



Historical bird and terrestrial mammal extinction rates and causes

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ABSTRACT

Aim Conservation of species is an ongoing concern.

Location Worldwide.

Methods We examined historical extinction rates for birds and mammals and contrasted island and continental extinctions. Australia was included as an island because of its isolation.

Results Only six continental birds and three continental mammals were recorded in standard databases as going extinct since 1500 compared to 123 bird species and 58 mammal species on islands. Of the extinctions, 95% were on islands. On a per unit area basis, the extinction rate on islands was 177 times higher for mammals and 187 times higher for birds than on continents. The continental mammal extinction rate was between 0.89 and 7.4 times the background rate, whereas the island mammal extinction rate was between 82 and 702 times background. The continental bird extinction rate was between 0.69 and 5.9 times the background rate, whereas for islands it was between 98 and 844 times the background rate. Undocumented prehistoric extinctions, particularly on islands, amplify these trends. Island extinction rates are much higher than continental rates largely because of introductions of alien predators (including man) and diseases.

Main conclusions Our analysis suggests that conservation strategies for birds and mammals on continents should not be based on island extinction rates and that on islands the key factor to enhance conservation is to alleviate pressures from uncontrolled hunting and predation.

Keywords

Biodiversity, conservation, deforestation, endangered species, extinction risk, reserve design.

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INTRODUCTION

There are three dominant forces commonly posited to be causing elevated extinction rates: habitat loss; human exploitation; and effects of invasive species, including diseases, as well as their combined effects (De Castro & Bolker, 2005; Smith *et al.*, 2006; Brook *et al.*, 2008; Frick *et al.*, 2010), with climate change assumed to be a future risk factor (Brook *et al.*, 2008; Stork, 2010). Deforestation is presumed to be a serious part of the extinction crisis (e.g. Gurd, 2006). Most countries have established parks and preserves to protect at-risk species, because human activity is generally considered the prime cause of risk of extinction for the vast majority of species (Wilcove

et al., 1998; Venter *et al.*, 2006). But do human habitat disturbance and habitat alteration really cause extinctions? This question is important because designating reserves for all at-risk species with conflicting requirements seems implausible at best (e.g. Ceballos *et al.*, 2005). Conservation funds are limited, and there is a risk that they may be used in the wrong places for actions that are not effective. Tests of the efficacy of existing conservation efforts are quite limited (Brooks *et al.*, 2006).

In this study, we examined historical data to ask what factors led to historical extinctions and to identify more effective conservation strategies. We focused particularly on birds and mammals, two taxa that are better studied and catalogued. We

did not examine estimated extinctions, predicted extinctions or calculated extinctions (see Stork, 2010). Rather, we conducted an analysis of actual historical record of extinctions with the purpose of understanding the nature and scope of extinctions from habitat reduction or other causes. We have analysed global extinctions of species (not subspecies) rather than local extinction (extirpation), which is a separate and valuable study.

METHODS

There are two main lists used by scientists to track extinctions. The 'Red List', maintained by the International Union for the Conservation of Nature and Natural Resources (IUCN), lists species that are either extinct or at risk of extinction (<http://www.iucnredlist.org>). The CREO list, from the Committee on Recently Extinct Organisms at the American Museum of Natural History (<http://creo.amnh.org>), addresses mammals but not birds. It has established very clear criteria for declaring a species extinct, not extinct or unresolved that have been uniformly applied to the historical record of extinctions of mammals and fish in the last 500 years. These criteria include adequate taxonomy (including DNA comparisons if available), sufficient hypodigm (actual specimens of the species) and adequate surveying of the species' habitat to verify extinction. The class Mammalia, which includes marsupials and monotremes, was used in our analysis. The conclusions of the CREO list are noted in the Red List and vice versa. Although the two lists are not very different, the CREO list provides a greater level of detail than the Red List. Thus, we have used it for mammal extinctions and the Red List for birds. Both lists are limited in their treatment of older extinctions (> 100 year) because of limited research on the topic, particularly on remote islands.

