RESEARCH PAPER

Patterns of ant species richness along elevational gradients in an arid ecosystem

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ABSTRACT

Aim In this study, we examine patterns of local and regional ant species richness along three elevational gradients in an arid ecosystem. In addition, we test the hypothesis that changes in ant species richness with elevation are related to elevation-dependent changes in climate and available area.

Location Spring Mountains, Nevada, U.S.A.

Methods We used pitfall traps placed at each 100-m elevational band in three canyons in the Spring Mountains. We compiled climate data from 68 nearby weather stations. We used multiple regression analysis to examine the effects of annual precipitation, average July precipitation, and maximum and minimum July temperature on ant species richness at each elevational band.

Results We found that patterns of local ant species richness differed among the three gradients we sampled. Ant species richness increased linearly with elevation along two transects and peaked at mid-elevation along a third transect. This suggests that patterns of species richness based on data from single transects may not generalize to larger spatial scales.

Cluster analysis of community similarity revealed a high-elevation species assemblage largely distinct from that of lower elevations. Major changes in the identity of ant species present along elevational gradients tended to coincide with changes in the dominant vegetation. Regional species richness, defined here as the total number of unique species within an elevational band in all three gradients combined, tended to increase with increasing elevation. Available area decreased with increasing elevation. Area was therefore correlated negatively with ant species richness and did not explain elevational patterns of ant species richness in the Spring Mountains. Mean July maximum and minimum temperature, July precipitation and annual precipitation combined to explain 80% of the variation in ant species richness.

Main conclusions Our results suggest that in arid ecosystems, species richness for some taxa may be highest at high elevations, where lower temperatures and higher precipitation may support higher levels of primary production and cause lower levels of physiological stress.

Key words ants, climate, diversity, elevational gradient, Nevada, NPP, species richness, U.S.A.

INTRODUCTION

Understanding variation in the number of species has been a central aim of community ecology for decades (Pianka, 1966; MacArthur, 1972; Ricklefs & Schluter, 1993; Rosenzweig, 1995). The need both to document and understand patterns in species richness, especially for little known but important taxa, is increasingly important as threats to biodiversity

escalate (Wilson, 1992). To date, we know little about the factors that govern species richness, especially along environmental gradients such as the elevational gradient. Two general patterns have emerged. Until recently, the most widely accepted pattern was a decline in species richness with increasing elevation (e.g. Brown, 1988; Stevens, 1992). However, a growing body of evidence suggests that, for a wide variety of taxa, mid-elevation peaks in species richness are perhaps more general (Rahbek, 1995).

Climatic, biological, geographical and historical factors have been suggested as causes of variation in species richness along elevational gradients (Rahbek, 1995; Rosenzweig, 1995; Lomolino, 2001). In this paper, we examine the effect of three factors on ant diversity: area, temperature and

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precipitation. The effect of area on species richness is one of ecology's few laws (Schoener, 1976; Lawton, 1999). However, it has rarely been applied to studies of species richness along elevational gradients (but see Rahbek, 1995; Sanders, 2002). Unless there are major plateaus along an elevational gradient, area should decrease with increasing elevation. If area influences ant species richness on the spatial scale of a mountain range, then we would expect that species richness would decline with increasing elevation.

Climate could have both direct and indirect effects on ant diversity along elevational gradients. The physiological stress of climatic extremes, such as might be found at extremes of elevation, could limit species distributions (Ricklefs & Schluter, 1993). Climate might also affect ant diversity through its effects on primary productivity. In general, both annual precipitation and mean temperature change over elevational gradients (Krebs, 2001). As a result, net primary productivity (NPP) should peak at elevations where there is sufficient moisture, but temperatures are not too extreme. Many studies have shown that the richness of consumer taxa increases with increasing NPP (Mittelbach et al., 2001), and there are several hypotheses to explain this pattern (Srivastava & Lawton, 1998). One explanation is that higher net primary production permits consumers to maintain higher population densities, thereby reducing the probability of local extinction due to stochastic processes (Janzen, 1973; Siemann, 1998; Srivastava & Lawton, 1998; Kaspari et al., 2000).

In this study, we characterize both local and regional patterns of ant diversity along elevational gradients in the Spring Mountains, Nevada, U.S.A. Ants are almost ubiquitous in terrestrial communities, where they can constitute a large portion of the animal biomass (Adis et al., 1984; Pisarski, 1978). Ants play numerous roles in communities and ecosystems, serving as scavengers, predators and herbivores (Hölldobler & Wilson, 1990). Mutualisms between ants and other species are common, and include seed dispersal and protection of other organisms against natural enemies (Beattie, 1985). Their nesting habits can alter the soil nutrient concentrations and biogeochemical cycles (Wagner et al., 1997; MacMahon et al., 2000). The presence of particular ant species has been used as an indicator of environmental stress and the diversity of other arthropod taxa (Alonso, 2000; Kaspari & Majer, 2000). Thus, understanding patterns in ant species richness, and the factors that cause them, may be important in understanding the functioning of ecosystems.

