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ORIGINAL ARTICLE

Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain Rapoport's rule?

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ABSTRACT

Aim Relationships between elevation and litter-dweller harvestman (Arachnida: Opiliones) species richness along three elevational gradients in the Brazilian Atlantic Forest were evaluated. Specifically, three candidate explanatory factors for the observed patterns were tested: (1) the mid-domain effect, (2) the Rapoport effect, and (3) the influence of environmental variables on species density and specimen abundance.

Location Cuscuzeiro, Corcovado and Capricórnio mountains, in Ubatuba (23°26′ S, 45°04′ W), a coastal municipality in São Paulo state, south-eastern Brazil.

Methods We recorded harvestman species and abundance through active sampling using 8 × 8-m plots in both summer and winter. At each plot we measured the temperature, humidity and mean litter depth. Harvestman species richness per elevational band was the sum of all species recorded in each band, plus the species supposed to occur due to the interpolation of the upper and lower elevational records. Differences between observed and expected species richness per elevational band, based on the mid-domain effect, were examined through a Monte Carlo simulation. The Rapoport effect was evaluated using both the midpoint method and a new procedure proposed here, the 'specimen method'. We applied multiple regression analysis to evaluate the contribution of each environmental variable (elevation, temperature, humidity and litter depth) on species density and specimen abundance per plot.

Results Harvestman abundance and species richness decreased at higher elevations in the three mountains. The decrease in species richness was not monotonic and showed a plateau of high species richness at lower elevations. The number of harvestman species per elevational band does not fit that predicted by the mid-domain effect based solely on geometric constraints assuming hard boundaries. Species with their midpoints at higher elevations tended to cover broader elevational range sizes. Both the midpoint method and the specimen method detected evidence of the Rapoport effect in the data. At fine spatial scales, temperature and humidity had positive effects on species density and specimen abundance, while mean litter depth had no clear effect. These relationships, however, were not constant between seasons.

Main conclusions Our results suggest that harvestman species density declines at higher elevations due to restrictions imposed by temperature and humidity. We found a pattern in species range distribution as predicted by the elevational Rapoport effect. However, the usual rescue effect proposed to explain the Rapoport effect does not apply in our study. Since the majority of harvestman

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species covering broader elevational ranges do not exhibit reduced abundance at low elevations, an alternative rescue effect is proposed here. According to this alternative rescue effect, the decrease in species richness at higher elevations occurs due to differential upper limits of species with source populations below mid-elevations. The seasonal differences in the relationships between environmental variables and species richness/specimen abundance per plot is an indication that species occurrence on elevational gradients is seasonally dependent. Thus relationships and hypotheses based on data recorded over short time periods, or in a single season, should be viewed cautiously.

Keywords

Altitudinal gradient, Arthropoda, Brazilian Atlantic Forest, Gonyleptidae, leaf litter, mid-domain effect, mountain ecology, Sclerosomatidae, source–sink populations, tropical rain forest.

INTRODUCTION

The search for causal explanations and general patterns of species distribution along geographical and environmental gradients is a long-standing goal of biogeographers and ecologists. Non-random changes in community parameters (such as richness, composition and relative abundances) along elevation gradients have been documented for several taxonomic groups since von Humboldt's first observations in the Andes in the early 1800s (von Humboldt, 1849). Despite the long interest in this issue, there are few studies on the effects of altitude on non-insect arthropods, which comprise a considerable proportion of the Earth's biota. This taxonomic bias needs to be remedied if we want to test the generality of hypotheses and search for widespread patterns of elevational species diversity.