In evaluating extinction data, it is useful to consider islands as a special case. It is well known that island biota are generally at a higher risk of extinction (Diamond, 1989; Alcover *et al.*, 1998; Baillie *et al.*, 2004; Blackburn *et al.*, 2004; Duncan & Blackburn, 2004; Pimm *et al.*, 2006; Sax & Gaines, 2008; Fordham & Brook, 2010; Lane, 2010). Corlett (2010) showed that the impact of invasive species has been greater on more remote islands. The reasons for greater extinction risk on islands are asserted to be the result of species naive about predators (Cronk, 1997), ground nesting by birds on predator-free islands (e.g. Duncan & Blackburn, 2004), less competition because of reduced species richness (Corlett, 2010), perhaps reflected in slower rates of evolution (Wright *et al.*, 2009), and smaller geographic ranges. If these particular causes are mainly operative on islands, then implications drawn for conservation priorities on much more spacious continents may not be valid (see Walter, 1998, 2004). Thus, we divided extinctions into two groups: (1) extinctions of species living on isolated islands or on Australia, and (2) extinctions of continental species. We excluded Greenland and Antarctica from consideration because they are almost totally covered by ice and have very few species of birds or mammals. We excluded marine mammals from our counts.

To compare extinctions on a per unit area basis, we summed the area in islands and continents. We define islands following Alcover *et al.* (1998) as those substantially not connected to the continents during the last glaciation. We also included Australia, in spite of its size, because of its lack of exposure to the modern fauna of the major continents before the modern era. The prehistoric human population of Australia also lacked agriculture, which kept population low and did not possess the bow and arrow, which reduced its hunting impact (Trueman *et al.*, 2005; Prideaux *et al.*, 2010). Island area was computed by summing the areas of Australia, New Zealand, Tasmania, Madagascar, Malaysia, Indonesia, Philippines, Japan, Taiwan and other major islands. The high arctic islands were not included because they are connected by ice every winter and are thus not isolated. The British Isles and Mediterranean islands were not included because of Pleistocene land connections and/or early and heavy human occupation (Alcover *et al.*, 1998). To capture smaller islands missed, this number was multiplied by an arbitrary 1.1 to be conservative. This yielded 1.31×10^7 km² area for islands. The total world land area is 1.489×10^8 km². To obtain the continental land area, we subtracted island area as well as Greenland and Antarctica areas, as these areas are almost entirely covered by ice. This yielded 1.196×10^8 km² continental area.

RESULTS

Island extinctions have dominated the total record of extinctions. On all continents, only three mammals are recorded as having gone extinct in the last 500 years. These were as follows: Bluebuck antelope, hunted to extinction, South Africa; Algerian gazelle, unknown cause, Algeria; and Omilteme cottontail rabbit, unknown cause, Mexico (Table 1). The remaining global mammal extinctions (58 or 95%) occurred on islands. Alcover *et al.* (1998) document 188 mammal island species that have gone extinct since the end of the Pleistocene, mostly because of human occupation (according to the authors). Not having access to the exact species they identified, we can only approximately identify 130 island (insular) mammal species as extinct because of prehistoric island invasions by humans and their commensals. Of the 128 extinct bird species, 122 (95.3%) were island extinctions and six were on continents. Of the continental bird species extinctions, three were prolific terrestrial bird species hunted to extinction and three were single-habitat freshwater bird species. These freshwater bird species suffered from hunting pressure, predation from introduced fish and habitat alteration.

Other studies have documented far more island bird (mainly) species that were driven to extinction during prehistoric (outside our 500-year window) or historical times (e.g. Steadman, 1995, 2006; Pimm *et al.*, 2006), perhaps, in the thousands. However, to avoid problems of subjectivity, we have used standard databases. The implications of the higher estimates are mentioned in the discussion.