METHODS

The Spring Mountains are located in the eastern Mojave desert of southern Nevada. The surrounding Mojave desert, c. 900–1000 m elevation, is sparsely populated by low woody shrubs in the genera *Larrea* and *Ambrosia*. The lower slopes of the Spring Mountains are dominated by the shrubs *Coleo-*

gyne and *Yucca*, rising to juniper-pinyon woodland and then mixed conifer forest at high elevation. The highest point in the Spring Mountains is 3630 m.

Patterns of species richness

We sampled ants with pitfall traps constructed from 120 mL plastic cups (6 cm diameter) embedded so that the lip of the cup was flush with the soil surface. Cups were partially filled with a 50 : 50 mixture of propylene glycol and water. After 48 h we retrieved the traps. The contents of the traps were strained through fine mesh and stored in 70% ethanol until identification.

Our goal in this study was to detect the majority of ant species at each sampling site. To determine the sampling effort necessary to detect at least 80% of the species present, we conducted preliminary trapping experiments at 1900 (pinyon–juniper woodland) and 2200 m (pine forest) in Kyle Canyon. At each site, we arranged 30 pitfall traps 10 m apart in a 50×60 m grid and recorded the number of species caught in each trap. For each elevation, we randomly extracted 100 samples of 1–30 traps, without replacement, and calculated the mean and standard deviation of the number of ant species caught for a given trapping effort. We plotted the mean species richness as a function of trap number, and estimated the total species richness as the point at which species number no longer increased with increasing sampling effort. This simulation analysis, which is similar to rarefaction, indicated that a sampling effort of 12 traps per site captured 80% of the species at one site, and over 93% of species at the other site.

We sampled ant species diversity along the three elevational transects that offered the greatest range of elevations in the Spring Mountain Range: Clark Canyon, on the west side of the mountain range, and Kyle and Lee Canyons, on the east side. In July 2000, we placed sets of 12 traps every 100 m in elevation along each transect. All canyons were trapped within a 2-week period, prior to the onset of summer rains. At each site along the transect, traps were 10 m apart and perpendicular to the elevational transect. We also recorded the dominant shrub and tree species present at each site along the transect. Representatives of all ant species detected at each elevation were pinned and identified using Wheeler & Wheeler (1986) and by comparison to specimens in the Natural History Museum of Los Angeles County.

For the purposes of this paper, we define local species richness as the number of species present in an elevational band within each canyon transect. We define regional diversity as the number of species in each band for all of the transects combined. Because some canyons offered access to higher elevations than others, our three transects did not cover exactly the same elevational span. This variation in sampling among elevations could affect our estimates of regional species richness. Therefore, for analyses of regional richness, we used data from only the 13 elevations sampled in all three transects.

We applied both linear and polynomial regression models to patterns in species richness along each transect and report the model that explained the most variation in species richness.

We also compared community composition among elevational bands. We calculated Jaccard's index of similarity (S_j) for every combination of elevations within each of the three transects as:

$$S_j = \frac{a}{a + b + c}$$

where a = the number of species shared by samples A and B, b = number of species unique to sample B, and c = number of species unique to sample A. The index ranges from 0, when adjacent communities share no species in common, to 1, when adjacent communities are identical. We then grouped elevations within transects by community similarity using single-linkage cluster analysis (Jongman *et al.*, 1995). Cluster analyses were converted to dendrograms (Jongman *et al.*, 1995). The dominant plant species were noted on dendrograms to illustrate the relationship between changes in the ant community to changes in the dominant plant species present.

Area, precipitation and temperature

We determined the area of each elevational band along our transects by estimating the width of the band, in m, on 1 : 100 000 USGS topographic maps. We averaged the band widths over the three transects and tested the hypothesis that average area was related positively to regional species richness using correlation analysis.

We examined the influence of climate on ant species richness, both as an estimate of productivity and because extremes of climate may have direct effects on the distribution of species. Direct data on productivity are generally difficult to obtain, but climatic data, such as annual averages of rainfall and temperature, can serve reasonably well as indirect measures of productivity (Rosenzweig, 1968; Kaspari *et al.*, 2000). Mid-summer temperatures are typically very high in the Mojave. We hypothesized that July temperature and precipitation may act as direct factors acting on the distribution and abundance of species. Because data from permanent weather stations in the Spring Mountains range were not available, we estimated how climate varies with elevation by compiling climate data from the 68 southernmost weather stations in Nevada maintained by the Western Regional Climate Center (http://www.wrcc.dri.edu/). From these 68 weather stations, we calculated the average annual precipitation, average July precipitation and maximum and minimum July temperature at each elevational band. Because these factors covary, we applied principal components analysis to generate a smaller number of orthogonal variables (McGarigal *et al.*, 2000). We then tested whether the principal component scores were related to regional species diversity using multiple regression analysis. Because species richness might be expected to peak at intermediate temperatures, we included a quadratic temperature term in the multiple regression model.

We used S-PLUS and JMP statistical software for data analyses. Data were transformed when necessary to meet assumptions of normality.