The most frequent relationships between elevation and richness are, in order, a hump-shaped species-richness curve; a plateau of high species richness at lower elevations; and a monotonic decrease in species richness with increasing elevation (McCoy, 1990; Rahbek, 1995; McCain, 2005). Several hypotheses have been proposed to explain the former relationship between species richness and elevation, including increased overlap of species ranges toward mid-elevations in gradients with marked hard boundaries (the so-called mid-domain effect proposed by Colwell & Lees, 2000); highest net photosynthetic accumulation at mid-elevations (Janzen, 1973; Janzen *et al.*, 1976); and environmental constraints on the distributions of populations (the 'ends are bad', Gagne, 1979; Smiley & Rank, 1986; Randall, 1982). Proposed hypotheses for the inverse relationship between species richness and elevation assert that this occurs due to nearly monotonic decrease or increase in several environmental features. According to these hypotheses, species richness increases with elevation as a consequence of a decrease in primary productivity/resource abundance (Lawton *et al.*, 1987; Srivastava & Lawton, 1998); habitat complexity (Rahbek, 1995; Kerr & Packer, 1997); and total available area (the species–area relationship; MacArthur, 1972). Additionally, some authors have argued that species richness decreases at higher elevations due to an increase in unfavourable (more variable and/or more extreme) climatic conditions (MacArthur, 1972; Tenow, 1973), and isolation from areas with similar elevation (MacArthur, 1972). The peak in species richness at lower-elevation plateaux can be interpreted as a consequence of combined effects of the mechanisms promoting both the monotonic decrease and the hump-shaped pattern. In fact, some authors have stressed that empirical patterns of species distribution should be interpreted as the emerging property of many convergent and contrasting processes (Heaney, 2001; Lomolino, 2001; Tews *et al.*, 2004).

Another debated pattern relating to the distribution of species along elevational gradients is the positive relationship between the elevational range size and the midpoint of the species (Stevens, 1992; Colwell & Hurtt, 1994; Blackburn & Gaston, 1996; Gaston *et al.*, 1998). This relationship was called 'Rapoport's rule' by Stevens (1989, 1992; after Rapoport, 1982) or, more appropriately, the 'Rapoport effect' by Blackburn & Gaston (1996). Although initially proposed for latitudinal gradients, Stevens extended the Rapoport effect to explain patterns of species distribution in elevational and bathymetric gradients (Stevens, 1992, 1996). Stevens's hypothesis for the elevational Rapoport effect postulates that: (1) high-elevation species have wider tolerance to environmental changes, such as climatic variability, than low-elevation species, and, consequently, (2) species from higher elevations have few constraints to expand their lower limits of elevational range, whereas low-elevation species are constrained by their upper elevational limits. Thus species at higher elevations could cover broader elevational ranges. The predicted consequence of Stevens's hypothesis is inflation in species richness at lower elevations through greater emigration rates of species from higher to lower elevations. This latter effect is an expansion to species level of the 'rescue effect' proposed by Brown & Kodric-Brown (1977).

For arthropods, especially insects, there is empirical evidence of monotonic decrease in species richness at higher elevations, and peaks in species richness at mid-elevations (Janzen *et al.*, 1976; Fernandes & Price, 1988; McCoy, 1990;

Olson, 1994). However, few studies have addressed the elevational Rapoport effect for arthropods (but see Fleishman *et al.*, 1998; Sanders *et al.*, 2003), and only one recent work looked specifically at arachnids (Chatzaki *et al.*, 2005). The Opiliones are the third major order within the arachnids, comprising nearly 6000 described species (Hallan, 2005). Harvestmen are strictly terrestrial, wandering arthropods that occur mainly in humid environments. The representatives of the order are a conspicuous element of the ground fauna worldwide, and in tropical rainy forests they are found on the vegetation, below woody debris and among the leaf litter (Pinto-da-Rocha, 1999). Although there is a large amount of information in the form of faunistic lists and some quantitative samplings worldwide, there have been few attempts to understand the general patterns of harvestman species richness along geographical gradients (Martens, 1984; Komposch & Gruber, 1999).

Our aim in this study was to investigate patterns in harvestman species distribution along three elevational gradients in a Neotropical rain forest and to propose a new method to test the Rapoport effect. Specifically, we addressed the following questions: (1) Is species richness related to elevation? (2) Is there support for the mid-domain effect or for the Rapoport effect on harvestman species distribution? (3) Do local environmental features and seasonality affect species density and specimen abundance at a fine spatial scale?

MATERIALS AND METHODS

Study area

We conducted the sampling of leaf litter harvestmen in three mountains 20–40 km apart in Ubatuba (23°26′ S; 45°04′ W), a coastline municipality in São Paulo state, south-eastern Brazil. The three mountains are covered by Atlantic Rain Forest, a vegetation type that is mostly distributed from low to medium elevations (*c.* 1000 m) of the eastern slopes of the mountain chain, running along the coastline from southern to north-eastern Brazil. For more details on the vegetation and geology of the Atlantic Forest in the areas sampled, see Suguio & Martin (1978); Oliveira-Filho & Fontes (2000), respectively.