Per million square kilometres, historical (past 500 years) extinction rates (not per year) for birds were 9.38 species on

Table 1 Extinct continental species.

| Species | Year | Source | Comments (quotes from source when available) |
|--|-------|----------|---|
| Bluebuck (<i>Hippotragus leucophaeus</i>) | 1800 | Red List | '...hunted by European settlers throughout the 1700s. The last of the species was killed around 1800'. |
| Labrador duck (<i>Camptorhynchus labradorius</i>) | 1878 | Red List | 'Shooting and trapping on the winter quarters were certainly proximate factors in the species' extinction. Overharvest of birds and eggs on the breeding ground could also have been a factor'. |
| Algerian gazelle (<i>Gazela rufina</i>) | 1894 | CREO | Reason for extinction unknown, this species known only from an adult male skull and a flat skin. |
| Carolina parakeet (<i>Conuropsis carolinensis</i>) | 1904 | Red List | Hunted for food and the millinery trade, killed for crop protection and because it competed with bees. |
| Slender-billed grackle (<i>Quiscalus palustris</i>) | 1910 | Red List | 'It had a small distribution in the Lerma marshlands, in the state of México, Mexico...last recorded in 1910, and presumably became extinct soon after as a result of the draining of its tule-cattail and sedge habitat'. |
| Passenger pigeon (<i>C. carolinensis</i>) | 1914 | Red List | '...Newcastle disease, extensive hunting, and the breakdown of social facilitation'. |
| Colombian grebe (<i>Podiceps andinus</i>) | 1950s | Red List | '...wetland drainage, siltation, pesticide pollution, disruption by reed harvesting, hunting and predation by introduced rainbow trout <i>Salmo gairdneri</i> '. |
| Atitlán grebe (<i>Podilymbus gigas</i>) (found only on Lake Atitlan, Guatemala) | 1986 | Red List | 'Its population dropped from c. 200 to 80 as a result of competition and predation by large-mouth bass <i>Micropterus salmoides</i> , introduced into the lake in 1960, but recovered to a high of 232 in 1975 when the numbers of bass plummeted. However, increasing pressure on breeding sites from local reed-cutting and from tourism development, along with the murder of the government game warden for the national park during the political unrest of 1982 and falling lake levels following the earthquake of 1976, drove the population down to 30 by 1983, and extinction by 1986. Drowning in gill nets and disturbance by increasing boat traffic have also been suggested as contributory factors'.* |
| Omitlame cottontail rabbit (<i>Sylvilagus insonus</i>) | 1991 | CREO | Reason for extinction unknown, species is known only from 3 specimens collected in 1991. |

CREO, Committee on Recently Extinct Organisms.

*Interestingly, this bird has since been replaced on Lake Atitlan by a similar grebe of the same genus, *Podilymbus podiceps*. In fact, there is significant disagreement among biologists about whether *P. gigas* is just a subspecies of *P. podiceps*, but we have included it to be on the safe side.

Table 2 Extinctions since 1500 according to IUCN and CREO, with per species and per unit area rates.

| | Number | % | Per 10 ⁶ km ² | vs. Fossil turnover |
|-------------|--------|--------|-------------------------------------|---------------------|
| Mammals | | | | |
| Continents | 3 | 0.081% | 0.025 | 0.89–7.4 |
| Islands | 58 | 7.4% | 4.43 | 82–702 |
| Ratio (I/C) | | 91 | 176 | 95 |
| Birds | | | | |
| Continents | 6 | 0.062% | 0.050 | 0.69–5.9 |
| Islands | 122 | 8.86% | 9.38 | 98–844 |
| Ratio (I/C) | | 143 | 187 | 143 |

IUCN, International Union for the Conservation of Nature and Natural Resources; CREO, Committee on Recently Extinct Organisms.