RESULTS

Local scale patterns of species richness

We detected 34, 39 and 32 species in Clark, Lee and Kyle canyons, respectively (Fig. 1). Ant species richness increased linearly with increasing elevation in Clark (Fig. 2a, $F_{1,11}$ = 18.66, $P < 0.001$, $r^2 = 0.61$, $y = 0.0037x + 3.0967$) and Lee (Fig. 2b, $F_{1,14}$ = 25.69, $P < 0.001$, $r^2 = 0.65$, $y = 0.0037x + 3.0967$) Canyons and peaked at mid-elevation in Kyle Canyon (Fig. 2c, $F_{2,10}$ = 7.69, $P = 0.01$, $r^2 = 0.43$, $y = -9 \times 10^{-6}x^2 + 0.0288x - 12.901$). To determine if a polynomial regression may have better explained variation in species richness than did simple linear regressions, we compared the sum of squares for the polynomial (quadratic) and linear models following Zar (1999). For both Clark and Kyle canyons, polynomial regressions did not fit the data significantly better than did simple linear regressions (Clark: $F_{1,11}$ = 0.384, $P > 0.25$, Lee: $F_{1,11}$ = 0.035, $P > 0.25$). Examination of Fig. 2c suggests that the interpretation of a unimodal pattern of species richness depends heavily on the number of species at the highest elevation. Indeed, when the highest elevation point is removed, the quadratic regression is no longer significant ($F_{2,9}$ = 2.1, $P = 0.18$, $R^2 = 0.32$). There was no evidence of autocorrelation in species richness values among adjacent transects (runs test of regression residuals, one-tailed $P > 0.05$ for all canyons; Sokal & Rohlf, 1995).

We did not determine whether ant abundance varied with elevation, although there is often a relationship between abundance and richness (Srivastava & Lawton, 1998; Kaspari *et al.*, 2000). Because we used pitfall traps to sample richness, it was impossible for us to determine the abundance of colonies at each elevational band.

In general, species in the subfamilies Dolichoderinae and Myrmicinae were more common at lower elevation than at higher elevation, while ant species in the subfamily Formicinae were more common at high elevation (Fig. 3).

Cluster analyses revealed distinct differences between high-elevation and lower elevation assemblages along all three transects (Fig. 4). The boundary between high- and low-elevation assemblages falls between 2000 and 2200 m, depending on the canyon. A less distinct break between mid- and low-elevation assemblages falls between 1700 m and 1800 m. In general, breaks in the similarity of ant species among elevations correspond to changes in the dominant vegetation present at the site (Fig. 4).
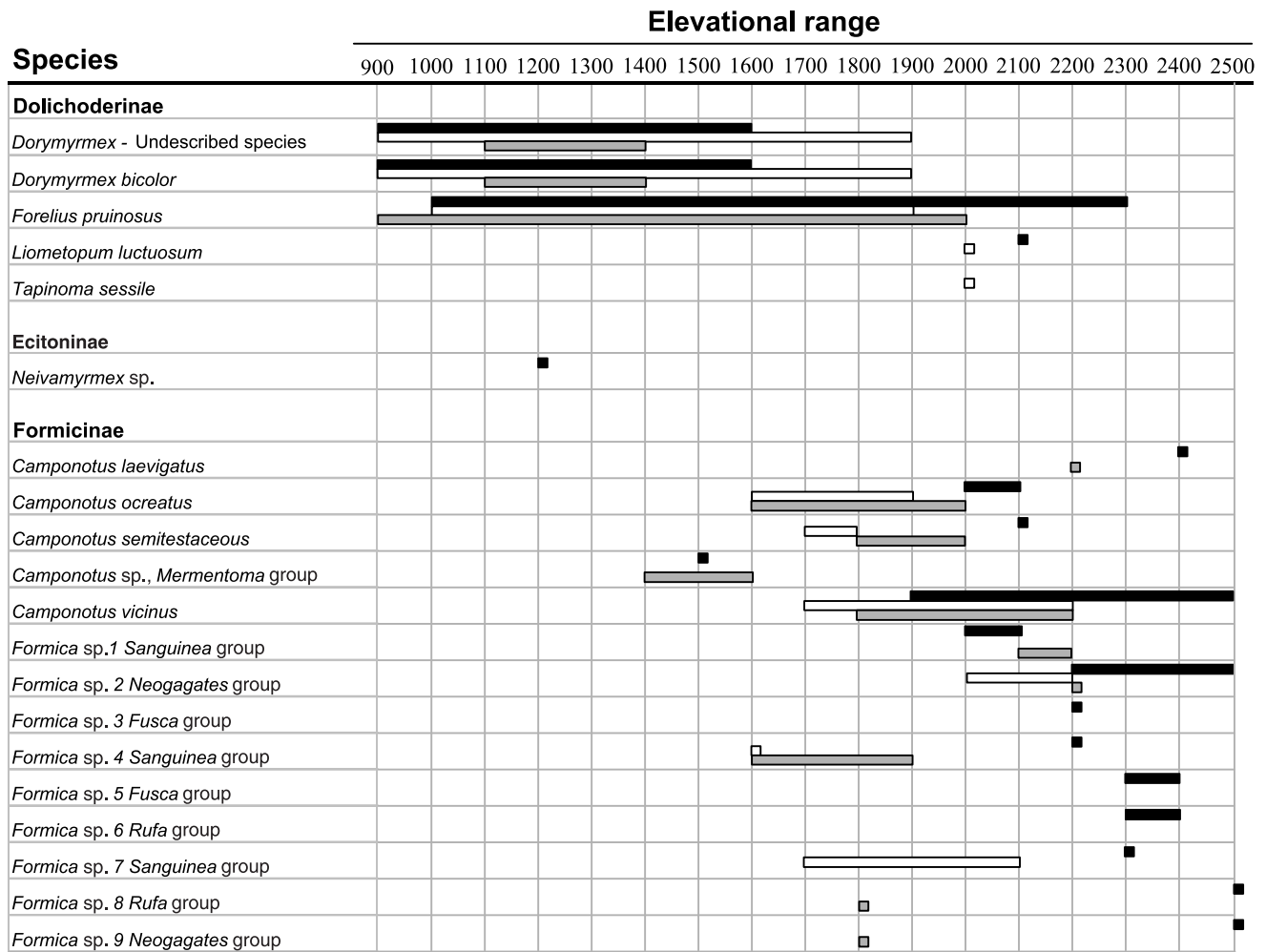
Fig. 1 The elevational ranges of ant species recovered from pitfall traps in three canyons of the Spring Mountains, Nevada. Black bars = Clark Canyon, white bars = Lee Canyon, grey bars = Kyle Canyon. Small square bars indicate that the species was detected at one elevation only.

