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Patterns in the geographical range sizes of ectotherms in North America

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Abstract The distributions of homeothermic mammals and birds in continental North America show a distinct pattern in the configuration of their geographical ranges. Smaller ranges tend to be elongated north-south while larger ranges tend to be elongated east-west. To examine the generality of this pattern in ectotherms, we analyzed the distribution on continental North America of 139 species of mosquitoes, 164 amphibians, and 221 reptiles. Unlike birds and mammals, small ranges of ectotherms were not elongated north-south and the small ranges of snakes were elongated east-west. The distribution of ectotherms with small ranges does not appear to be affected by the major topographic features of North America which tend to run north-south. Like birds and mammals, large ranges of mosquitoes and reptiles but not amphibians are elongated east-west. The east-west orientation of mosquitoes with large ranges is not attributable to the three largest genera in North America taken singly, *Aedes*, *Culex*, or *Anopheles*, but appears only when all genera are pooled. The east-west orientation of reptiles with large ranges is attributable to turtles and snakes but not lizards. Climatic zones may thus affect the distribution of mosquitoes, turtles, and snakes with large ranges but are not the major determinants of range dimensions among ectotherms in general.

Key words Biogeography · Amphibian · Mosquito · Reptile · Ectotherm

Introduction

The study of species and community diversity has been pursued with renewed interest in recent years due to the increased awareness of the rapid loss of both habitats

and species and the anticipated effect of this loss on all levels of biodiversity. It has become apparent that many aspects of biodiversity and community structure will not be understood readily without consideration of the ecological and evolutionary factors that determine the patterns of geographical distribution (Gaston 1991). In particular, the interactions of characteristics such as body size, local abundance, and probability of extinction with geographical range size have been examined (Brown and Maurer 1987, 1989; Gaston and Lawton 1988; Gaston 1990; Lawton 1993). This approach has led to the discovery of a number of intriguing general patterns and correlations. Ecologists in search of a greater understanding of biodiversity have begun to examine distribution and abundance data at many spatial scales from local to continental.

A continental approach was taken by Brown and Maurer (1989) who examined the size and shape of geographical ranges of terrestrial mammals and birds of North America. They plotted the north-south range against the east-west range on a logarithmic scale. By comparing the observed distribution of points to the 1:1 line which would be generated if the ranges were of equal size in both dimensions, a number of patterns emerged. Species with small ranges tended to fall above the 1:1 line, suggesting that small ranges were elongated in a north-south direction. Species with large ranges tended to fall below the line, suggesting that large ranges were elongated east to west. Brown and Maurer (1989) proposed that species with small ranges may be limited by habitat associations or major topographic features such as mountain ranges, river drainages or coast lines, which in North America are predominately north-south in orientation. Species with large ranges may be relatively insensitive to these variables and, instead, are limited by major climatic zones and biome types, which are determined in large part by latitudinal gradients that are predominately orientated from east to west.

These mechanistic processes proposed by Brown and Maurer (1989) do not appear, as they point out, to depend on endothermy; yet both of the taxa they consider

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are vertebrate endotherms. To test whether the patterns observed in birds and mammals apply to ectotherms as well as endotherms, we examined the relationships between east-west and north-south range dimensions for North American mosquitoes, amphibians, and reptiles. If the pattern observed for vertebrate endotherms is general, then, a plot of north-south against east-west ranges on a full logarithmic scale should (1) exhibit a slope of less than 1.0, (2) show greater north-south than east-west orientation in species with small ranges, and (3) show greater east-west than north-south orientation in species with large ranges.

Materials and methods

Neither Brown (1995) nor Brown and Maurer (1989) describe their methodology other than saying that they examined "land birds" and "terrestrial mammals." For the purposes of this study we considered geographic range as the extent of occurrence (sensu Gaston 1991), defined as the area encompassing all known localities. We chose extent of occurrence for the simple reason that we were interested in the pattern of range extension in latitude and longitude, not the pattern of occupancy within a species' known range. The extents of species ranges were taken directly from range maps (Stebbins 1954; Conant 1975; Darsie and Ward 1981) by measuring the largest longitudinal and latitudinal extent of the range. We excluded from the analysis all species occupying exclusively peninsular Florida, to eliminate potential bias due to the extreme north-south elongation imposed physically by the surrounding marine habitats. Since the ranges of several species extended to an unknown extent into Central and South America, we also excluded from analyses all species whose entire range extended only 200 km north of the Mexican border or was contained entirely in Texas south of 30° N. The resulting data set included 139 species of mosquitoes, 164 amphibians, and 221 reptiles. Mosquitoes were considered as a whole and by the three major genera in North America: 16 species of *Anopheles*, 22 species of *Culex*, and 72 species of *Aedes*. Amphibians were subdivided into 89 species of salamanders and 75 species of anurans. Reptiles were subdivided into 44 species of turtles, 72 species of lizards, and 105 species of snakes.