islands and 0.0502 on continents (Table 2). This equal area rate was 187 times (not per cent) higher on islands. For mammals, the extinction rates per million square kilometres were 4.43 species on islands and 0.0251 species on continents,

and the relative risk was 176.5 times higher on islands. If we consider Australia to be a continent, then there are 23 continental and 38 island extinctions, but the island rate per million square kilometres is still 45 times as high. In this case, we would have to explain why 82% of the mammal extinctions are marsupials, returning us to the conclusion that species of Australia were/are uniquely sensitive. If prehistoric impacts of humans had been included, the difference would be even greater because many species were exterminated prior to our 500 year cut-off. Alcover *et al.* (1998), for example, estimated that 130 island mammal species went extinct during the prehistoric Holocene, most of which they attributed to human invasion of islands. A similar number of continental species are not available, although Alcover *et al.* (1998) assert that it is much lower because of long coexistence with humans on the continents. Similarly, they estimate that 60% of 3500 island endemic birds went extinct during the Holocene following human occupation, although this number is very rough. Steadman (1995, 2006) and Pimm *et al.* (2006) give similar high numbers. Some of these extinctions may have resulted from post-Pleistocene climate changes and sea-level rise.

The approximate total number of recent mammal species (including recently extinct) from IUCN (and Alcover *et al.*, 1998) is 4629, of which 117 are marine and 787 are island species. This gives 3725 living continental land species. The continental per species extinction rate is then 3/3725, or 0.081% per 500 years, or 1.61 per million species years (MSY). Similarly, the per capita island extinction rate is 58 of 787 total island species (IUCN) or 7.4% per 500 years or 147.4 per MSY. The island rate per MSY is 91.6 times the continental rate.

We can compare these numbers to estimated fossil mammal turnover rates (species/species per million years) of 0.21 (Alroy, 1998), 0.4 (Regan *et al.*, 2001), 0.46 (Foote, 1997) and 1.8 (Barnosky *et al.*, 2011). This means that continental rates of extinction are 0.89 as high to 7.4 times higher than for fossil fauna. In contrast, assuming comparable island preservation, island extinction rates are 82–702 times higher on a species pool basis. These numbers are subject to great uncertainty because of difficulty in estimating past extinction rates (Boyajian, 1986; Jablonski, 1994; Boucot, 2006).

For birds, the number of continental species is 9672. The six continental extinctions represent 0.062% per 500 years or 1.24 per MSY. For islands, we have 122/1377 or 8.86% per 500 years or 177.2 per MSY. The island rate per MSY is 142.9 times higher than the continental rate.

Comparison to background extinction rates is difficult for birds because so many of them are small, with bones that preserve poorly. An extensive search did not turn up any estimates. If we assume that birds have mean species durations comparable to the large range postulated for mammals above (550,000 year to 4.8 Myr), we can make some assessments. On this basis, the recent continental bird rate is 0.69 as high to 5.9 times higher than background. For islands, it is 98–844 times higher than background on a per species basis.

We can also evaluate continental extinction rates relative to the species pool. The three extinct mammals represent approximately 0.08% of the continental species pool. Even if we assume that all three went extinct in the past 100 years (vs. 500 year), it would take, at this rate, 1235 years for 1% of continental mammals to go extinct. Similarly for birds, the six species represent 0.062% of the 9672 species pool and it would take 1613 years to lose 1% of extant species at current rates even if the recorded extinctions all took place over the last 100 years. Even if true continental extinctions are ten times higher than our estimates, the results for relative risk change little because true island extinctions are also much higher than our estimates, especially for birds.

The above analyses are summarized in Table 2. Whether we compare per area rates, species turnover rates or per species pool rates, island extinctions are two to three orders of magnitude higher than continental rates.

DISCUSSION

It can be objected that we did not capture all relevant extinctions. We used established authorities as our standard, rather than guessing about individual species. Even if the true

rates are higher, the relative risks on continents vs. islands will hold. If anything, more uncounted extinctions would be included from islands (especially for birds) because of the lack of adequate surveys of islands (see Alcover *et al.*, 1998), making our relative rankings even more extreme.