Regional scale patterns of species richness

Taken together, our three gradient surveys detected 52 unique species in the Spring Mountains between 900 and 2500 m elevation. Using only those elevations for which data for all three transects were available, ant species richness increased as elevation increased (Fig. 5, $F_{1,11} = 37.79$, $P < 0.0001$, $R^2 = 0.77$). A quadratic regression did not explain more of the variation in ant species richness than the linear regression ($F_{1,11} = 17.18$, $P < 0.0006$, $R^2 = 0.77$).

Area, precipitation and temperature

Available area did not explain variation in ant species richness in the Spring Mountains. The width of elevational bands decreased as elevation increased along each of the three transects ($r < -0.60$, d.f. = 14 or 15, $P < 0.01$). Ant species richness was therefore negatively related to our estimate of available area ($r = -0.88$, d.f. = 11, $P < 0.01$).

Climate data from weather stations throughout southern Nevada supported the assumption that both precipitation and temperature change with elevation in the region. Mean July temperature decreased with increasing elevation ($r < -0.80$, d.f. = 64, $P < 0.001$), whereas mean annual precipitation increased with increasing elevation (Fig. 6a, $r = 0.56$, d.f. = 63, $P < 0.01$). Mean July precipitation was positively but weakly correlated with elevation (Fig. 6b, $r = 0.31$, d.f. = 63, $P < 0.05$).

Variation in ant species richness over the elevational gradient was partially explained by climate. The first three principal components generated from climate variables explained 99% of the variation in climate. Principal components (PC) were
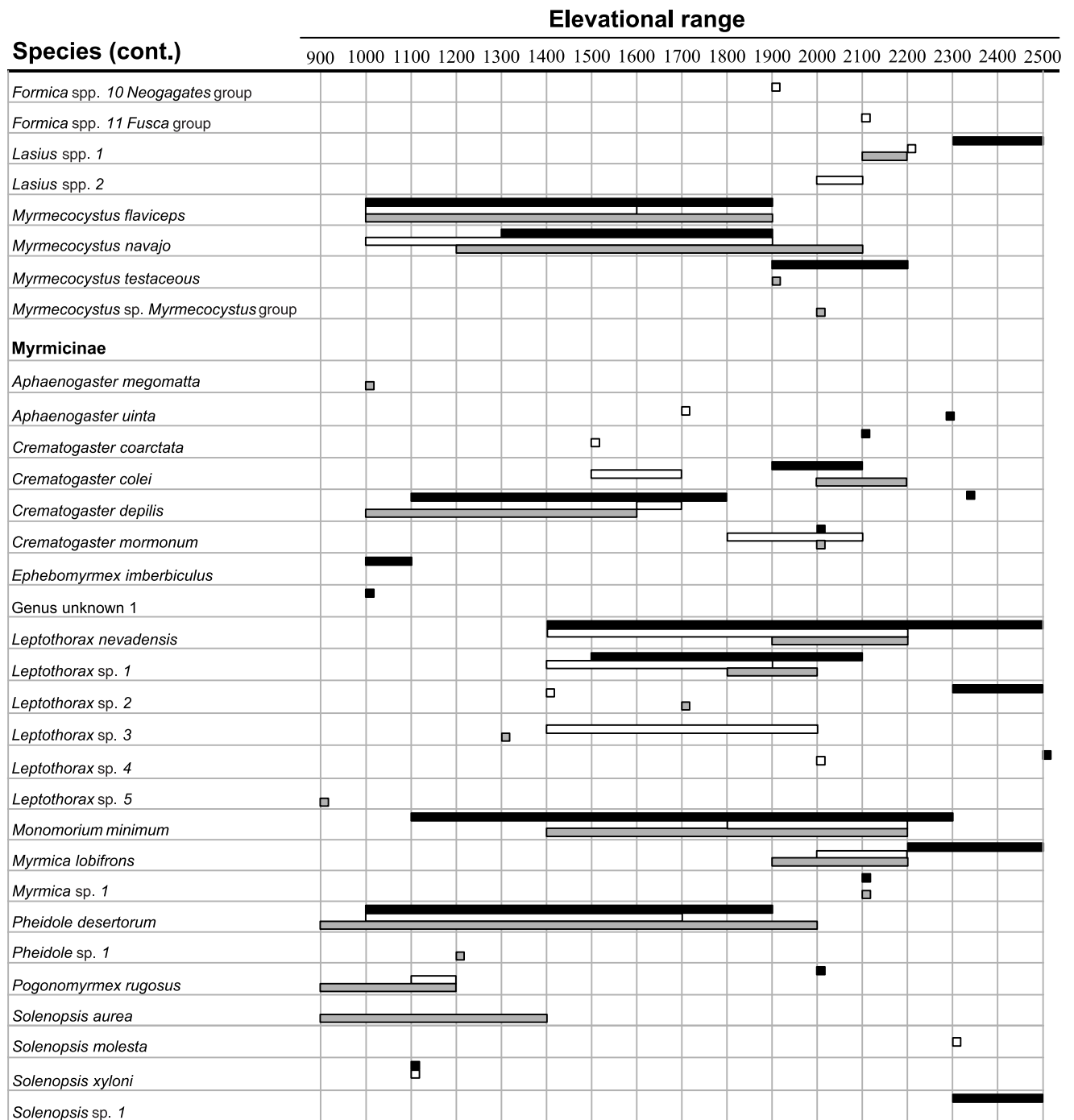
Elevational range