Since we were interested in the relationship between latitudinal and longitudinal range extent, and not the prediction of one from the other, we determined the slope and 95% confidence interval of the principal axis of their bivariate distribution. Progressive deviation from equal range dimensions in latitudinal and longitudinal extent would result in a curvilinear relationship. When plotted on a full logarithmic scale, this curvilinearity would result in a slope significantly different than 1.0. For instance, if larger ranges tend towards increased east-west elongation, the slope and its upper 95% confidence interval would be less than 1.0; conversely, if the larger ranges tend towards increased north-south elongation, the slope and its lower 95% confidence interval would be greater than 1.0.

Brown (1995) and Brown and Maurer (1989) make no explicit tests of their suggested patterns; we do make explicit tests of each of our three predictions.

Prediction 1: a plot of north-south against east-west ranges on a full logarithmic scale should exhibit a slope of less than 1.0.

If μ_X and μ_Y are the two means and Var_X , Var_Y , and $\text{Cov}_{X,Y}$ are their respective variances and covariance, then for a sample size of N , the slope of the principal axis is (Sokal and Rohlf 1969, Sect. 15.6)

$$\beta_1 = \frac{\text{Cov}_{X,Y}}{\lambda_1 - \text{Var}_X} \quad (1)$$

where

$$\lambda_1 = \frac{\text{Var}_X + \text{Var}_Y + D}{2}, \quad \lambda_2 = \frac{\text{Var}_X + \text{Var}_Y - D}{2}, \quad (2)$$

and

$$D = \sqrt{(\text{Var}_X + \text{Var}_Y)^2 - 4(\text{Var}_X \text{Var}_Y \text{Cov}_{X,Y}^2)} \quad (3)$$

and the intercept of the principal axis is

$$\alpha_1 = \mu_X - \beta_1 \mu_Y \quad (4)$$

The upper and lower 95% confidence intervals are

$$L_{\text{LOW}} = \frac{\beta_1 - A}{1 + \beta_1 A} \quad \text{and} \quad L_{\text{UPR}} = \frac{\beta_1 + A}{1 - \beta_1 A} \quad (5)$$

where

$$A = \sqrt{\frac{H}{1-H}}$$

and

$$H = \frac{\chi_{1,\alpha}^2}{N\left(\frac{\lambda_1}{\lambda_2} + \frac{\lambda_2}{\lambda_1} + 2\right)} \quad (6)$$

When only one principal axis is being determined, $\chi_{1,0.05}^2 = 3.84$ and the slope of the principal axis is significantly different from 1.0 if the range L_{LOW} to L_{UPR} does not contain the value 1.0. When more than one principal axis is being tested, the actual protection level must be increased to assure a table-wide protection level of $\alpha = 0.05$. To achieve this table-wide protection, we used a sequential Bonferroni (Rice 1989). First, we adjusted the value of χ^2 in Eq. 6 until L_{LOW} or L_{UPR} equalled 1.00 and then used that value of χ^2 with 1 *df* to determine the exact probability that $\beta_1 = 1.00$. Second, we ranked these probabilities and applied the sequential Bonferroni to determine, hierarchically, whether $P < 0.001$, $P < 0.01$, $P < 0.05$, or $P > 0.05$.

