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# VARIATION IN SPECIES LOSSES FROM ISLANDS: ARTIFACTS, EXTIRPATION RATES, OR PRE-FRAGMENTATION DIVERSITY?

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*Abstract.* Species are being lost from isolated reserves as predicted by ecological theory, prompting calls for larger reserves with higher species immigration rates. However, some large islands have lost a large proportion of their species, whereas some small islands have not lost any. Conservation efforts would be more efficient if the cause of such variation in the relationships among number of species lost, island size, and immigration rate were known. Observed species losses could be affected by the time since islands were isolated, species immigration rates, species extirpation rates, the pre-fragmentation diversity of the region relative to steady state, or overestimation of the pre-fragmentation diversity of islands. To test the last three hypotheses, I compared the intersection points of the island, intraprovincial, and interprovincial species–area relationships of terrestrial mammals from nine archipelagos of land-bridge islands and terrestrial habitat isolates. Species losses from three archipelagos were greater than expected due to reduced immigration rates alone, although I could not resolve if this was due to increased extirpation rates or overestimation of the pre-fragmentation diversity of the islands. Analysis of six archipelagos indicates that the diversity of mammals in two regions of North America is currently below steady state, probably due to the extinction of mammals and glacial retreat during the late Pleistocene. These results have direct implications for reserve planning. When provincial diversity is below steady state, some combinations of reserve size and species immigration rate will allow reserves to maintain their pre-isolation diversity. However, the diversity of provinces relative to steady state is likely to vary, so conservation of a given proportion of a province may not always conserve the same proportion of its species. I present a new species–area relationship for islands formed by fragmentation that replaces the parameter *c* (fitted constant) with a rotation point. Estimation of this rotation point will allow reserve planners to separate the effects of extirpation and immigration rates on species losses from islands, identify provinces that are below steady-state diversity, and estimate the combinations of reserve size and immigration rate that will prevent loss of species from reserves.

*Key words: extinction; extirpation; immigration; land-bridge islands; macroecology; mammals; reserves; speciation; species–area relationships; species diversity.*

## Introduction

Anthropogenic activities cause habitat loss and leave remaining habitat as isolated fragments. This process of habitat fragmentation is thought to have caused recent species extinctions (Pimm and Askins 1995, Turner 1996) and is considered a threat to the persistence of many other species (Soulé 1991, Wilcove et al. 1998, Owens and Bennett 2000). The primary strategy to counter habitat loss is to create habitat reserves (Soulé 1991, Margules and Pressey 2000), but this may be only a temporary conservation strategy. Theory predicts that isolated reserves will experience reduced immigration rates and lose species (MacArthur and Wilson 1967). As predicted, reserves are currently experiencing species losses (Newmark 1987, 1995, 1996, Gurd and Nudds 1999, Brashares et al. 2001, Wiersma and Nudds 2001, Parks and Harcourt 2002), prompting recommendations for larger reserves connected by immigration corridors (Soulé and Terborgh 1999). Although larger reserves are undoubtedly better, knowing how and why the proportion of species conserved varies with reserve size and immigration rate would help to direct limited resources toward efficient conservation (Soulé and Sanjayan 1998).

Regions that were fragmented during the change in climate that ended the last glacial period have served as empirical models of the consequences of fragmentation. Melting glaciers increased sea levels, creating land-bridge islands that were formerly connected to continents. Plant communities shifted to higher elevations, creating habitat ''islands'' isolated at the top of mountains. Studies invariably indicate that species have been lost from such islands (Brown 1971, Diamond 1972, 1984, Terborgh 1974, Case 1975, Wilcox 1978, 1980, Patterson 1984, Crowell 1986, Lawlor 1986, Richman et al. 1988, Lomolino et al. 1989, Foufopoulos and Ives 1999), but the proportion of species

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lost varies widely. Wilcox (1980) estimated that Sunda Shelf land-bridge islands as large as 750 000 km$^2$ have lost 40% of their nonvolant mammal species; this predicts a bleak future for many mammals in much smaller reserves (Soulé et al. 1979). Paradoxically, recently isolated reserves in North America between 12 000 and 22 000 km$^2$ have not lost mammal species (Newmark 1987, Gurd et al. 2001).

At least five hypotheses may explain such variation in species losses from islands. First, time lags may delay species losses from recently created reserves (Brooks et al. 1999, Ferraz et al. 2003). Second, species' immigration rates may differ between islands. Third, extirpation rates on historical land-bridge islands may have increased following isolation. For example, climate change may have increased extinction rates on islands by altering the area of individual habitats independent of changes in total island area (Pregill and Olson 1981, Goodfriend and Mitterer 1988). Fourth, the pre-isolation diversity of historical land-bridge islands may be overestimated because it must be estimated from contemporary continental diversity, which may have increased following isolation due to shifts in species' ranges in response to climate change (Graham et al. 1996), or may never have been representative of the province from which the islands were formed. Fifth, some provinces may have been closer to steady-state diversity than others at the time of fragmentation. Islands should loose a smaller proportion of species if there were fewer species present initially. The first two hypotheses are well-known effects of isolation. Instead of detecting these effects, I attempt to control for them. The latter three hypotheses predict variation in species losses due to effects other than isolation. Such effects have been dismissed based on anecdotal evidence in one case (Richman et al. 1988), but I am not aware of any systematic attempt to detect them.