Species (cont.)

Species	Elevational range

Fig. 1 *continued.*

clearly interpretable: PC1 was negatively correlated with mean annual precipitation ($r = -0.98$), PC2 was correlated negatively with mean July precipitation ($r = -0.98$), and PC3 was correlated positively with both mean maximum and minimum July temperatures ($r > 0.80$). Approximately 80%

of the variation in regional ant species richness along our elevational transects was explained by the combination of climate variables ($F_{4,8} = 8.4$, $P = 0.006$). Both mean July temperature (PC3) and mean July precipitation (PC2) contributed significantly to the model (Table 1). Mean annual
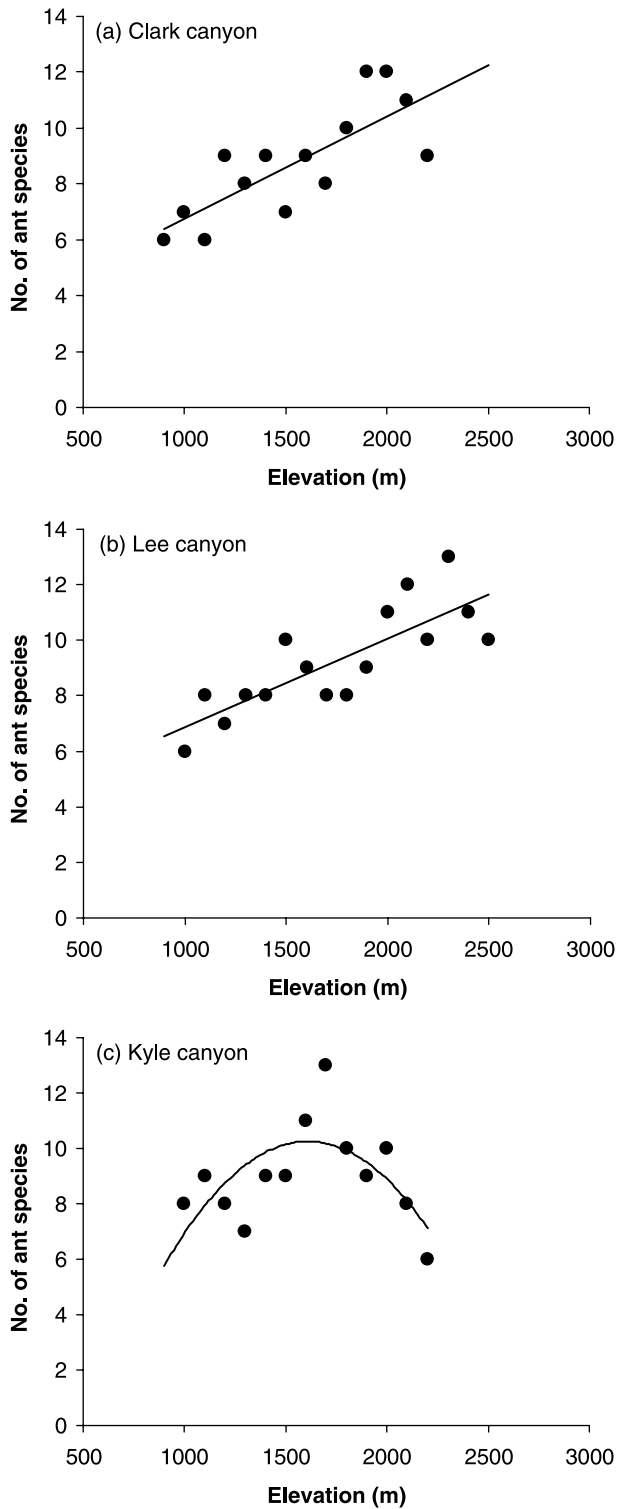
Fig. 2 The relationship between local ant species richness and elevation in Clark, Lee and Kyle canyons in the Spring Mountains, Nevada.
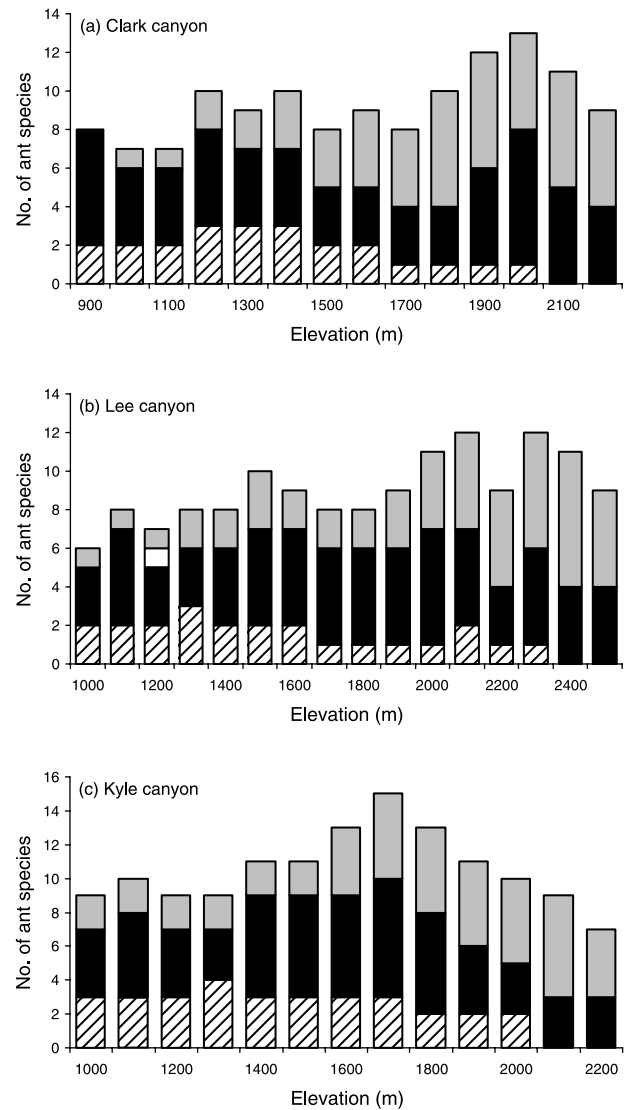

