, 2011). These remnants are now found all over the oceans, from the tropics to the poles to the deep sea. Some of them represent collapses that took place 30-50 years ago, yet they have still managed to avoid extinction (Roberts, 2007). Overfishing has drastically reduced most populations from their sizes prior to exploitation. Lotze and Worm (2009) investigated records of 256 exploited fish populations and found an 89% decline from known historic levels. Populations that have sustained losses of this magnitude are generally considered to have collapsed. A collapsed state means that the population has become so depressed that it no longer plays an effective role in the ecosystem. In terms of its biological and commercial value, a collapsed population has become a shadow of its former self and its chances of continued survival are greatly diminished.

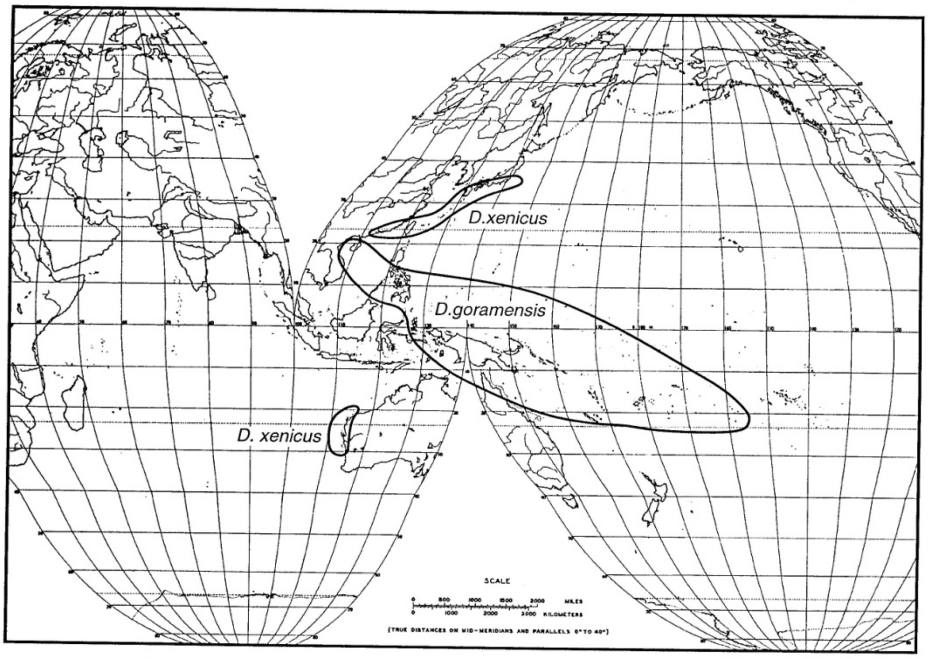

Fig. 1 The relict populations of*Diplogrammusxenicus* separated by *D. goramensis.* After Fricke (1983).

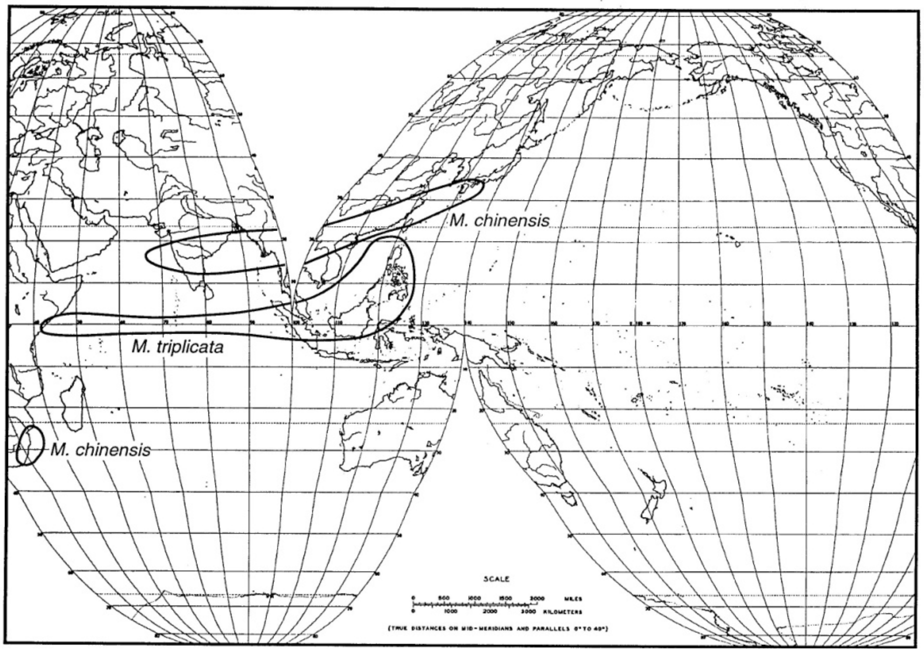

Fig. 2 The antiequatorial populations of *Mitra chinensis* separated by *M. triplicata.* After Cernohorsky (1976).