The Capricórnio and Cuscuzeiro mountains range from sea level to 890 and 1240 m, respectively, and both are mostly covered by old-growth forest (*sensu* Clark, 1996). The Corcovado Mountain ranges from sea level to 1150 m, but the forest does not extend further than 1000 m. Below 200 m, most of the sampled areas in the Capricórnio and Corcovado mountains presented signs of human disturbance, such as selective logging and hunting trails. However, we do not believe that such disturbance will have affected our samples, because we avoided sampling on gaps and trails. Moreover, the leaf litter depth in these places did not differ from similar altitudinal bands in the undisturbed Cuscuzeiro Mountain.

The climate in the study area has two well defined seasons: a warm-wet season from October to April, and a cold-dry season from May to September. During the warm-wet season the mean monthly temperature ranges from 23 to 25 °C and the total precipitation may reach 2000 mm, whereas in the cold-dry season the mean monthly temperature ranges from 16 to 18 °C and the total precipitation drops to 680 mm.

Sampling design

Sampling was carried out from 19 December 1995 to 24 February 1996 (hereafter called summer) and from 10 to 27 July 1996 (hereafter called winter). For practical purposes, the mountains were divided into the coastal forest band (0–50 m) and into 100 m bands from 50 to 950 m (to 850 m in Capricórnio Mountain). These samples cover the entire forested elevational gradient in the Capricórnio and Corcovado mountains, and nearly 80% in the Cuscuzeiro Mountain.

Study sample units were 8 × 8-m ground plots. Although pitfall traps are the most commonly used technique for the capture of ground-dweller harvestmen (Curtis, 1978; Adams, 1984; Schaefer, 1986), we used an active-capture method since harvestman activity decreases at lower temperatures (Machado *et al.*, 2004; Mestre & Pinto-da-Rocha, 2004). Thus we seek to avoid bias due to differences in mobility and vagility between species, which is known to occur in passive methods such as pitfall traps (Adis, 1979; Lang, 2000).

To establish the position of a plot, we adopted the following sequence of three randomizations along the trail: (1) the exact altitude within each elevational band, (2) the side of the trail (right or left), and (3) the distance (0–30 m) from the trail to the plot. Two plots were sampled within each elevational band in the summer, whereas one plot per band was sampled in the winter. A total of 96 plots (6144 m^2) were sampled.

We delimited the perimeter of the plots with ropes and ground strips *c.* 30 cm wide cleaned of litter. Each plot was completely enclosed by a nylon net (60 cm high, 1 × 1-mm mesh) attached to aluminium stakes. The bottom of the net was secured to the ground with sticks, stones and leaf litter. After placement of the net, five to eight people stirred the litter on hands and knees, using garden forks. Holes on the ground were examined superficially with flashlights and rotting logs were rolled in order to search for harvestmen. Searches were conducted between 07:00 and 18:00 h, and all leaves and litter within the plot were overturned.

To assess the effect of local environment on harvestman species density (*sensu* Lomolino, 2001) and abundance at fine spatial scales (plot scale), we recorded the following variables in each plot: mean litter depth, measured at 1.5 m from each corner and at the centre of the plot; and temperature and humidity, measured with an ordinary thermometer (−5 to 60 °C) and a psychrometer, respectively, 1.5 m high from the ground in one corner of the plot.

All harvestmen collected during this study were preserved in 70% ethanol, but only adult individuals, which accounted for 98.8% of the total, were identified to species level and used in the analyses. Voucher specimens were deposited at Museu de Zoologia da Universidade de São Paulo (MZSP), Museu Nacional do Rio de Janeiro (MNRJ), and Museu de

História Natural da Universidade Estadual de Campinas (ZUEC).

Analyses

We examined patterns in species distribution within individual mountains and by combining the three mountains in a regional-scale analysis (Sanders *et al.*, 2003). The former are represented by the number of species present in an elevational band within each mountain, whereas the latter is the number of species in each elevational band for all mountains combined. Only bands from 0 to 850 m were considered in statistical analyses for regional patterns because the highest elevational band recorded in the Capricórnio Mountain was 850 m. As an exhaustive sampling effort was not conducted for each elevational band, a species was considered present in a particular elevational band only if it was recorded both in a higher and a lower band. This interpolation of species occurrence has been used in many studies to correct for possible sampling problems (e.g. Grytnes & Vetaas, 2002). We applied interpolation for species occurrence only for bands with higher and lower species records in the same mountain.

