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Elevational gradients in ant species richness: area, geometry, and Rapoport's rule

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Studying the distributions of plants and animals along environmental gradients can illuminate the factors governing and maintaining species diversity. There are two general predictions of how species richness and elevation are related: either species richness decreases monotonically with increasing elevation or richness peaks at mid-elevations. Several processes might contribute to this pattern. In this paper, I examine patterns in ant species richness along elevational gradients in three states in the western US: Colorado, Nevada, and Utah. I test for the effects of available area and the geometric constraints model on species richness patterns. I also test Rapoport's rescue hypothesis, which relates the extent of species' elevational ranges to patterns in species richness. In each state, species richness peaked at mid-elevations. Area explained more variation in species richness than the geometric constraints model in Colorado and Utah, but not in Nevada. Area and geometric constraints together explained 90%, 99%, and 57% of the variation in species richness in Colorado, Nevada, and Utah, respectively. Even though there were peaks at mid-elevations, I still found a strong Rapoport effect. This work suggests that the influences of area and geometric constraints cannot be overlooked when examining patterns in species richness along environmental gradients.

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A frequently documented ecological pattern is the relationship between species richness and elevation. Two general patterns emerge: a monotonic decrease in species richness with increasing elevation (e.g., MacArthur 1972, Stevens 1992) or a humped-shaped relationship, with a peak in richness at intermediate elevations (see Rahbek 1995 for a detailed review). Both patterns have been documented in a variety of habitats and taxa (e.g., Terborgh 1977, Stevens 1992, Brown 1995, Rahbek 1995, Rosenzweig 1995, Brown and Lomolino 1998), but Rahbek (1995, 1997) and others (Lees et al. 1999, Colwell and Lees 2000) have pointed out that perhaps mid-elevational peaks are more common.

If peaks in species richness at mid-elevations are a common pattern, then the next step is to understand the mechanisms contributing to the pattern. Traditionally, such explanations have focused on relating species richness to elevation via productivity. That is, productivity varies along elevational gradients, and productivity is the driving force behind patterns in richness; elevation merely serves as a surrogate for productivity. Species richness can be related to productivity in at least two ways: 1) as productivity increases, species richness increases monotonically (Hutchinson 1959, Preston 1962a, b, Connell and Orians 1964, MacArthur 1965, 1969, 1972, Brown 1988, Brown and Lomolino 1998) or 2) as productivity increases, species richness increases, peaks at mid-levels of productivity, and then decreases at high productivities (Tilman 1982, Rosenzweig and Abramsky 1993, Rosenzweig 1995). However, hard data demonstrating that elevation is a fair surrogate for productivity remain elusive (Rahbek 1997).

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Like productivity, another important influence on species richness is area. In fact, one of ecology's few laws is that large areas often support more species than do smaller areas (Schoener 1976). But few studies have examined the relationship among area, elevation, and species richness. For insects feeding on bracken in Britain, there was no relationship between richness and elevation after the effects of area were removed (Lawton et al. 1987). Rahbek (1997) found that when not accounting for the effect of area, there was a monotonic decrease in neotropical bird diversity with increasing elevation. However, when the influence of area was factored out, the relationship between diversity and elevation became hump-shaped with peaks at mid-elevations (Rahbek 1997).

Colwell and Lees (2000) have suggested another hypothesis, the mid-domain effect, which seems to be very robust among different taxa. A mid-domain peak in richness is generated when there is increasing overlap of species ranges toward the center of the domain because the extent of the elevational ranges of species are bounded by the highest and lowest elevation possible in the region (Colwell and Hurtt 1994). Thus, regardless of variation in climatic variables such as productivity, a peak in species richness at mid-elevations may be due simply to the limits imposed by geographic boundaries.