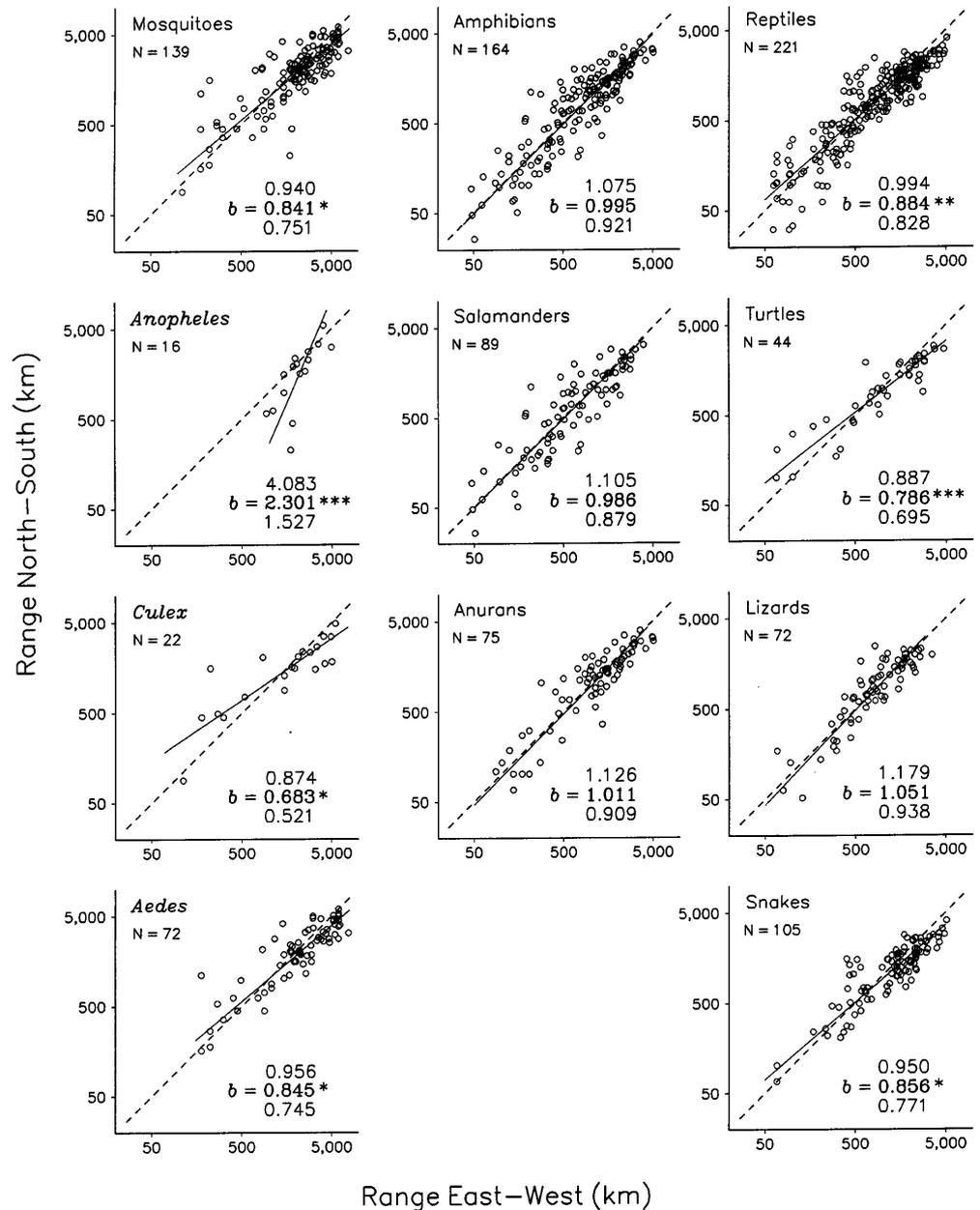
Predictions 2–3: a plot of north-south against east-west ranges on a full logarithmic scale should show (2) greater north-south than east-west orientation in species with small ranges and (3) greater east-west than north-south orientation in species with large ranges

To test the prediction that smaller ranges are predominately elongated in a north-south direction, we calculated the mean and standard error of the value $\log(\text{north-south}/\text{east-west})$ for each taxonomic group and compared it to the null expectation of no difference in range dimensions. Both the lower 50th and 20th percentile of range sizes were considered in this analysis. Similarly, to test the prediction that large ranges tend toward greater east-west elongation, we examined the upper 50th and 20th percentiles of range sizes. We performed a total of 44 *t*-tests of mean $\log(\text{NS} \div \text{EW})$ for significant deviation from zero (11 taxonomic groupings \times 2 percentiles \times 2 range sizes) whose significance we assessed by applying the sequential Bonferroni test, as above.