Fig. 3 The number of ant species in each subfamily at each elevation in Clark, Lee and Kyle canyons in the Spring Mountains, Nevada. In each panel, grey bars represent the Formicinae, black bars represent the Myrmicinae, hatched bars represent the Dolichoderinae and the white bar represents the Ecitoninae.

precipitation did not contribute significantly to the model, although the low *P*-value associated with PC1 suggests that mean annual precipitation may also play a role in ant species richness (Table 1).

DISCUSSION

Using data from three replicate transects, our results from the Spring Mountains, Nevada indicate that regional ant species richness increases with increasing elevation. If there is an

Table 1 Results of multiple regression analysis testing the effects of mean annual precipitation, mean July precipitation and mean maximum and minimum July temperature on the number of ant species in the Spring Mountains, Nevada

Term	Estimate	SE	t	P
Intercept	17.1	0.75	22.8	< 0.0001
PC1 (mean annual precipitation)	−1.3	0.8	−1.7	0.06
PC2 (mean July precipitation)	−1.6	0.8	−2.0	0.04
PC3 (mean July temperature)	−3.7	0.8	−4.8	0.005
PC3^2	−1.3	1.0	−1.3	0.2

elevation at which ant species richness peaks in this region, it lies above the upper range of our survey. This pattern differs from that reported by many previous studies of ant species richness along elevational gradients. Most such studies have found the highest ant species richness at low or intermediate elevations (Olson, 1994; Fisher, 1996, 1998; Samson *et al.*, 1997; Brühl *et al.*, 1999). Of those studies that found a peak in ant species richness, the peak occurred at elevations below the maximum elevation used in this study (Samson *et al.*, 1997; Fisher, 1998).