We found that 95% of all recorded bird and mammal extinctions are island or Australian species. We suggest that human predation (e.g. unregulated hunting and gathering of eggs) was a major factor in most confirmed extinctions, particularly on islands. Several lines of evidence support the primacy of hunting as the cause of extinctions. Most of the extinctions we evaluated in the IUCN and CREO databases list exploitation as the primary cause of their demise. Sax & Gaines (2008), using the IUCN database, found that predation (including human hunting) alone or in concert with competition from invasive species accounted for 98% of all vertebrate extinctions (although this again reflects expert opinion as recorded in the database). Duncan *et al.* (2002) showed that species whose remains were found in human middens on New Zealand were more likely to go extinct, as were ground-dwelling birds, which are more easily hunted and tend to nest on the ground. Worthy & Holdaway (2002), Duncan & Blackburn (2004) and Steadman (2006) also documented the importance of hunting. We can also note the long coexistence of species with early humans on Australia (Trueman *et al.*, 2005; Prideaux *et al.*, 2010). These peoples lacked agriculture (and thus had low populations) and the bow and arrow and thus were slower to extirpate species (Trueman *et al.*, 2005; Prideaux *et al.*, 2010). The loss of small bird species and rodent-like species (rodents and small marsupials) can probably be attributed to introduced rats, dogs and (more recently) cats. The correlation of deforestation with species loss on oceanic islands (Didham *et al.*, 2005) may be partially explained by the fact that forest loss is an indicator of population size, which is itself an indicator of exploitation pressure. This would explain why extensive deforestation on continents has not led to many extinctions.

The role of disease is difficult to assess. While theoretically important, it leaves few traces for extinctions not directly observed in recent years. For example, in order to demonstrate even the presence of an introduced disease in an extinct species, Wyatt *et al.* (2008) had to conduct DNA analyses on museum specimens, and even then, the extent to which the disease contributed to the extinction was only suggestive. Likewise, estimates of the contribution of infectious disease to extinction of < 4% of species extinct since 1500 (Smith *et al.*, 2006) is based on expert opinions expressed in the IUCN database. On the other hand, the argument that introduced disease per se can only predispose a population to extinction (De Castro & Bolker, 2005) ignores the reservoir effect of disease carried by an introduced species and the sensitivity of a naive species (particularly on islands). The fact that flightless birds such as rails were far more likely to have gone extinct (Steadman, 1995, 2006; Pimm *et al.*, 2006) also suggests hunting and introduced predators (e.g. rats) as a major cause of extinctions, rather than disease. Similarly, more rapid loss of

species when human populations were larger also suggests hunting and/or habitat alteration rather than disease. Disease can, of course, have been important in some cases and is clearly important today in cases such as bat decline in eastern North America and amphibian decline in South America.

Invasive species seem to be a major secondary cause of extinctions on islands. Australian and island species were extremely vulnerable to pressure from invasive predators (e.g. Recio *et al.*, 2010), competitors and disease species. This was because of the ground-nesting habit of many island species such as rails (e.g. Pimm *et al.*, 2006) and the tendency of many species to not flee from predators or humans. Many extinct island mammals on the CREO list are rodents, which probably perished because of competition with introduced rats. Although it occurred over a number of years, this initial introduction of continental species into island habitats is now better understood and attempts are being made to avoid new introductions and to actively control old ones. Habitat loss has, of course, played a role in the extinction of some continental species. However, it is worth noting that to date, no continental mammal or bird in our databases has been documented to have gone extinct solely because of habitat reduction. Early prehistoric waves of extinction (America around 12,000BP and Australia over 50,000 year ago) also were not because of habitat alteration (except fire) but largely because of hunting and other exploitation (e.g. egg gathering) (Trueman *et al.*, 2005; Sodhi *et al.*, 2009; Prideaux *et al.*, 2010; Ripple & Van Valkenburgh, 2010). All extinctions of marine mammals are strictly because of hunting and are obviously not because of habitat alteration or introduced predators.