Another pattern along elevational gradients is a positive correlation between elevation and the elevational range of species; this pattern has been called Rapoport's rule (Stevens 1992) or effect (Blackburn and Gaston 1996). It posits that climates at higher elevations are more variable, so species at higher elevations can tolerate more variability and therefore have larger elevational ranges. Richness is inflated at low elevations because of the proximity of nearby core areas for these "low elevation" species, but these species cannot persist at higher elevations. As a result, species richness decreases monotonically with elevation. This pattern has been documented in butterflies (Fleishman et al. 1998), trees, mammals, reptiles, some amphibians, and grasshoppers (references cited in Stevens 1992).

For insects, there is considerable empirical evidence for both peaks in species richness at low elevations (e.g., Wolda 1987, Fernandes and Price 1988, McCoy 1990, Kearns 1992, Stevens 1992, Olson 1994, Sparrow et al. 1994) and peaks in species richness at intermediate elevations (Janzen 1973, McCoy 1990, Olson 1994, Sanchez-Rodriguez and Baz 1995, Fleishman et al. 1998). However, to my knowledge, only Lawton et al. (1987) have explored the relationship between insect species richness and elevation when area is controlled for and Fleishman et al. (1998) are the only researchers to have tested for Rapoport's rule in insects.

A few studies of ants have examined the effects of elevation on species richness, with differing conclusions. Several studies demonstrated that there are fewer species at higher elevations than at lower elevations, or that there are no species above a certain elevation (Weber 1943, Brown 1973, Janzen 1973, Janzen et al. 1976, Collins 1980, Atkin and Proctor 1988). Species richness of leaf litter ants in a Malaysian rainforest decreased exponentially with increasing elevation (Brühl et al. 1999). Similarly, studies performed in a Panamanian rainforest (Olson 1994) and in Madagascar (Fisher 1996) showed a monotonic decrease in ant species richness with increasing elevation. In contrast, Fisher (1998), in another study in Madagascar, detected peaks in species richness at mid-elevations in leaf litter ants, and Samson et al. (1997) reported a peak in species richness at mid-elevations in forests in the Philippines. To date, no studies have examined the relationship among elevation and ant species richness while considering the effects of area and the mid-domain effect.

To examine the relationship between elevation and species distributions, this study considers the distributions of ant species in the western US. The data on ant distributions come from extensive faunistic surveys of three states in the western US: Colorado (Gregg 1963), Nevada (Wheeler and Wheeler 1986), and Utah (Allred 1982). Although there are unknown biases in sampling effort, species identifications, and locality information with these three studies, these references include a comprehensive review of richness in these states and trustworthy data on locality from which most species were collected. I use the data on ant distributions from each of these states as a sample, so when I refer to the Colorado ants, I simply mean the data from Gregg's monograph on Colorado ants; the ants do not respond differently just because they are from a particular state. Since the range of altitudes (ca 150–4400 m) in the three states is so great, it is possible to get a fair estimate of the elevational range size of each species. Furthermore, the influences of abiotic factors on species richness patterns are not confounded by latitudinal gradients because the states are at roughly the same latitudes (McCoy 1990).

Here, I test the generality of patterns in ant species distributions along elevational gradients in two ways. First, I use data from intensive faunistic surveys of three states (Colorado, Nevada, and Utah). Second, I compare my results across subfamilies in the Formicidae. If the same pattern of distributions along elevational gradients exists among the three states and the most common subfamilies, then they are likely to be general mechanisms. Specifically, this study asks: 1) What is the influence of available area and geometric constraints on ant species richness patterns along elevational gradients in Colorado, Nevada, and Utah? 2) Do the patterns in richness differ among states? 3) Are the results consistent with Rapoport's rule?

Methods

Ant taxonomy has been extensively revised since the publication of these regional surveys I used. I elevated every subspecies listed in each of the three sources to the appropriate species-level taxon using Bolton (1994). In total, 226 species were identified and over 11 700 ant specimens were recorded in the three states.