This disparity in the pattern of diversity with elevation among studies may be due, in part, to underlying changes in the relationship between climate and elevation over space. A
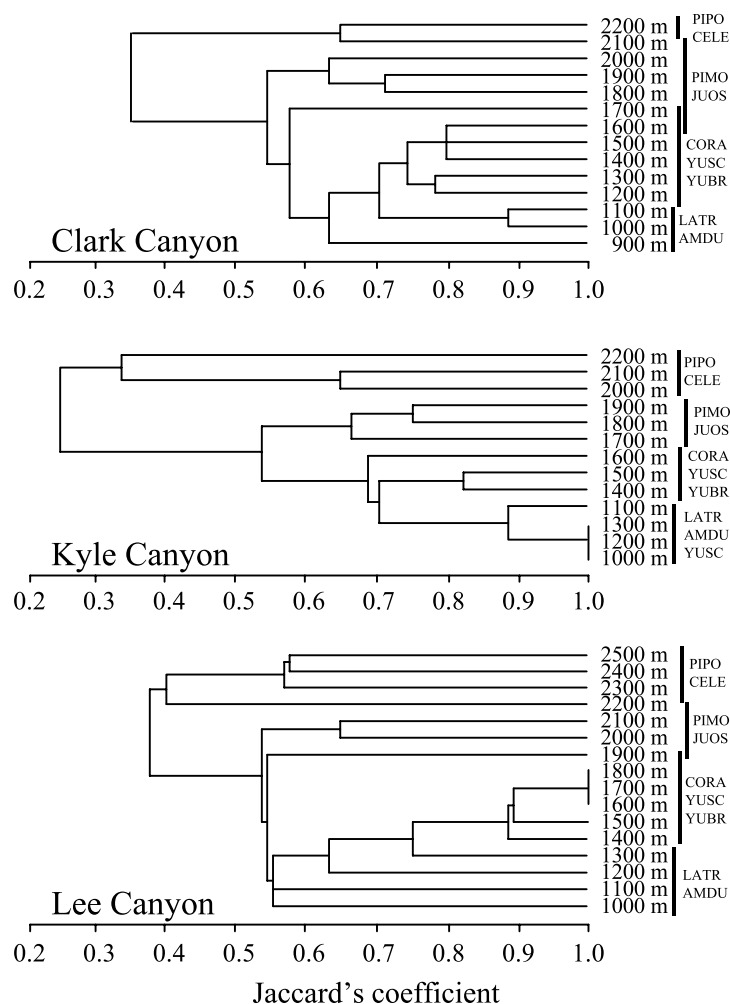

Fig. 4 Dendrograms of ant community similarity within three canyons of the Spring Mountains. Dendrograms illustrate the results of single-linkage cluster analyses using Jaccard's coefficient, an index of community similarity calculated from the presence and absence of ant species (Jongman *et al.*, 1995). Thick, vertical bars show the elevational range of plant communities, as characterized by the dominant shrubs and trees. AMDU = *Ambrosia dumosa*, CELE = *Cercocarpus ledifolius*, CORA = *Cercocarpus ramossisima*, JUOS = *Juniperus osteosperma*, LATR = *Larrea tridentata*, PIMO = *Pinus monophylla*, PIPO = *Pinus ponderosa*, YUSC = *Yucca schidigera*, YUBR = *Yucca brevifolia*.
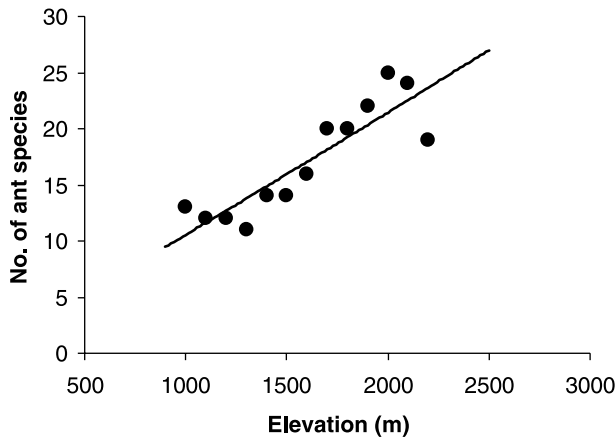
Fig. 5 The relationship between elevation and regional ant species richness in the Spring Mountains, Nevada. Symbols represent species richness at elevations for which all three canyons were sampled. The line is the best-fit line.
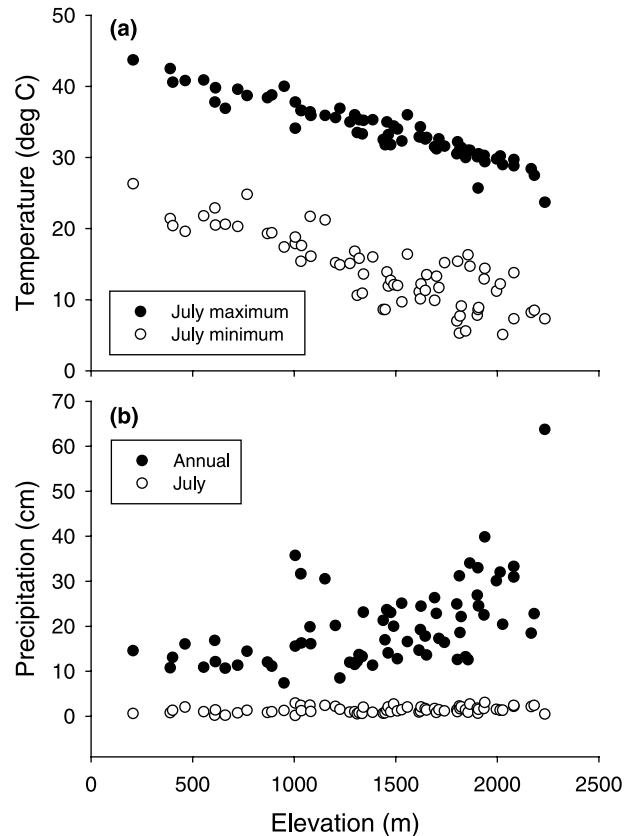

Fig. 6 The relationships between climate and elevation from 68 weather stations in southern Nevada. (a) Mean July maximum and minimum temperature. (b) Mean annual and July precipitation.

similar elevational range studied in the tropics and the temperate zone would probably yield a different combination of temperature and precipitation along each. For example, in the tropics, rainfall generally decreases with elevation, but in many temperate and arid habitats, rainfall increases with increasing elevation (Brown, 1995). If species richness is related to climate, then the relationship between species richness and elevation should change over space as well (McCoy, 1990). In a comparison of 20 studies of insect diversity along elevational gradients, McCoy (1990) found a weak negative correlation between the latitude and the elevation of peak insect diversity. In addition, major topographical features, such as proximity to mountains or oceans, are also likely to affect the relationship between climate and elevation.