I tested whether these three hypotheses can account for variation in the number of mammal species lost from islands in nine different archipelagos. I used Rosenzweig's (1995) conceptual framework of island, intraprovincial, and interprovincial species–area relationships in a comparative, graphical analysis. By comparing the intersection points of these three relationships, and by recognizing that the species–area relationship of islands formed through fragmentation must rotate around a single point, I will show that mammal diversity in some North American provinces is below steady state and that some archipelagos of historical islands have lost more species than expected due to isolation reducing immigration rates. Finally, I will discuss how the three types of species–area relationships can be used to guide reserve planning.

### *Inferences from dynamic, scale-dependent species–area relationships*

Provinces and islands can be defined by the relative contribution of extinction, extirpation, speciation, and immigration to their diversity (Rosenzweig 1995). Provinces are self-contained regions whose species originate entirely by speciation within the province and are lost by extinction. Islands are self-contained regions whose species originate entirely by immigration from outside the island and are lost through extirpation. Few strict examples of islands and provinces exist, but these definitions create a continuum of the relative contribution of speciation and extinction vs. immigration and extirpation in determining the diversity of a region's biota (e.g., Losos and Schluter 2000).

The distinction between islands and provinces leads to three types of species–area relationships (Rosenzweig 1995): island (I), intraprovincial (P), and interprovincial (IP). The relative position of these relationships in log area–log species space will differ if factors other than isolation have contributed to species losses from islands and predict conditions under which islands will maintain their pre-isolation diversity. If provincial diversity is at steady state ($S'_P$) (i.e., the speciation rate is equal to the extinction rate) at the time of island formation, the three relationships will intersect at a single point (Rosenzweig 1995). Under this scenario, islands will always lose species following isolation (Fig. 1A). If provincial diversity is below steady state at the time of island formation, some islands will be able to maintain their pre-isolation diversity, depending on their size and immigration rate (Fig. 1B). If provincial diversity is at steady state at the time of island formation, but extirpation rates on islands increase following isolation (Fig. 1C), or the current intraprovincial relationship overestimates the pre-isolation diversity of the islands (Fig. 1D), then the island and intraprovincial relationships will intersect to the right of the interprovincial relationship, giving the false impression that islands must be larger than the province they were derived from in order to avoid the effects of reduced immigration rates and maintain their pre-isolation diversity.

The prediction that some islands can maintain their pre-isolation diversity if provincial diversity is below steady state (Fig. 1B) requires additional comment. One might argue that some species may persist on islands due to immigration from the continent. If these species' source populations were to disappear from the continent, island diversity would decline, causing $S_R$ (the diversity coordinate of the rotation point in a species–area relationship) to decline with $S_P$. However, for a decline in $S_R$ to occur, the species lost from the continent must have existed on all the islands prior to the continental extinction event. $S_R$ is common to all island relationships, so a decline in $S_R$ of one species implies a loss of one species from every island. It is difficult to explain why a species would be resistant to extirpation from small, isolated islands and be prone to extinction on the continent. A more plausible scenario would suggest that species lost from the continent are