To examine the relationship between species richness and elevation, I divided the range of elevations into 100 m bands and found the total number of species in each band in each state. I assumed that each species was present in all bands between its highest and lowest reported elevations.

I determined the relationship between area and elevation in each state by calculating the number of square kilometers in an elevational band. To calculate the area at each elevational band in Colorado, I used a Digital Elevation Model (DEM) from ESRI's Arcview GIS Data and Maps 1999. For the Nevada data set, I used a 1:100 000 scale DEM from the Nevada Div. of Wildlife. To determine the area at each elevation in Utah, I used a DEM contour map with intervals at 500 ft and calculated the area at each interval.

I used Colwell's RangeModel software (Colwell 2000) to generate a null distribution predicted by the mid-domain effect based on 1000 runs of N_i species, where N_i is the number of species in each state i. The output of the simulation is the expected number of species at each elevation band.

To examine the influence of area and the mid-domain effect on ant species richness patterns in each state, I determined for each state the relationship between species and area by log transforming the number of species in each elevational band and the area at each elevational band; this is the species-area curve for each state. I also log transformed the number of species predicted by the geometric constraints model. I used simple linear regressions with area and the predicted number of species alone as independent variables. I then used both area and the predicted number of species from the mid-domain effect in a multiple regression to examine their combined effects on species richness patterns. All p values reported here are simply indices of relative fit of the dependent and independent variables. They are not really "tests of statistical significance" because elevational bins are not independent (Colwell pers. comm.).

To examine the relationship between the extent of the elevational range size of ants and elevation, I calculated the elevational range of each species in each state by subtracting the lowest elevation at which a species was collected from the highest elevation at which it was collected for each species collected at two or more elevations. I assumed that a species was present at all intervals between its highest and lowest recorded elevational distributions. To overcome statistical non-independence of spatial data, I used the "midpoint method" as a measure of central tendency (Rohde et al. 1993); a midpoint for each species was calculated as the mean of the highest elevation and lowest elevation at which a species was collected.

I used correlation analysis with $\alpha = 0.05$ to test for associations between elevation and elevational range size. In Figs 3–5, best fit lines are only to aid the reader's eye; they are not meant to suggest causality. To test if the strength of the relationship between elevation and range size was independent of state and subfamily, I performed a test similar to a chi-square analysis using

$$\chi^2 = \Sigma(n_i - 3)(z_i - z_w)^2,$$

where n_i is size of sample i, z_i is Fisher's transformation (Fisher 1915), and z_w is the weighted mean correlation coefficient for all samples. I also performed post hoc comparisons using Tukey tests to test for differences between each sample (Zar 1999).

Results

Species richness for each state peaked at mid-elevations (Fig. 1). The total richness from the three states combined also peaked at mid-elevations. The numbers of species in each subfamily also peaked at mid-elevations, so there is likely to be no phylogenetic effect on ant distributions.

The area in an elevational band was generally greatest at mid-elevations (Fig. 1). The species-area curves for each state are plotted in Fig. 2. Area explained a significant amount of the variation in each state (Colorado: $y = 0.8969x - 1.8546$, $r^2 = 0.75$, $p < 0.0001$; Nevada: $y = 0.4028x + 0.1222$, $r^2 = 0.71$, $p < 0.0001$; Utah: $y = 0.5234x - 0.5014$, $r^2 = 0.53$, $p = 0.0003$).

The patterns in species richness for each state are consistent with the mid-domain effect (Colorado: $y = 0.261x + 0.768$, $r^2 = 0.13$, $p = 0.04$; Nevada: $y = -1.30 + 1.72$, $r^2 = 0.91$, $p < 0.0001$; Utah: $y = -1.21 + 1.70$, $r^2 = 0.37$, $p = 0.004$).

The combined effects of area and geometric constraints explained a considerable amount of the variation in species richness in each state (Colorado: $r^2 = 0.90$, $p < 0.0001$; Nevada: $r^2 = 0.99$, $p < 0.0001$; Utah: $r^2 = 0.57$, $p = 0.0008$).