Studies of ant diversity over elevational gradients have been conducted chiefly in the tropics. Over the approximate elevational range we studied (900–2500 m), these tropical studies found that ant species richness decreased with increasing elevation. In contrast, two studies of ant species richness in the temperate zone (both from the Mojave desert) found richness increased with increasing elevation (Bernstein, 1971; this study). In a widespread survey of leaf litter ant diversity, Ward (2000) found that species richness peaked at mid-elevations in the tropics but decreased continuously with elevation in temperate regions. Thus, the disparity in elevational patterns of ant diversity across studies may be explained partly by latitude. Topographical features may also play a role in our results. As a result of a rain shadow effect, as well as global circulation patterns, low elevation areas in the Mojave can be extremely hot and dry. Perhaps because of this topographic effect, our findings and those of Bernstein (1971) suggest that the elevation at which ant species richness peaks is higher in the Mojave than in the tropics. Similarly, butterfly diversity in

the Toquima range of the Great Basin also peaked at high elevations (Fleishman et al., 2000).

Our data indicate that both temperature and rainfall vary along elevational gradients in southern Nevada (Fig. 5). As mean July temperature decreased and average annual rainfall increased with increasing elevation, ant species richness tended to increase, except at the highest elevations. The combined effects of temperature and rainfall explained 80% of the variation in ant species richness. Our multiple regression analysis suggests that ant species richness is better predicted by mean July temperature and precipitation than by mean annual precipitation (Table 2). Other studies have also found an association between ant diversity and precipitation. Precipitation and ant species richness were positively correlated in deserts of the California, Arizona and New Mexico (Davidson, 1977), but not in Australia (Morton & Davidson, 1988) or South America (Medel, 1995). In an exhaustive study of patterns in ant species richness at 15 sites along the latitudinal gradient in the Americas, Kaspari et al. (2000) found that rainfall was related positively to, and explained

45% of the variation in, ant species richness within a habitat. Maximum temperature was not an important predictor of ant species richness, but minimum temperature was related positively to, and explained 33% of the variation in, ant species richness (Kaspari *et al.*, 2000). Davidson (1977), in contrast, found that the annual rainfall was a better predictor of ant species richness than mean July temperature.

At local scales, we found that ant species richness increased along two transects, but peaked at mid-elevations for a third. It is likely that disturbance at high elevations in Kyle Canyon, associated with the city of Mount Charleston (*c.* 2100 m), contributed to the reduction in diversity at high elevations along that transect. However, because the unimodal pattern observed at Kyle Canyon depends heavily on the single highest point we sampled, it is also possible that the pattern results from an outlier. Taken at face value, the results suggest that the relative influences of area, precipitation, temperature and disturbance on ant species richness in the Spring Mountains are canyon-specific (e.g. Fleishman *et al.*, 2000). An important implication of such specificity is that a pattern detected at a local scale may not generalize to the larger, more regional scale.

Another hypothesis to explain patterns in species richness along elevational (and latitudinal) gradients is gaining support (Colwell & Lees, 2000). Because the extent of elevational ranges of many species are bounded by 'hard' limits imposed by geography (e.g. mountain-tops), there is increasing overlap of species ranges toward the centre of the domain (Colwell & Hurtt, 1994; Colwell & Lees, 2000). Although this mid-domain effect may have explanatory value for patterns of ant species richness along elevational gradients (Sanders, 2002), we did not explore the possibility that the mid-domain effect influences ant species richness in this study for two reasons. First, we did not detect a mid-elevation peak in species richness, except for Kyle Canyon. Secondly, the species ranges we calculated from our three transects were not abutted by hard boundaries, as the mid-domain effect requires.

Our surveys found that the proportion of species in three subfamilies varied with elevation (Fig. 2). At low elevations along our three transects, samples were dominated by species in the subfamilies Myrmicinae and Dolichoderinae, but the proportion of species in the Myrmicinae and Dolichoderinae decreased with elevation, and the proportion of species in the Formicinae increased. Since species in the same subfamily probably share many traits because of their recent evolutionary history, it may be that some species in the Formicinae (e.g. *Formica* and *Lasius* spp.) are better able to tolerate colder temperatures at higher elevations (and latitudes) than are species in the Myrmicinae or Dolichoderinae.

In conclusion, we suggest that future studies of the causes of variation in species richness along environmental gradients consider the multiple mechanisms that contribute to the pattern. Our study indicates that climate, and in particular summer temperature and precipitation, influences regional diversity of an ecologically important taxon in an arid ecosystem. At local scales, human disturbance may be important. Studies that explore the mechanisms of variation in richness will be necessary in order to assess and preserve ant species richness and the important roles that ants play in the functioning of a variety of ecosystems.

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