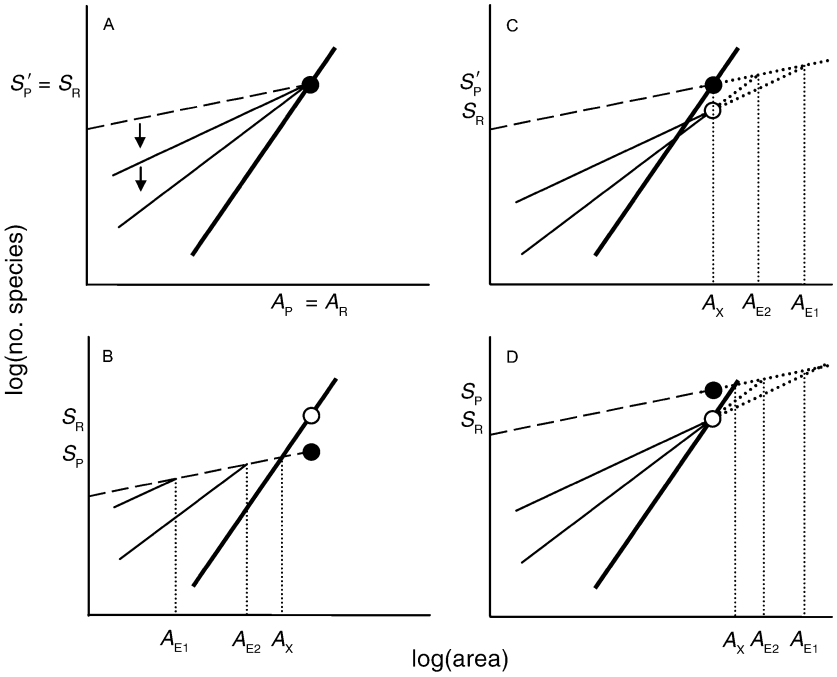


FIG. 1. Interpretation of the intersection points of hypothetical intraprovincial (dashed line), island (thin lines), and interprovincial (thick line) species–area relationships and their implications for conservation of species in reserves. If provincial diversity is at steady state at the time of island formation (A), the three relationships will intersect at a single point, and the intersection of the intraprovincial and interprovincial relationships will define the area ($A_P$) and steady-state diversity ($S'_P$) of the province (solid circle) (see Rosenzweig 1995). As islands become increasingly isolated, immigration rates decline, and species are lost (arrows), causing the island relationship to rotate around a point (Diamond et al. 1976, Rosenzweig 1995, 1999) defined by ($A_R$, $S_R$) (open circle, hidden under solid circle). Under this scenario, a provincial biota cannot be conserved in an area smaller than the province because islands will always lose species (i.e., $S'_P = S_R$) (Rosenzweig 1995). If provincial diversity is below steady state at the time of island formation (B), then $S_R > S_P$, and some islands will be able to maintain their pre-isolation diversity. Islands of size $A_{E1}$ and $A_{E2}$ both contain their pre-isolation diversity, but $A_{E2}$ must be larger than $A_{E1}$ because it is more isolated and has a lower immigration rate. If provincial diversity is at steady state at the time of island formation, but extirpation rates on islands increase following isolation (C), $S_R$ and the island relationship will decline, increasing the value of $A_{E1}$ and $A_{E2}$. If the current intraprovincial relationship overestimates the pre-isolation diversity of the islands (D), the number of species lost from the islands will be exaggerated, causing $A_{E1}$ and $A_{E2}$ to be overestimated. Under scenarios (C) and (D), $A_E$ will fall to the right of the area intercept ($A_X$) of the intersection of the intraprovincial and interprovincial relationships, while $A_E = A_X$ under scenario (A), and $A_E < A_X$ under scenario (B), regardless of the degree of island isolation or time lags delaying species losses from islands.

likely to have persisted only on large islands with high immigration rates, limiting diversity only on the largest islands. The net result would be an island species–area relationship with a break point that coincides with the intersection with the intraprovincial relationship (Fig. 1B). This scenario is consistent with data indicating that species' distributions on land-bridge islands are nested and dependent on island area (Wright et al. 1998).

## METHODS

I used published data on the distribution of terrestrial, native, nonvolant mammals on nine island archipelagos to test for evidence of the patterns illustrated in Fig. 1. I used data for the tropical Indonesian islands of the Sunda Shelf (Lawlor 1986) and temperate islands of Lake Michigan (Hatt et al. [1948], referenced in Lomolino [1986]), the Gulf of Maine (Crowell 1986), coastal British Columbia (Lawlor 1986), and the southern coast of Alaska (Conroy et al. 1999). I excluded the five smallest islands from the Lake Michigan data set because they greatly inflated variation in the intersection estimates due to the ''small-island effect'' (Lomolino and Weiser 2001). Data for terrestrial habitat islands were from montane forests in the Great Basin (Brown 1971), Colorado Basin (Lomolino et al. 1989), and southern Rocky Mountains (Patterson 1984) of the southwestern United States and isolated reserves in the temperate, mixed forest of southeastern Canada (Gurd and Nudds 1999). The reserves were isolated by anthropogenic habitat change by European colonists within the last 300 years (Gurd and Nudds 1999), whereas the other eight archipelagos were formed at the end of the last glacial cycle ~9000–12 000 years ago. The Canadian reserves and islands of Lake Michigan and the Gulf of Maine belong to the Allegheneian-Illinoian (AI) mammal region, the Pacific coast islands to the Vancouverian-Montanian (VM) mammal region,

and the montane forest islands to the Coloradan mammal region (Hagmeier 1966).

Intraprovincial data were taken from Wilcox (1980) for the Sunda Shelf; Brown (1971) and Patterson (1984) for the Coloradan mammal region; and Gurd and Nudds (1999) for the AI and VM mammal regions. In five cases, the island and intraprovincial data came from the same, or related, sources in which authors ensured that the same habitat was sampled. The Pacific coast, Lake Michigan, and Maine island data came from different sources than the intraprovincial data, but the intraprovincial data sampled the continental region from which the islands were derived at a scale commensurate with the size of the islands, providing the best estimate of the pre-isolation diversity of the islands. Recall that the comparability of island and intraprovincial data is not an assumption of this study, but a condition that I am testing.