An important point about these documented extinctions is that because of the unique sensitivity of island species, the recent historical rate of island extinctions cannot continue at the same pace into the future. On many islands, most or all of the flightless rails, for example, are already extinct (Steadman, 1995, 2006). Thus, it is not valid to conceive of a rate of X species per year as continuing, although, of course, many species are currently at risk.

Our results do not support statements or projections by others of grossly elevated extinction rates for continental bird and mammal fauna over the last 500 years compared with background rates. This is particularly noteworthy because mammals (Ceballos *et al.*, 2005), large-bodied animals (Sodhi *et al.*, 2009) and carnivores (Safi & Pettorelli, 2010) are widely assumed to be at greater risk than other species. For example, Sodhi *et al.* (2009) projected that current extinction rates are 100–10,000 times background vs. the very modest rise we estimated of 0.89–7.7 times the background rate for continental mammals and 0.69–5.9 times background for continental birds. We do find very high rates for islands, several hundred times background. Wilson (1992) estimated from theory that 540–1088 continental bird and mammal species had been lost the past few hundred years, depending on which of his assumptions are used. Twenty other studies (Table 1 in Stork, 2010) make similar high estimates. Sax & Gaines (2008) estimate 13,500–27,000 total species (all taxa) lost or doomed

per year just because of tropical deforestation. Most of these estimates are based on the species–area curve, which is an empirical relationship between the number of species found and the area surveyed. The idea is that when area is lost to development, the change in species that can be supported can be estimated from this model. In contrast, our compiled IUCN and CREO continental bird and mammal extinctions and references cited earlier do not support these projections. In fact, habitat loss only contributed to a handful of extinctions, even on islands.

Our relatively low estimates for extinction rates could theoretically be because of some species requiring a relatively long time period to reach extinction (an extinction debt, Labrum, 2011). For example, Wilson (2001) notes that ‘...species in a reduced habitat may take from 25 to 100 years to go extinct’ and that research has shown that the rate of these delayed extinctions drops off exponentially with time. Even with this assumption, the long history of deforestation should have led to hundreds of extinctions. We have, however, seen only a handful. If true extinction debt relaxation times are more like thousands of years (as in prehistoric Australia following human arrival), then the recent continental rates are explainable, but none of the references to current extinction rates we found (e.g. Sax & Gaines, 2008; Stork, 2010) make this assumption. Under this assumption, conservation efforts would be much more hopeful.

Several other factors may at least partially be responsible for lower observed extinction rates than expected based on estimates of background extinctions. Stork (2010) suggests that conservation efforts have been a successful mitigation effort. It is true that species such as the California condor have been saved and reintroduced into the wild. Many other species have been protected or are currently found only in zoos. However, this number is far below what is needed to reconcile our results with extinction rates predicted by others. Stork also suggests that secondary forest could be providing adequate habitat for at least some species assumed to require old growth (undisturbed) forest. Finally, some species predicted as extinct may not have ever been described in the scientific literature. However, it is unlikely that hundreds of extinct continental bird and mammal species have not been documented and only the unknown species should have gone extinct.

We suggest that the ‘habitat loss’ theory of extinction risk is deficient. What might explain this deficiency? On continents, species are often able to roam widely and this mobility prevents speciation except under exceptional circumstances. For example, in the eastern United States, most mammals and birds can move freely and for this reason occupy the entire zone from Florida and into Canada but will be locally found in their preferred habitats such as wetlands or meadows. It does not follow logically that these species require this entire region to persist. Evidence from islands suggests that they do not. On the Galapagos, each of the tiny islands has a unique tortoise species and finch species. These islands are each home to a unique species only because they are isolated but testify to the fact that species can persist in a small area, as documented by Walter

(1998, 2004). Further, the very large number of bird species on oceanic islands is largely because of isolation and drift, resulting in more species per unit area than on continents.