Results

The results of our analysis of the principal axes of range dimensions showed a mixed pattern (Fig. 1). In mosquitoes and reptiles, but not amphibians, the slope of the principal axis was significantly less than 1.0. Within mosquitoes, the slope of the principal axis was greater than 1.0 in *Anopheles*, and less than 1.0 in *Culex* and in *Aedes*. Within reptiles, the slope of the principal axis was less than 1.0 in turtles and snakes, but not significantly

Fig. 1 Geographic ranges (km) of North American mosquitoes, amphibians, and reptiles. The dotted line illustrates a slope of 1.0, the solid line shows the principal axis of the bivariate distribution of north-south and east-west range extensions. The slope of the principal axis (b) is provided with its upper and lower 95% confidence limits for a nominal protection level of $\alpha = 0.05$. The probability that $b = 1.00$ after application of a sequential Bonferroni is given by *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$; otherwise, $P > 0.05$

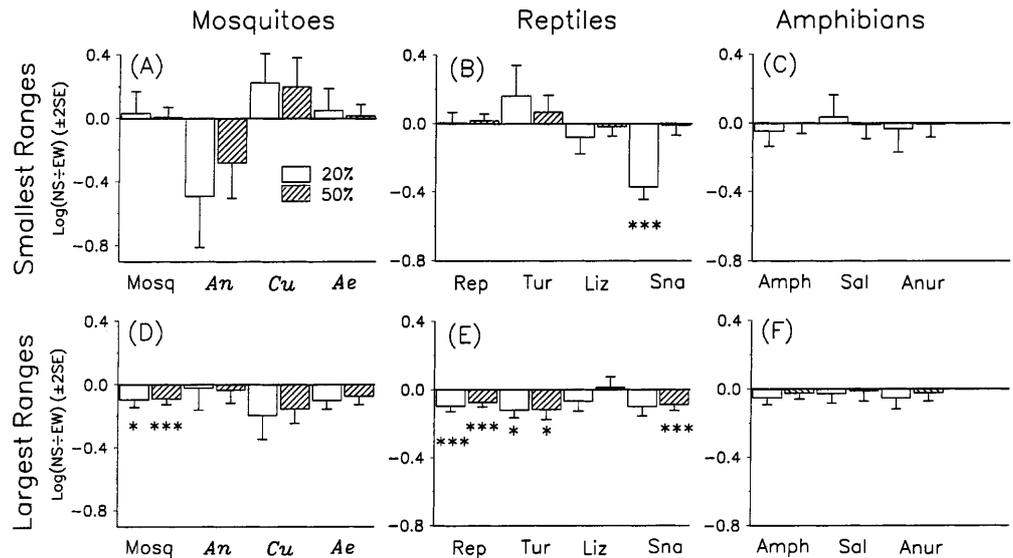


different from 1.0 in lizards. Within amphibians, the slope of the principal axis was not significantly different from 1.0 in either salamanders or anurans.

Among species with small ranges (Fig. 2A–C), there was no instance of a significant north-south orientation. Neither salamanders, anurans, nor amphibians as a whole showed a significant bias in the orientation of small ranges. Snakes showed a significant east-west bias in the range extensions of the smallest 20% but not 50% of ranges; there was no significant bias in range orientation of reptiles in general, lizards, or turtles. Taken together, these results showed mainly an absence of significant bias in the orientation of small ranges and, when a significant bias did occur, it was towards a larger east-west than north-south orientation.

There were six taxa in which the slope of the principal axis was less than 1.0 (Fig. 1). The large ranges of four of these taxa showed a significant east-west orientation (Fig. 2D–F): mosquitoes in general but not the genera *Aedes* and *Culex*, reptiles in general, turtles, and snakes. In the far north, the distance from Labrador to the Aleutian Islands exceeds the distance from the Gulf of Mexico to the north coast of North America, thereby injecting a potential physical bias in the east-west ranges of animals with extreme ranges. Six species of *Aedes* – *A. punctator*, *A. canadensis*, *A. excrucians*, *A. fitchii*, *A. communis*, and *A. cinereus* – have east-west ranges that exceed the north-south dimensions of continental North America north of Mexico. To determine whether the east-west orientation of *Aedes* with large ranges was due