Estimating the interprovincial relationship poses some difficulties. Ideally, provinces should differ only in size, but delimiting large, evolutionarily independent areas with similar habitats and climates with reasonable replication is difficult, if not impossible. In addition, defining provinces by habitat alone assumes that habitats have not changed in area over evolutionary time. Because habitat type and climate are highly correlated, and their effects on mammal diversity are well known, I chose to define provinces using continental boundaries to control variation in provincial area. By including habitat and climatic variation between provinces, I have increased variation in the interprovincial relationship and, therefore, variation in the intersection points, leading to a more conservative test. Comparison of an interprovincial relationship (from provinces that vary in climate and habitat) to island and intraprovincial relationships (from a specific habitat and climate) will be biased. However, these biases can account for my results in only one comparison (see *Discussion*).

To estimate the interprovincial species–area relationship, I counted the number of terrestrial, native, nonvolant mammals that occur on landmasses with a large proportion of endemic species: the five continental landmasses (Africa, southwest of the Suez Canal; Asia; Australia; North America; South America, south of Mexico), the islands of New Guinea and Madagascar, and some islands of the Galapagos and the West Indies, based on distribution data from Honacki et al. (1982), Morgan and Woods (1986), Steadman et al. (1991), and Woods et al. (2001). I included species that became extinct after European colonization of these provinces.

I used least-squares regression to fit the power form of the species–area relationship ($S = cA^z$, where $c$ and $z$ are fitted constants) to each data set following logarithmic transformation. Results did not differ qualitatively when nonlinear regressions were estimated using maximum likelihood, but least-squares models accounted for more variation in diversity. I then used the least-squares regression equations to estimate the area intercept at which, respectively, the island and intraprovincial ($A_E$) or intra- and interprovincial ($A_X$) species–area relationships intersect. I estimated variation in $A_E$ and $A_X$ by calculating the intersection points from 2000 bootstrapped parameter estimates for each regression (Efron 1981). Insufficient data ($n \leq 5$) existed to bootstrap the intraprovincial regression for the Coloradan or the Sunda Shelf mammal regions. As a result, variation in $A_E$ and $A_X$ will be underestimated for these provinces, but bias will be limited because the intraprovincial regression is used to estimate both $A_E$ and $A_X$.

I did not test whether island regressions from the same province share a single rotation point. Robust and precise estimates of the rotation point require data from at least three archipelagos (two nonparallel lines will always intersect) that became isolated at different points in time and were sampled using the same techniques. I was unable to find sufficient data that met these criteria. Because I could not estimate the island rotation point, and $A_P$ (provincial area) cannot be estimated independently of the intersection of the intraprovincial and interprovincial regressions, I could not resolve between the patterns in Fig. 1C, D.

## Results

Values of $z$ were of the order expected for the three types of species–area relationships: interprovincial > island > intraprovincial (Table 1). The reserves, which were isolated most recently, had the lowest value of $z$ among the island regressions. Regression analyses of the four terrestrial archipelagos and the Lake Michigan and Gulf of Maine archipelagos indicated that $A_E < A_X$, whereas analyses of the British Columbia, Alaska, and Sunda Shelf archipelagos indicated $A_E > A_X$ (Fig. 2). The distribution of the bootstrapped estimates (Fig. 3) indicated that the differences between $A_E$ and $A_X$ were greater than expected due to chance (median test; $N = 2000$ bootstrap estimates, $P < 0.001$ for all comparisons). For the British Columbia, Alaska, and Sunda Shelf archipelagos, $A_E$ was one to two orders of magnitude greater than $A_X$ and three orders of magnitude greater than the values of $A_E$ estimated from the other archipelagos (Table 2).

## Discussion

I found no evidence that diversity in any province is at steady state. Results from six archipelagos, including islands and terrestrial isolates, indicated that diversity in two North American provinces is currently below steady state. Analyses of the British Columbia, Alaska, and Sunda Shelf archipelagos could not infer whether the VM mammal region is at steady state, but they did indicate that factors other than isolation have increased the differences in diversity between the intraprovincial and island regressions.

TABLE 1. Parameter estimates and statistics for island, intraprovincial, and interprovincial species–area relationships (where $\log S = \log c + z \log A$) for nonvolant, terrestrial mammals from four different regions.