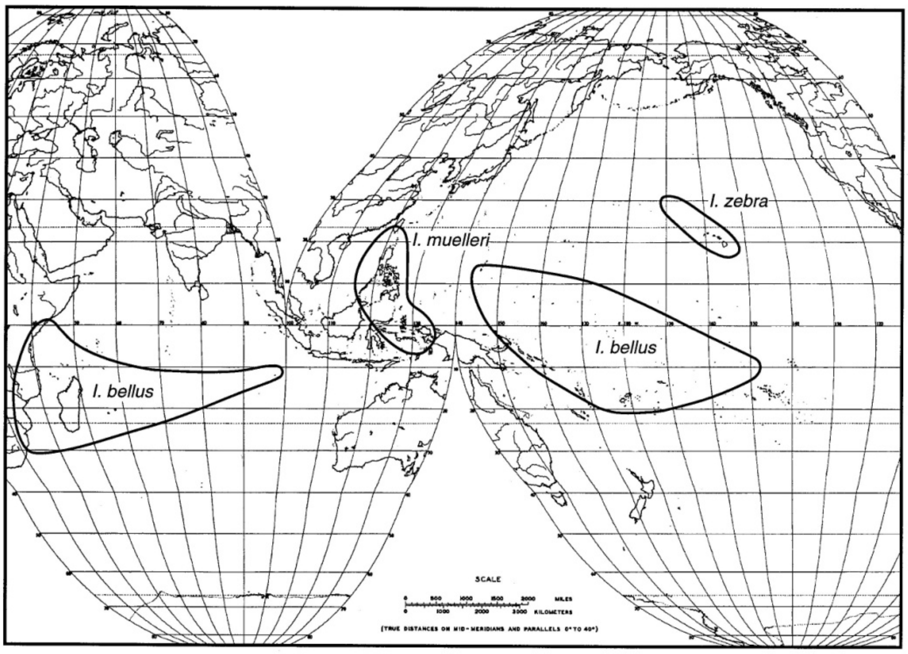

Fig. 3 The east-west disjunct populations of *Istiblennius bellus*and *I. zebra* separated by *I. muelleri.* After Springer and Williams (1994).

5 Global Considerations

The contrast between continental and island extinction rates is critical to conservation planning and needs to be addressed. On the continents, extinctions recorded for the past 500 years are remarkably few. Among the insects, the three best known surrogate groups reveal no extinctions, but all other insect groups indicate a loss of 66 species. However, more than 38 of the latter were island inhabitants, leaving continental extinctions as a vanishingly small part of a total of 3.4 million living species. Among the vertebrates, three mammals and six birds became extinct. If those losses are some indication of the extinction rate among all continental vertebrates, and if the insect extinctions can be taken as an indication of all invertebrate losses, this means that the world's continents have suffered very few extinctions in their vertebrate and invertebrate faunas. Although some continental habitats, like mountain tops and deserts, are space-restricted, they have not made significant contributions to the extinction total; the probable reason is that most of those habitats have been short-lived due to frequent Pleistocene climate changes.

Why so few insect extinctions? Mayhew (2007), in his comprehensive review, concluded that the ultimate factors most likely responsible for low extinction rates are small body size, high population density, high dispersal propensity through flight, and phytophagy. To these, I would add an early beginning to terrestrial life starting about 479 million years ago (Ma) (Misof et al., 2014). This provided an evolutionary advantage over the vertebrates who did not achieve terrestrial life until about 395 Ma (Clack, 2012). The more numerous molluscan extinctions can be attributed to a propensity for rapid evolution in isolated habitats and a vulnerability to subsequent invaders (Régnier et al., 2009).

The rarity of extinctions on the continents and in the oceans, can be seen as a continuation of a low extinction rate that was evident through most of the Pleistocene. In spite of the glacial/interglacial cycles, there is little or no evidence of any insect species becoming extinct at this time (Coope, 2004). The response of insect species to climatic change was to track the whereabouts of acceptable conditions as these changed their locations. Average rates of extinction for the Pleistocene interval as a whole are less than 2%, one of the very lowest extinction levels recorded for any time interval in Earth history (MacLeod, 2013). The extinctions of the large animals (megafauna) on the continents, and the extinctions of Pacific island birds (Steadman, 1995), both of which coincided with human invasions, were notable events but they had little effect on the overall extinction rate. Historical extinctions appear to be concentrated into pulses as the result of drastic environmental changes. The most recent pulse, or a series of regional pulses, took place at the very beginning of the Pleistocene. Those extinctions are generally taken to represent a culling of species that were unable to cope with the onset of the rapid climatic changes typical of that epoch (Jablonski, 2008).

Based on the fossil record of average longevities for different taxonomic groups, a range from 5 to 10 million years translates roughly into an extinction rate of one species per year (MacLeod, 2013). This result indicates that since the year 1500 we should have witnessed the extinction of about 515 species. This figure is close to the 566 extinctions recorded for the Mollusca, and only somewhat less than the 746 total faunal extinctions recognized in the IUCN Red List. However, it is the great contrast between ocean/continental and island/freshwater environments that needs to be explained. In the first category, extinctions have been rare; but in the second, they have been relatively common.