The elevational extent of species tended to increase with increasing elevation, as Rapoport's rule predicts ($n = 364$, $r = 0.453$, $p < 0.001$) (Fig. 3). Even though there is considerable scatter around the best fit line, there is a positive correlation between the elevational range size and the midpoint of the range size for most taxa; species at higher elevations had broader ranges.

For each subfamily, elevational extent tended to increase with increasing elevation, as Rapoport's rule predicts (Dolichoderinae: $n = 18$, $r = 0.536$, $p < 0.05$; Formicinae: $n = 196$, $r = 0.442$, $p < 0.001$; Myrmicinae: $n = 145$, $r = 0.343$, $p < 0.001$) (Fig. 4). The responses for each taxon were not significantly different from one another ($\chi^2 = 1.57$, DF = 2, $p > 0.20$), so there is probably little or no phylogenetic effect. The elevational extent of species in each state increased with increasing range size (Colorado: $n = 137$, $r = 0.622$, $p < 0.001$; Nevada: $n = 134$, $r = 0.400$, $p < 0.001$; Utah: $n = 93$, $r = 0.569$, $p < 0.001$) (Fig. 5), but states differ in the strength of the correlation between elevational range size and the midpoint of the range ($\chi^2 = 6.46$, DF = 2, $p < 0.05$). The Rapoport effect for Colorado ant distributions is significantly different from that of Nevada ("Tukey" test, $q = 3.50$, $p < 0.05$), but neither Colorado and Utah ($q = 0.84$, $p > 0.05$) nor Nevada and Utah ($q = 2.31$, $p > 0.05$) were significantly different.

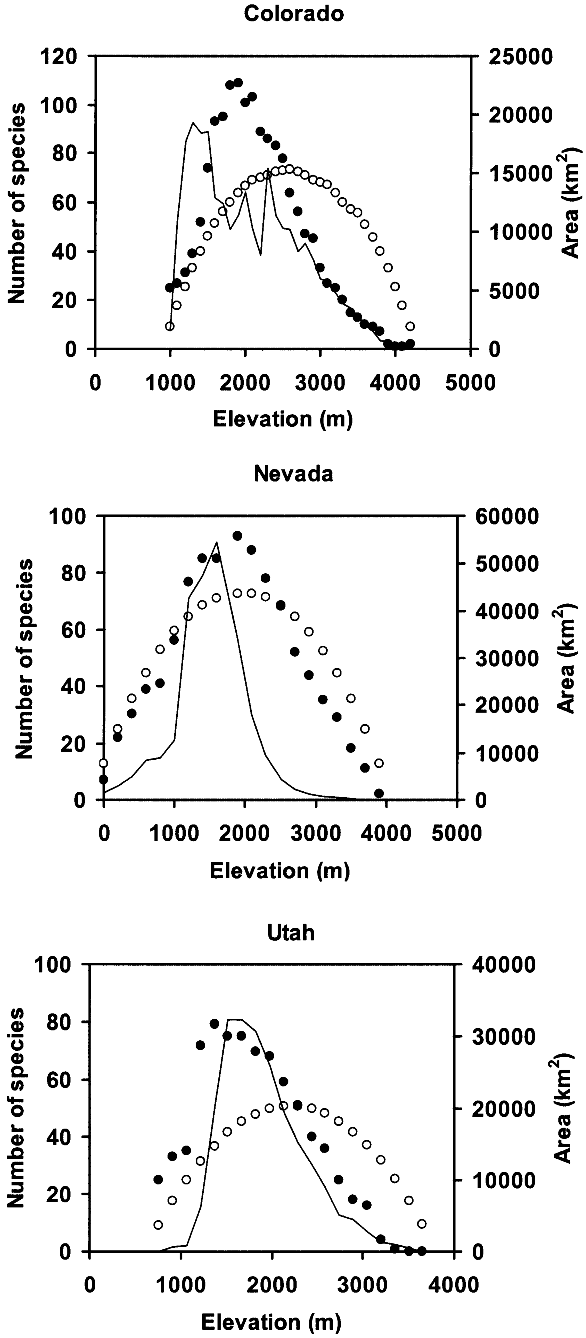

Fig. 1. The relationship between species richness, area, the mid-domain effect, and elevation. In each figure, the filled circles show the observed number of species present, the open circles show the expected number of species predicted by the mid-domain effect, and the solid line shows the amount of available area in that elevational band.