| Relationship | *N* | Log *c* | SE log *c* | *P*† | *z* | SE *z* | *P*‡ | $R^2$§ |
|---|---|---|---|---|---|---|---|---|
| Alleghenian–Illinoian | | | | | | | | |
| Canadian reserves | 8 | 1.32 | 0.102 | <0.0001 | 0.09 | 0.035 | 0.05 | 0.50 |
| Lake Michigan islands | 9 | 0.17 | 0.054 | 0.019 | 0.29 | 0.048 | 0.0006 | 0.83 |
| Gulf of Maine islands | 24 | 0.68 | 0.033 | <0.0001 | 0.25 | 0.021 | <0.0001 | 0.86 |
| Intraprovincial | 56 | 1.57 | 0.017 | <0.0001 | 0.01 | 0.006 | 0.10 | 0.05 |
| Coloradan | | | | | | | | |
| Colorado Basin islands | 27 | −0.18 | 0.114 | 0.117 | 0.39 | 0.051 | <0.0001 | 0.70 |
| Great Basin islands | 17 | −0.46 | 0.208 | 0.0415 | 0.43 | 0.077 | <0.0001 | 0.68 |
| Rocky Mountain islands | 27 | −0.27 | 0.185 | 0.15 | 0.36 | 0.057 | <0.0001 | 0.61 |
| Intraprovincial | 5 | 1.16 | ⋯ | ⋯ | 0.06 | ⋯ | ⋯ | ⋯ |
| Sunda Shelf | | | | | | | | |
| Islands | 27 | 0.54 | 0.064 | <0.0001 | 0.25 | 0.022 | <0.0001 | 0.84 |
| Intraprovincial | 2 | 1.19 | ⋯ | ⋯ | 0.17 | ⋯ | ⋯ | ⋯ |
| Vancouverian–Montanian | | | | | | | | |
| British Columbia islands | 75 | 0.11 | 0.036 | 0.0035 | 0.21 | 0.021 | <0.0001 | 0.58 |
| Alaska islands | 24 | 0.39 | 0.123 | 0.005 | 0.18 | 0.044 | 0.0005 | 0.43 |
| Intraprovincial | 58 | 1.53 | 0.025 | <0.0001 | 0.03 | 0.009 | 0.0034 | 0.14 |
| Interprovincial | 15 | −1.67 | 0.295 | <0.0001 | 0.58 | 0.053 | <0.0001 | 0.90 |

*Note:* Ellipses indicate that statistics are not given where $N \leq 5$ observations; *N* is the number of reserves, islands, intraprovincial areas, or provinces sampled.

† The probability that $\log c = 0$.

‡ The probability that $z = 0$.

§ The proportion of variation in log *S* explained by log *A*.

Given the history of the late Pleistocene, it is not surprising that many of the analyses indicate that mammal diversity is below steady state. Within the last 50 000 years, over half of the 150 genera of large mammals (>44 kg) have become extinct (Barnosky et al. 2004). At the Wisconsin maximum 18 000–20 000 years ago, glaciers covered ~48% of North America. Not only did much of the world recently contain more, and larger, mammal species, but also the ice-free area of North America was much smaller. The extinction of large mammals is consistent with the explanation of how declines in provincial diversity could limit the diversity of large islands. Large mammals are likely to have persisted only on large islands with high immigration rates, so their extinction should not have affected the diversity of small, isolated islands.

Although some mammal provinces in North America may be below steady-state diversity, this may not be the case for all provinces or taxa. Some provinces, particularly those in Africa and Asia, may have maintained a larger portion of their Pleistocene fauna (Barnosky et al. 2004) and some provinces may have decreased in size since the Pleistocene. Provinces consisting of small, dense pockets of endemic mammals are priority areas for conservation (Myers et al. 2000), but may tend to be closer to steady-state diversity than less diverse regions; thus they require reserves that are larger or have higher immigration rates to maintain their diversity. Other taxa may not have experienced high extinction rates during the Pleistocene, leading to provinces closer to steady-state diversity. A plot of the three species–area relationships for frugivorous birds of wet tropical forests (Rosenzweig 2003) appears to predict a single intersection point. Consequently, conserving a given proportion of a province may not always conserve the same proportion of species.

For the British Columbia, Alaska, and Sunda Shelf archipelagos, it is plausible that island extirpation rates increased following isolation, or that contemporary intraprovincial relationships overestimate the pre-isolation diversity of the islands. All three archipelagos are mountainous and contain different habitats along an elevation gradient. As climate change occurred at the end of the last glacial period, these habitats may have ascended to higher elevations and decreased in area, similar to the montane forests in the southwestern United States. Evidence also suggests that the diversity of the continental Pacific coast has increased since the islands of British Columbia and Alaska were formed. The land bridge connecting these islands to the continent was in place 13 500–10 500 years ago (Barrie et al. 1993, Josenhans et al. 1997), but the range of many North American mammals continued to shift north after it was flooded (Graham et al. 1996). Alternatively, extinctions may have been caused by humans settling on islands prior to European colonization (Steadman 1995).

The archipelagos in which $A_E < A_X$ were less influenced by these effects, possibly for two reasons. First, these archipelagos are less isolated than those of the Pacific coast and Sunda Shelf. Some immigration has occurred between the montane forest islands (Lomolino et al. 1989) and periodic ice bridges have facilitated immigration to the Gulf of Maine and Lake Michigan

