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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

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

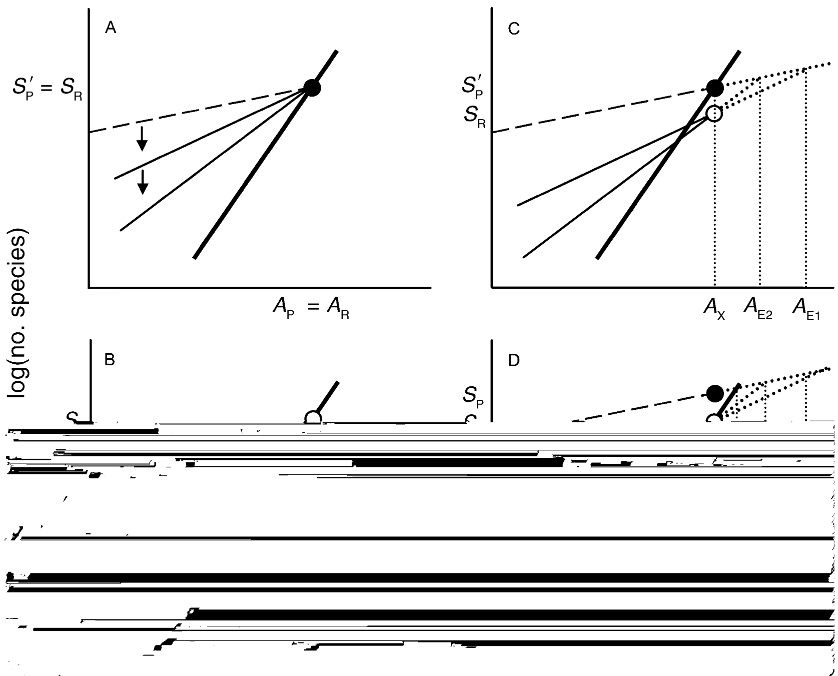


FIG. 1. Interpretation of the intersection points of hypothetical intraprovincial (dashed line), island (thin lines), and interprovincial (thick line) species–area relationships and their implications for conservation of species in reserves. If provincial diversity is at steady state at the time of island 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.

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 in-

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 $z = 0$.

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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

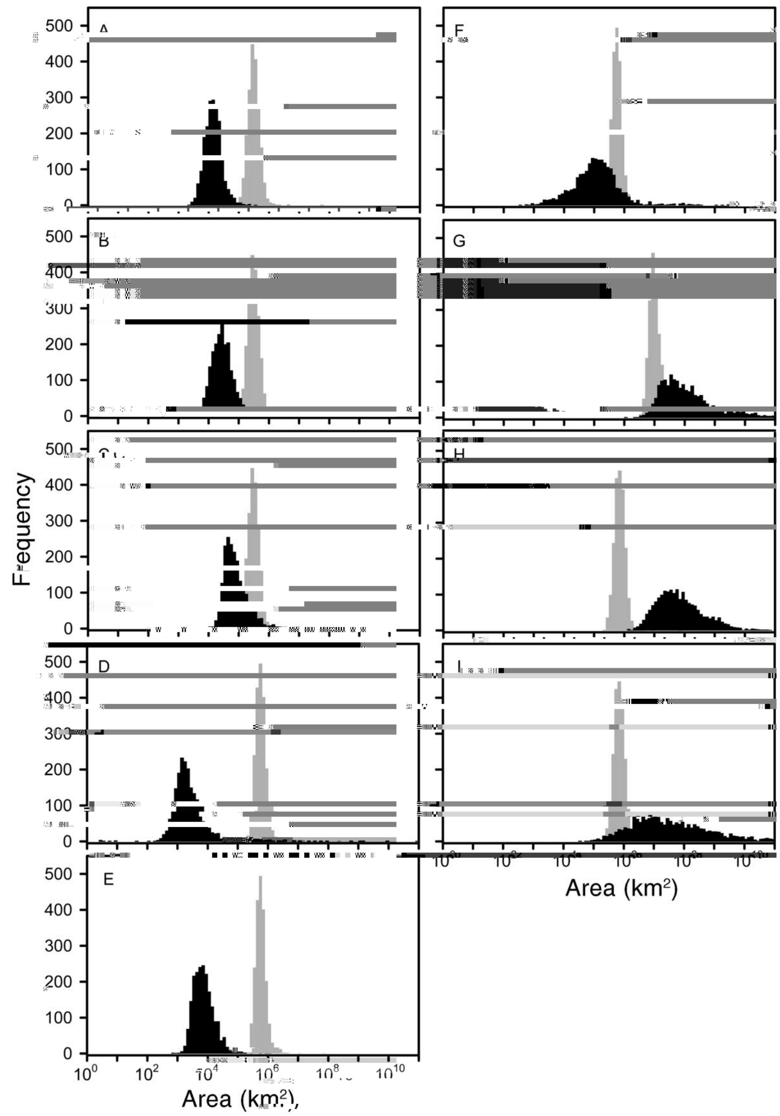


FIG. 3. The distribution of 2000 bootstrap estimates of the intersection of the island and intraprovincial species–area relationships (

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 percenta 8.2 468.5 0 -0 8.2 223.149 671 Tm 0 |
|---|---|---|---|---|---|---|---|
| | | Bootstrapped values | | | Bootstrapped values | | |
| Archipelago | Obs. | Mean | Median | Obs. | Mean | Median | |

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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