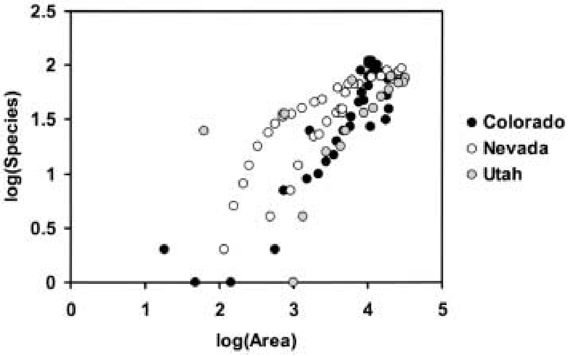

Fig. 2. Species-area curves for each state. Shown are the log transformed numbers of species and number of km^2 in each elevational band in each state.

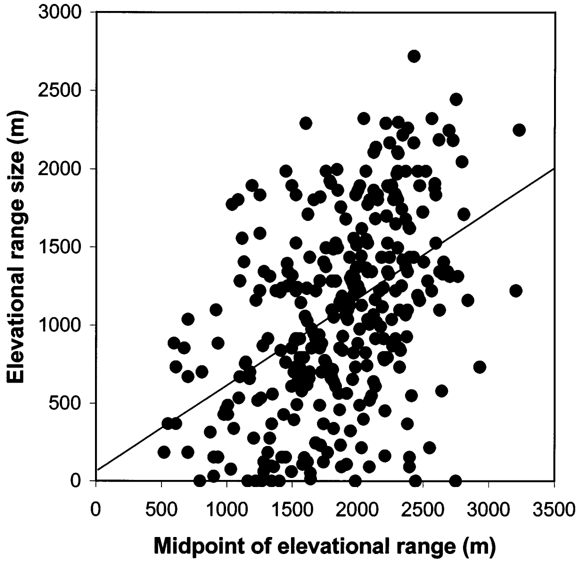

Fig. 3. Rapoport effect on elevational ranges of ants from all three states combined. The line is the least squares linear regression line ($y = 0.5554x + 60.916$).

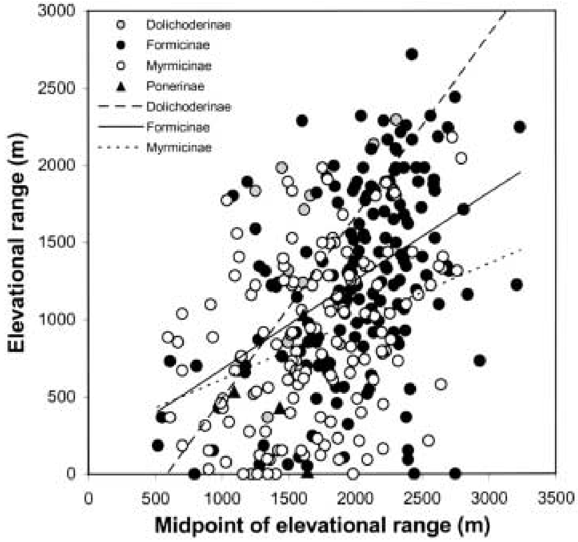

Fig. 4. Rapoport effect on elevational ranges of the three most abundant subfamilies, the Dolichoderinae, Formicinae, and Myrmicinae. The line is the least squares linear regression line. (Dolichoderinae: $y = 1.1739x - 681.79$, Formicinae: $y = 0.5697x + 111.44$, Myrmicinae: $y = 0.3744x + 240.01$.)