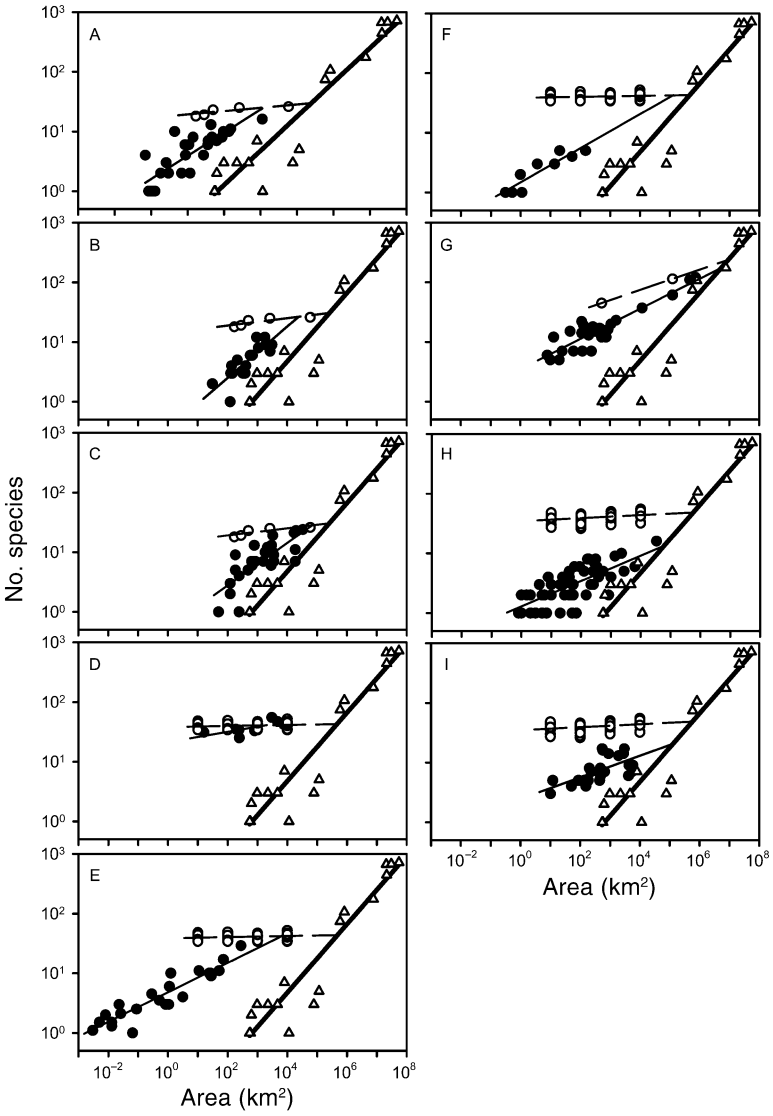


FIG. 2. The observed island (solid circles, thin line), intraprovincial (open circles, dashed line), and interprovincial (open triangles, thick line) relationships for terrestrial mammals: (A) Colorado Basin, (B) Great Basin, (C) Rocky Mountains, (D) Canadian parks, (E) Gulf of Maine, (F) Lake Michigan, (G) Sunda Shelf, (H) British Columbia, (I) Alaska.

islands (Crowell 1986, Lomolino 1986). Higher immigration rates would have increased the probability that species with expanding ranges colonized these islands. Second, the montane islands were defined a priori by a single habitat type and the Gulf of Maine and Lake Michigan islands have low relief, providing a stronger relationship between island area and habitat area. Species typical of surrounding habitats may have been included in samples of the montane forests and Canadian parks, reducing the value of $A_E$. However, $A_E$ was not less than $A_X$ entirely due to ''spillover'' of species into terrestrial islands, because values of $A_E$ were comparable between the Gulf of Maine and Lake Michigan islands and the terrestrial islands. In addition, I calculated that $A_E < A_X$ for two other archipelagos of ice-bridge islands in the AI mammal region: islands in the St. Lawrence River (Lomolino 1982) and Georgian Bay (Schmiegelow and Nudds 1987).

Although the interprovincial relationship should be estimated from provinces that differ only in area, I was forced to include provinces with different climates and habitats in the analysis, potentially biasing my results. Because mammal species diversity is greater in tropical regions and lower in temperate regions, I overestimated $A_X$ for the tropical provinces and underestimated $A_X$ for the temperate provinces. In all but two cases, these biases are in the opposite direction to the effects that I detected. Consequently, the North American provinces are even farther below steady state and a greater proportion of the difference in diversity between the