A second aspect of the species–area curve approach is that this curve is a sampling artefact (He & Hubbell, 2011) rather than a mechanistic model. There is a hysteresis in the relationship such that reductions in habitat must be more extreme to cause a loss (extinction) of species compared to the rising accumulation curve. Thus, the widespread assumption that island biogeographic theory and the species–area curve provide a sound basis for conservation at the landscape scale (see Gurd, 2006; citations in Stork, 2010) is not supported by our results. This is especially true for mobile species such as birds and mammals. Others have similarly urged caution when applying these models (e.g. Walter, 1998, 2004; Botkin *et al.*, 2007; Smith, 2010). The lack of applicability of the species–area curve for complete loss of habitat is even more true for mere habitat alteration because of activities such as grazing and forestry.

There is an obvious difference between continental and island extinction rates even if exact values are uncertain. When total island area is considered, the difference is even more extreme. Owing to their isolation and size, islands are often limited in the number of founding taxa and speciation events possible. Thus, predators, in particular, may be missing or (in case of Australia) not as effective as continental predators. Humans are especially effective as predators. Thus, human spread across islands such as those of the South Pacific was accompanied by rapid extinctions (Alcover *et al.*, 1998). Continental species, in contrast, have evolved in the context of modern predators for a very long time, and thus, man as predator has much less effect (Alcover *et al.*, 1998). Nevertheless, most continental birds and mammals currently at risk from extinction are in this predicament because of human predation. A recent study (Fisher & Blomberg, 2011) throws a further light on this question. They show that mammal species have often been rediscovered after having been declared extinct. If the threat to the species was habitat loss, then the species was most likely to be rediscovered. If the threat to the species was introduced predators, overhunting or disease, the species was least likely to be rediscovered. This suggests, according to the authors, that risks caused by habitat loss are substantially overestimated.

We also suggest that it is inappropriate to accept ‘risk of extinction’ ratings as if they were data. For example, Safi & Petteorelli (2010) developed models to predict extinction risk, but the IUCN Red List information they used was in fact subjectively defined risk rankings. Gage *et al.* (2004) performed a similar analysis. Thus, because projections of future extinction risk are based on models which we have shown do not match historical data, they should not be given too much weight.

CONCLUSIONS

Our analysis is not meant to imply that habitat loss, forest fragmentation or loss of species diversity are incidental or

unimportant issues or that extinctions will rise or fall in the future. This is an analysis of historical record to date. Because mammals and birds are more mobile than other taxa, we also do not consider our results to necessarily extend to other taxa, which make up a significantly higher proportion of total extinctions.

There are implications from our study for conservation practice. We suggest that conservation should be spatially focused on islands for birds and mammals because species on islands are uniquely sensitive. Furthermore, efforts to restore or protect a given area on islands will, in general, have a much higher pay-off than on continents, if our goal is to prevent extinctions. On islands, it is most important to control invasive species (particularly predators) and exploitation (unregulated hunting). Thus, preserves may not be effective on islands unless introduced predators are controlled. Predator removal can, in fact, lead to dramatic recovery (Jones, 2010). On continents, the role of habitat loss is overemphasized by models that do not predict correct extinction rates (He & Hubbell, 2011). Introduced or altered levels of predators on continents have rarely been documented to be the type of problem they are on islands because continents already have modern efficient predator species. Thus, on continents, it is control of hunting and other exploitation that would yield the largest benefit.

We do not extend our results to plants (e.g. Sax & Gaines, 2008) because they are so different from birds and mammals. Relative to forecasts of climate change effects (e.g. Brook *et al.*, 2008; Stork, 2010), we would note first that many such forecasts have been based on the species–area curve (critiqued by Botkin *et al.*, 2007) and second that before extrapolating to unknown future conditions it would be helpful to properly understand existing extinction records.

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BIOSKETCHES

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