It seems apparent that extinctions among the world's fauna have usually taken place in small habitats, primarily on oceanic islands but also in certain freshwater lakes. This tendency seems to indicate a temporal progression similar to the "source-to-sink" movements observed in population ecology (Pulliam, 1988). Paleontological work on the marine bivalve molluscs (Jablonski, 2008; Krug et al., 2009) found a Cenozoic global pattern indicating that extinctions were highest in the temperate zones. The latter authors suggested that the extinctions lowered the standing diversity and permitted invasions from warmer waters. The extinctions may have provided part of the mechanism to account for the out-of-the-tropics migrations of tropical lineages (Jablonski et al., 2006). Compared to the tropics, the temperate zones were exposed to more climatic extremes, probably accounting for the increased extinctions. This suggests that migrations from the more diverse tropics to higher latitudes might demonstrate a long term, source-to-sink phenomenon. We can therefore distinguish two migratory pathways to extinction, a long term (historical) one to higher latitudes and a contemporary one to oceanic islands and restricted freshwaters.

The general dynamic theory of oceanic island biogeography (Whittaker et al., 2008) provides a connection between island history and species extinction. New islands are colonized by dispersal, speciation takes place as the islands age, and extinction occurs as the islands become worn down and eventually disappear. Island existence can also be terminated by tectonic action or sea level rise. Over time, more new islands are formed to repeat the cycle. This provides a mechanism for continuous peripheral extinction and is consistent with an ecological source-to-sink flow. The same mechanism can be applied to species extinction in freshwater lakes. Most lakes are ephemeral (as are small islands) and, as they eventually disappear, their endemic faunas become extinct. In regard to both islands and lakes, this gradual process of extinction has been suddenly accelerated by human occupation, i.e., losses induced by overexploitation, habitat alteration, and introduction of predatory species (Blackburn et al., 2004). The common result is that migration to faraway places, with small living spaces, leads to disappearance without traces.

The two migration routes, here identified, are consistent with previous conclusions reached as the result of analyses of global marine dispersal patterns (Briggs and Bowen, 2013). It was found that dominant species appeared to arise within small centres of high species diversity and maximum competition. Species continually disperse from such centres of origin and invade less diverse communities (Briggs, 2013) where they are readily accommodated. The centres were judged to be part of a global system responsible for the increase or maintenance of biodiversity over much of the world. It seems apparent that, as species continued to move to less diverse systems, they eventually reached very small habitats, where they sometimes underwent adaptive radiation (Briggs, 2014a), but extinction was the final result as the habitats became degraded and eventually disappeared.

6 Conservation

The world's greatest conservation problem, on the continents and in the oceans, is exemplified by the thousands of species that were once numerous but are now represented only by very small populations. They are the remnants of species that were almost destroyed by human overexploitation, habitat destruction and pollution. These populations are threatened because they have suffered genetic loss due to their reduced size, inbreeding, and depensation (Allee effect). Genetic loss reduces the ability to respond to environmental change such as continued global warming. Furthermore, small populations are often confined to restricted habitats, from which they would be unable to migrate in response to climatic change. Formerly abundant species that now exist in small numbers are considered to be evidence of an extinction debt, one that will be paid when environmental change proves too difficult for them to adapt (Kuussaari et al., 2009). The huge numbers of species extinctions, estimated over the past 40 years, have been of great concern among conservationists. But, the lack of direct evidence demonstrates that fear of large-scale extinctions is not justified. An analysis of 100 assemblage time series, taken across the Earth for the past 40 years (Dornelas et al., 2014), failed to reveal a general loss of species diversity; and ongoing speciation may have contributed to a gain of biodiversity (Briggs, 2014b).These findings should alleviate fears of a mass extinction and permit a better concentration on the needs of threatened populations. The conservation plan, initiated by the World Wildlife Fund, and supported by the Zoological Society of London, the Global Footprint Network, and the European Space Agency, is promising. Their Living Planet Index (2012) provided information on the status of 9,014 vertebrate populations belonging to 2,688 species. The Index reported that the population sizes had undergone a 28% global loss since 1970; the greatest decline was in the tropics where the loss was 60%. The Living Planet Index, which identifies populations in need of help, needs to be expanded to cover invertebrates and plants.

7 Conclusions

In contrast to most of the current popular and scientific literature, species extinctions during the past 500 years have occurred at a very slow pace. Conclusions based on documented extinctions, instead of theoretical estimates based on the species-area relationship or habitat destruction, indicate that biodiversity loss on the world's continents and in the oceans has been minimal. This low extinction rate is apparently a continuation of the modest extinctions that were evident throughout the Pleistocene. Examination of the geographic locations of the extinctions reveals that the great majority have occurred on oceanic islands or in restricted freshwater habitats. This pattern illustrates geographical pathways toward extinction. The pathways are the result of the constant migration of species from high diversity centres and their invasions of ecosystems in low diversity, peripheral localities. Although human-caused extinctions on islands and in lakes have been extensive, there is no evidence of large-scale, global extinctions that would herald the beginning of a sixth mass extinction. Consequently, there is still time to save many of the small populations that are currently at risk.

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