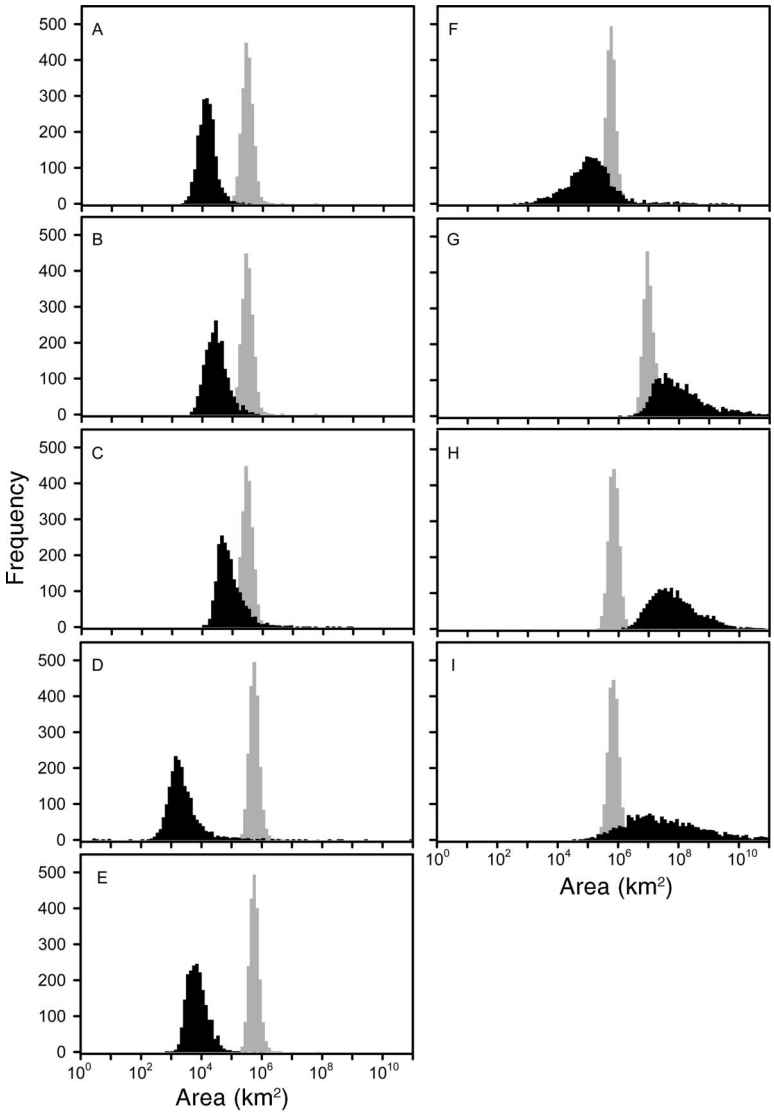


FIG. 3. The distribution of 2000 bootstrap estimates of the intersection of the island and intraprovincial species–area relationships ($A_E$; black bars) and the intersection of the intraprovincial and interprovincial relationships ($A_X$; gray bars) for (A) Colorado Basin, (B) Great Basin, (C) Rocky Mountains, (D) Canadian parks, (E) Gulf of Maine, (F) Lake Michigan, (G) Sunda Shelf, (H) British Columbia, and (I) Alaska. Distributions of some estimates were highly skewed. Values greater than $10^{11}$ km$^2$ are not shown.

intraprovincial and island relationships of the Sunda Shelf is due to factors other than isolation. The estimate of $A_X$ for the VM province is probably too low and more similar to $A_E$ than my analysis of the British Columbian or Alaskan archipelagos suggest.

These results indicate that land-bridge islands should be used cautiously as an empirical model of the effects of isolation on species richness of reserves. Soulé et al. (1979) estimated rates of species losses from the Sunda Shelf islands to predict the future diversity of East African reserves up to 5000 years following isolation. I calculated the $A_R$ of their reserve species–area relationship to be $10^{8.2}$ km$^2$, which is greater than the area of the seven continents combined, while $S_R = 181$ species. Soulé et al. (1979) conclude, not surprisingly, that the East African reserves are too small to avoid species losses due to reduced immigration rates: their model predicts that the continents are also too small to avoid these losses. Clearly, this result is problematic. There are far more than 181 species of mammals in the world and continental immigration rates are, for most terrestrial mammals, zero. The error is due to the model's assumption that species losses from the islands were entirely due to reduced immigration rates following isolation.

To separate the effects of decreased immigration rate and increased extirpation rate on island diversity, a rotation point should be part of an explicit definition

TABLE 2. Observed (Obs.) and bootstrapped estimates of the intersection of the island and intraprovincial species–area relationships ($A_E$) and the intersection of the intraprovincial and interprovincial species–area relationships ($A_X$) for nonvolant, terrestrial mammals.

| | $A_E$ (km$^2$) | | | $A_X$ (km$^2$) | | | $A_E$ as a percentage of $A_X$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Bootstrapped values | | | Bootstrapped values | | | Bootstrapped values | |
| Archipelago | Obs. | Mean | Median | Obs. | Mean | Median | Obs. | Mean | Median |
| Colorado Basin islands | $10^{4.09}$ | $10^{4.10}$ | $10^{4.09}$ | $10^{5.42}$ | $10^{5.44}$ | $10^{5.44}$ | 4.68 | 4.57 | 4.47 |
| Great Basin islands | $10^{4.37}$ | $10^{4.41}$ | $10^{4.38}$ | $10^{5.42}$ | $10^{5.44}$ | $10^{5.44}$ | 8.91 | 9.33 | 8.71 |
| Rocky Mountain islands | $10^{4.77}$ | $10^{5.87}$ | $10^{4.77}$ | $10^{5.42}$ | $10^{5.44}$ | $10^{5.44}$ | 22.39 | 269.15 | 21.38 |
| Canadian parks | $10^{3.27}$ | $10^{3.65}$ | $10^{3.24}$ | $10^{5.69}$ | $10^{5.71}$ | $10^{5.70}$ | 0.38 | 0.87 | 0.35 |
| Gulf of Maine islands | $10^{3.78}$ | $10^{3.81}$ | $10^{3.77}$ | $10^{5.69}$ | $10^{5.71}$ | $10^{5.70}$ | 1.23 | 1.26 | 1.17 |
| Lake Michigan islands | $10^{5.10}$ | $10^{5.14}$ | $10^{5.11}$ | $10^{5.69}$ | $10^{5.71}$ | $10^{5.70}$ | 25.70 | 26.92 | 25.70 |
| Sunda Shelf islands | $10^{7.90}$ | $10^{8.78}$ | $10^{7.86}$ | $10^{6.96}$ | $10^{7.00}$ | $10^{6.95}$ | 870.96 | 6025.60 | 812.83 |
| British Columbia islands | $10^{7.72}$ | $10^{7.82}$ | $10^{7.70}$ | $10^{5.78}$ | $10^{5.80}$ | $10^{5.79}$ | 8709.64 | 10 471.29 | 8128.31 |
| Alaska islands | $10^{7.38}$ | $10^{7.85}$ | $10^{7.42}$ | $10^{5.78}$ | $10^{5.80}$ | $10^{5.79}$ | 3981.07 | 11 220.18 | 4265.80 |