Fig. 2 Mean difference between log(north–south) and log(east–west) range extensions comprising the smallest 20% and 50% of ectotherm ranges in North America. After sequential Bonferroni applied figure-wide to 44 comparisons, the probability that a given difference equals 0.00 is given by *** $P < 0.001$, * $P < 0.05$; otherwise, $P > 0.05$ (*Mosq* mosquitoes, *An* *Anopheles*, *Cu* *Culex*, *Ae* *Aedes*, *Rep* reptiles, *Tur* turtles, *Liz* lizards, *Sna* snakes, *Amph* amphibians, *Sal* salamanders, *Anur* anurans)



to these extreme species, we deleted those *Aedes* from the data set and recalculated the asymmetry of the largest ranges. The results were consistent with the data set as a whole: log(north-south/east-west) ranges were still negative for both the 20% (mean \pm SE = -0.095 ± 0.015) and 50% (-0.069 ± 0.014) largest ranges.

Discussion

We agree with the sentiment of Brown (1995) that the general patterns of geographic ranges need to be established before we can seek the underlying causality. Brown and Maurer (1989) provide full logarithmic plots of north-south versus east-west ranges of North American birds and mammals that show three patterns. First, small ranges tend to be more north-south than east-west oriented; second, large ranges tend to be more east-west than north-south oriented, and third, as a consequence, the apparent slope of the relationship is less than 1.0. Brown (1995) and Brown and Maurer (1989) propose that species with small ranges are more limited by local topographic features such as mountain ranges, river valleys, and coastlines which, in North America, tend to run north-south. Consequently, animals with smaller ranges should be north-south oriented. By contrast, animals with larger geographic ranges should be limited more by major climatic zones which are stratified in latitudinal bands. Consequently, animals with larger ranges should be east-west oriented. As Brown (1995, p. 110) pointed out, if the patterns observed for birds and mammals really do “reflect the effect of the geography of North America on the configurations of geographic ranges, then other kinds of organisms should show similar patterns.” We agree with this prediction and have sought to test it by examining the ranges of ectothermic mosquitoes, reptiles, and amphibians.

We find no consistent repeatability among ectotherms for the range configuration observed in verte-

brate endotherms. First, in no case did we find that small ranges of mosquitoes, reptiles, or amphibians were significantly north-south oriented and, in one instance (snakes) they were oriented east-west (Fig. 2A–C). Second, we did find that the principal axis of range configurations (Fig. 1) had a slope significantly less than 1.0 in mosquitoes and reptiles (but not amphibians). In the case of reptiles, this departure could be attributed to turtles and snakes but not lizards. In the case of mosquitoes, this departure is probably attributable to the speciose genera *Aedes* and *Culex* but not *Anopheles* where the slope of the principal axis was actually positive. Third, a slope of the principal axis of less than 1.0 for range configurations is attributable to an east-west bias in the largest ranges but not a north-south bias in the smallest ranges. Hence, departure of this slope from 1.0, by itself, does not constitute evidence that small ranges are north-south oriented.

The differences between the orientation of small ranges in birds and mammals observed by Brown and Maurer (1989) and the orientation of small ranges in mosquitoes, reptiles, and amphibians in Fig. 2 indicate fundamental differences between endotherms and ectotherms in the environmental factors affecting their ranges. Major topographic features may be important to the distribution of birds and mammals with small ranges but they do not appear to affect the distribution of either vertebrate or invertebrate ectotherms with small ranges. We are unable to propose any reason why endotherms and ectotherms should differ in this manner.

Large range extensions of ectotherms compare inconsistently with birds and mammals. Large ranges of birds and mammals appear to be east-west oriented, similar to the large ranges of mosquitoes and reptiles but not amphibians. The mosquito pattern can be ascribed to *Aedes* and *Culex* and the reptilian pattern to turtles and snakes but not lizards. Brown (1995, Fig. 6.5) shows linear plots taken from an unpublished student report suggesting that range orientation of lizards and snakes