Discussion

Ant species richness peaked at mid-elevations in each state (Fig. 1). In this study, over 90% of the variation in species richness along elevational gradients in Colorado and Nevada was explained by available area and geometric constraints, and 57% of the variation in species richness in Utah was explained by area and geometric constraints.

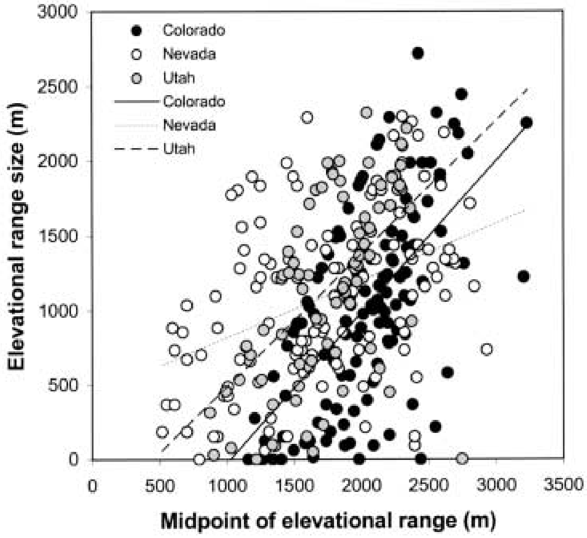

Fig. 5. Rapoport effect on elevational ranges in each state. The line is the least squares linear regression line. (Colorado: $y = 1.0112x - 1038.8$, Nevada: $y = 0.3802x + 440.1$, Utah: $y = 0.8931x - 408.39$.)

Reports of mid-elevation peaks in richness are common in the literature (e.g., Wolda 1987, Fernandes and Price 1988, McCoy 1990, Kearns 1992, Stevens 1992, Olson 1994, Sparrow et al. 1994, see Rahbek 1995 for a review), and such mid-elevation peaks are probably the rule rather than the exception. Several hypotheses have been suggested to explain mid-elevation peaks in richness. The "ends are bad" hypothesis states that distributions are limited by climatic severity and reduced availability of resources at upper elevations, and by climatic severity and predation at lower elevations (McCoy 1990). A second hypothesis is the "middle is good" hypothesis which posits that productivity is highest at mid-elevations because daytime temperatures allow for higher photosynthesis rates, and cool evenings allow for lower plant respiratory rates (Janzen 1973, Janzen et al. 1976). A third hypothesis is that lower elevations receive more disturbance, thereby reducing species diversity at lower elevations. A final hypothesis directly relates species richness along elevational gradients to productivity: as productivity increases, diversity first increases then declines, giving a hump-shaped pattern (Rosenzweig and Abramsky 1993 and references therein).

Many of these hypotheses are difficult to test. But authors have tested them, and results are equivocal. For example, some studies on the effects of habitat disturbance on ant species richness have shown that disturbance reduces richness or diversity (e.g., Greenslade and Greenslade 1977), while others have demonstrated little or no effect of disturbance (Room 1975, Torres 1984). It is unclear what the relationship between productivity and elevation is (Rahbek 1997), and studies to date on the relationship between productivity and ant species richness are equivocal. Desert ant species richness is positively correlated with productivity in North America (Davidson 1977) and negatively correlated in Australia (Morton and Davidson 1988) and South America (Medel 1995). In the most thorough study to date on the relationship between productivity and ant species richness, Kaspari et al. (2000) showed that ant species richness is positively correlated with productivity in 15 habitats throughout North America.