of a species–area relationship for islands formed through fragmentation of a province. Following the point-slope equation for a logarithmically transformed island relationship,

$$\log S_i - \log S_R = z_i(\log A_i - \log A_R)$$

which gives

$$S_i = S_R(A_i/A_R)^{z_i}. \quad (1)$$

This equation replaces the parameter $c_i$ with $S_R$ and $A_R$, which are functionally related to $S_P$ and $A_P$, respectively, supporting Gould's (1979) suggestion that $c_i$ includes other parameters related to the ecology and evolution of an archipelago's biota. An increase in $z_i$ will reflect a decrease in immigration rates, while a decrease in $S_R$ will reflect an increase in extirpation rates. To quantify the effect of factors other than isolation on species losses from the Sunda Shelf islands, I used Eq. 1 to force the island relationship calculated by Soulé et al. (1979) through the intersection of their intraprovincial relationship and the interprovincial relationship given in Table 1. The revised island relationship is $S_i = 3.72A_i^{0.21}$, whereas the original relationship is $S_i = 1.52A_i^{0.21}$, suggesting that over half of the species absent from the islands were lost due to factors other than decreased immigration rates.

When provincial diversity is below steady state, reserve planners can trade off immigration rate and reserve size, within limits, without affecting species persistence in reserves. Estimating the rotation point of the island species–area relationship will allow reserve planners to quantify this trade-off and to assess the costs of larger reserves compared to immigration corridors or active transport of species between reserves. This trade-off could be incorporated into reserve-selection algorithms (e.g., Rothley 1999, Margules and Pressey 2000) to design a system of reserves that meets goals for both the presence and persistence of species. For example, I estimated the combinations of $z_i$ and $A_E$ that would allow reserves in the AI mammal region to maintain their pre-fragmentation diversity by solving the equation

$$S_R(A_E/A_R)^{z_i} = c_P A_E^{z_P} \quad (2)$$

for $A_E$, given different values of $z_i$. I assumed that the point of rotation for the island relationship was given by the intersection of the island regressions fit to the Canadian reserves and Lake Michigan islands ($A_R = 10^{5.75}$ km$^2$; $S_R = 69$ species). The relationship between $A_E$ and $z_i$ is close to linear ($z_i = 0.118 + 10^{-5.75} A_E$) and suggests that a doubling of reserve area can compensate for a 50% increase in isolation. If the relationship between immigration rate and some measure of isolation were known, then the threshold isolation above which species would be lost could be calculated. Note that the relationship between $z_i$ and $A_E$ is likely to vary between provinces.

The rotation point can also be used to identify existing reserves that are in danger of losing species. The slopes of the interprovincial (0.58) and AI intraprovincial (0.01) relationships can be considered to be indexes of the minimum and maximum possible immigration rates. The slope of the line connecting a point on the intraprovincial relationship at 12 000 km$^2$ and the island rotation point, which is an index of the minimum immigration rate that a reserve can endure without losing species, is 0.14. This represents a maximum decline in immigration rate of 25%. If the actual immigration rate for a non-isolated reserve were known, then a minimum target immigration rate could be calculated and compared to immigration rates of existing isolated reserves of the same size. Reserves below the target will need to be larger or experience a higher immigration rate to avoid species losses in the future.

It is important to recognize that even if provinces are below steady state, careful planning of reserves may not avoid species losses indefinitely (Rosenzweig 2001, 2003). The persistence of species in reserves assumes that the quantity and quality of habitats within reserves are temporally stable. As discussed earlier, reduction

in habitat quality or quantity through stochastic events, such as climate change (Peters and Darling 1985) or fire (Pickett 1978), may cause species to be extirpated from reserves for long periods of time or even permanently. Ultimately, reducing a species' range size or population size to the confines of a system of reserves may never come without an increased risk of extinction. By devising ways to design more efficient reserves, perhaps more species will persist long enough for society to learn to create more habitat for them.

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