may conform to the pattern of birds and mammals. The numbers of species in the analysis, the source of the data, and the geographic limits of these data are not provided nor is any test made to determine whether the observed patterns depart from null expectation. Hence, we are unable to reconcile the lizard and snake patterns in Brown (1995) with those shown in Fig. 1. We have, however, taken our ranges from published and readily available range maps and have tested them against explicit expectations. We therefore conclude, first, that the differences in large range orientation between turtles or snakes and lizards that we show in Fig. 1–2 are real and, second, that real differences occur in range orientation among broader taxonomic categories of ectotherms, among genera within mosquitoes, and among orders or suborders within reptiles. The role of phylogenetic factors influencing the relationships between range size characteristics and other population parameters is the topic of a number of recent studies (Lawton 1993). Our observations point to the importance of not blindly seeking causality for general patterns observed in large taxonomic groups since specific lineages and ecologies may behave differently from the general pattern and need to be considered independently.

What factors do limit the ranges of ectotherms? Our analyses provide no direct answers but do provide several foci for future enquiry. It is clear that vertebrate endotherms with small ranges may be limited by major topographic features such as mountain ranges or river valleys while neither vertebrate nor invertebrate ectotherms are so limited. Hence, future research in the area of small species ranges should focus on potential costs of endothermy in limiting the range extensions of birds and mammals with smaller ranges.

Among ectotherms with large ranges, we found no east-west bias, and hence, no implication of range limitation due to climatic zones in any of the most speciose of North American mosquito genera, in lizards, or in amphibians (Fig. 2D–F). All three mosquito genera include species with the largest of ectotherm ranges (Fig. 1). This pattern suggests that range extension of these genera is limited more by the available land mass of North America than by climatic factors. The largest lizard ranges (no significant east-west bias) are smaller than those of turtles or snakes (significant east-west bias) (Fig. 1) and are smaller than those of birds or mammals that appear east-west biased (Brown and Maurer 1989). This pattern suggests that lizard ranges are constrained more by their dispersal ability than by their tolerance of northern climatic zones. Neither of these rationales, however, applies to amphibians (no significant east-west bias) whose large range extensions are less than those of the mosquito genus *Aedes* (no significant east-west bias) and equally as extensive as turtles and snakes (significant east-west bias).

The significant east-west bias of the largest ranges of snakes and turtles implies that their range expansions are limited by more northern climates, namely by (1) the increasing intensity of winter cold, (2) the increasing

duration of winter, or (3) the decreasing duration of the summer growing season. The intensity of winter cold is not likely to be limiting to snakes because red-sided garter snakes, for example, hibernate and aggregate in dens where the effects of winter cold are greatly mitigated (Gregory 1977). Similarly, northern populations of turtles that overwinter as freeze-susceptible eggs in the south can escape the exigencies of winter cold by hatching in the fall and either digging deeper in the soil or finding refuge in nearby bodies of water (Costanzo et al. 1995). The duration of the summer growing season is not likely to be limiting to snakes or turtles because both take several years to mature anyway. We therefore propose that it is the duration of winter that may impose the range limitation. Even hibernating ectotherms require energy for winter metabolism and for development and reproduction the following spring. Long winters may deplete snake or turtle reserves thereby reducing survivorship, retarding development, or reducing growth or reproduction.

The absence of a significant east-west bias in large ranges at broader taxonomic levels negates the proposition that the broader taxon is limited in its range expansion by the northern climate; but, this negation does not necessarily apply to all species within that taxon. The presence of a significant east-west bias implies, but does not demonstrate or test the proposition that some aspect of the more northern climate is limiting the range expansion of some of the species in that taxon. In the case of the significant east-west biases in the large ranges of snakes and turtles, we have proposed that the duration of winter rather than the intensity of winter cold or the duration of the summer growing season is the limiting component of northern climates. Testing this or alternate propositions (which we heartily encourage) will require specific knowledge of the regional phenology, thermal ecology, and demography of northern populations of species with large ranges.

Range configurations are certainly flexible in evolutionary time and likely in ecologically relevant time scales as well. The effects of range expansion and contraction on the patterns of species distributions are poorly understood. Species' ranges may have quite different properties under non-equilibrium conditions, such as range contraction and expansion, than under equilibrium conditions. These factors may have important implications for the conservation and management of species whose historical range is undergoing fragmentation or a reduction in area (Lawton 1993). Unfortunately, our ability to observe "natural" patterns of the configuration of species ranges is diminishing rapidly as historical ranges shrink and fragment in response to human activity.

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