The results reported in this study point to two other mechanisms creating hump-shaped patterns in species richness along elevational gradients: area and the mid-domain effect. At the regional scale in Colorado, Nevada, and Utah, there is more area at mid-elevations (Fig. 1). And the hard boundaries of the highest mountain tops and lowest elevations in states limit the range sizes of ant species, thereby generating a peak in species richness at mid-elevations.

Rosenzweig (1995) notes that if you sample a bigger area, you will find more species. He also lists several processes that contribute to this pattern. For the ants of Colorado, Nevada, and Utah, it seems likely that larger areas simply have higher habitat diversities, though I did not test this hypothesis.

Several recent studies (see Colwell and Lees 2000) have shown that the mid-domain effect is common among many different taxa. Area explained more of the variation in species richness than did the mid-domain effect in Colorado and Utah but not Nevada. However, the peak in species richness for Colorado and Utah was at a lower elevation than the peak predicted by the null model for each the ants in each state, and species richness was generally lower at higher elevations than the null model predicted (Fig. 1). These results are similar to Rahbek's (1997) result on tropical bird richness and suggest that factors other than the mid-domain effect, such as available area, influence patterns in species richness along elevational gradients. In Nevada, the peaks in the observed number of species and predicted number of species occurred at the approximately the same elevation (Fig. 1).

Many authors have equated the latitudinal gradient with the elevational gradient in species richness and argued that the underlying mechanisms are the same for both (Stevens 1989, 1992). Rahbek (1995) points out that though species richness patterns might be the same along elevational and latitudinal gradients, the underlying mechanisms need not be the same. However, both available area (e.g., Rosenzweig 1995) and the mid-domain effect (e.g., Colwell and Lees 2000) are important influences on the latitudinal gradient, just as they are on elevational gradients in ant distributions reported in this study.

The elevational range sizes of ants from Colorado, Nevada, and Utah increase with increasing elevation; this agrees with Rapoport's rule. Distributions of ants in the three most common subfamilies, Myrmicinae, Formicinae, and Dolichoderinae, show this pattern. Interestingly, range sizes of ants from different states respond differently to increased elevation, though all are positive. Why does Rapoport's rule not generalize across three samples? Differences among states in the strength of the Rapoport effect undoubtedly result from differences in sampling intensities, variation in the structures of the habitat types sampled, and different levels of disturbance among sampling sites, or a combination of factors.

Recall that Rapoport's elevational rule, according to Stevens (1992), relates to the rescue effect and is presented as an explanation for monotonic decreases in species richness with increasing elevation. But the ants from Colorado, Nevada, and Utah all show peaks at mid-elevations. How can these apparently conflicting patterns be reconciled? Colwell and Hurtt (1994) and Rahbek (1995, 1997) have pointed out that the data Stevens (1989, 1992) presented in support of his version of Rapoport's rule actually show a peak at mid-elevations (or latitudes for the latitudinal version of the rule). The distributions of ants reported here probably suffer from geometrical limits, and show a Rapoport effect by default (Colwell and Hurtt 1994), though I did not explicitly test this hypothesis. Perhaps Rapoport's elevational rule describes a spurious effect, or, if true, helps to explain peaks in species richness at mid-elevations rather than monotonically decreasing richness with increasing elevation. So far, there have been too few studies on Rapoport's rule for ecologists to make general conclusions about its generality or applicability (Gaston and Blackburn 1999). But, if anything, Rapoport's rule is not general (Rohde et al. 1993, Rohde 1996).

There is a lack of information on the elevational distributions of plants and animals, especially for such ecologically important organisms as ants. Most studies have been performed in the tropics along relatively short elevational gradients, and sampling regimes have varied considerably. This study shows that ant species richness is highest at mid-elevations in three states in the Western US as a result of more area at mid-elevations and the mid-domain effect. Other studies, on both ants and other taxa, have found very different results from those reported here. It could be very interesting to explore further the relationship between elevation and species richness for other taxa when the influence of area and the effects of geometric constraints are considered, though it is likely that area and geometry will be among the most important influences on species richness along elevational gradients.

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