The relationships between elevation and the local/regional number of harvestman species per elevational band were examined through simple linear regression. To compare the observed with the expected species richness by the mid-domain effect, we generated 95% prediction intervals through 50,000 Monte Carlo simulations of the elevational ranges within the domain using the software MID-DOMAIN NULL (McCain, 2004, 2005). The expected species richness in each elevational band was generated using the empirical range sizes sampled without replacement and randomly chosen range midpoints, to produce ranges within the domain limits (McCain, 2004). The simulations were performed with the lower hard boundary at 0 m for the three mountains, and upper hard boundaries at 850 m for Capricórnio and 950 m for Corcovado and Cuscuzeiro mountains. It is important to stress that the Cuscuzeiro Mountain was evaluated only for comparative purposes, given that its real upper limit is 1250 m. To evaluate whether the species richness predicted by the mid-domain effect based solely on geometric constraints assuming hard boundaries is congruent with the observed species richness, we tested the fit between the two sets of species richness through the determination coefficient of a least-squares linear regression.

The relationship between elevation and elevational range size (Rapoport effect) of harvestman species was evaluated using the midpoint method (Rohde *et al.*, 1993). However, we used species instead of elevational bands as sample units in regression analysis, as Fleishman *et al.* (1998) and Sanders (2002) for elevational data, and Diniz-Filho & Torres (2002) for latitudinal data. We adopted this approach because some lower bands, and all bands in elevations > 500 m, had few or no species with range midpoints within the elevational interval. As our total elevational range includes 10 or 11 bands, we chose an analysis that retains a higher number of sample units. The midpoint of each species was calculated as the equidistant elevation between the extremes at which a species was recorded.

Stevens's (1992) hypothesis for the elevational Rapoport effect states that species richness at lower elevations is inflated by the emigration of species from higher elevations. We propose here a new method, hereafter called the 'specimen method', to test the Rapoport effect through a measure that takes into account the abundance of each species along the elevational gradient. According to the specimen method, the mean elevation of each species was calculated as the weighted average midpoint, as follows:

$$\mathrm{WA}_i = \frac{\sum_{i=1}^{i=n} E_i N_i}{\sum_{i=1}^{i=n} N_i}$$

where WA_i = the weighted average midpoint of species i; E_i = the elevation of each band where species i is present; and N_i = the number of individuals of species i at each elevational band.

We propose that this specimen-based method is more appropriate for testing Stevens's hypothesis for the elevational Rapoport effect than a geometric measure (such as the midpoint). The specimen-based method gives a measure of central elevation that can detect more reliably if the species with broader elevational ranges are those from higher elevations (Sagarin & Gaines, 2002), that is, species with greater abundances at higher elevations. We also assumed that the optimum elevational range of each species is that where it has its maximum abundance (Whittaker, 1967; Grytnes & Vetaas, 2002). Logically, the specimen method is applicable only to data sets with standardized sampling at all elevations and equidistant elevational bands, to avoid biased measurement. Therefore, as our sampled bands were 100 m apart and we have a sampled band at 50 m, we did not consider the lowest band (sea level) in the analysis using the specimen method.

The elevational range of each species in each mountain was calculated as the highest minus the lowest elevation at which a species was recorded. As we did not perform complete sampling of the harvestman species in each elevational band, rare species might have had their ranges under-sampled. To minimize potential bias related to sample effort in the Rapoport effect analysis, we used the following criteria to include a species in both midpoint and specimen methods: (1) records in two or more elevational bands within a mountain, and (2) a minimum abundance of three specimens. To test the Rapoport effect, we applied least-squares linear regression.

Relationships between local environmental features and elevation, and the effects of the former on species density (*sensu* Lomolino, 2001) and specimen abundance per plot, were examined initially through Spearman's rank correlation. We checked if the effects of local environmental variables were consistent between seasons (summer vs. winter plots). The relationships between local environmental features for each season were tested separately to evaluate differences in responses to independent variables between seasons. The elevation of each plot and all local environmental features significantly correlated with species density and/or specimen abundance were included as independent variables in multiple linear regressions. We examined the variance inflation factor (Belsley, 1991) of each independent variable to detect multicollinearity in multiple regression analysis.

Species richness in two nearby elevational bands should be, on average, more similar than species richness in distant bands (Vetaas & Grytnes, 2002) due to spatial autocorrelation in species richness and/or spatial autocorrelation in an explanatory variable that is spatially structured. Thus our regression analyses between species richness and elevation have a primarily descriptive value, and should not follow the strict assumptions of inferential statistics due to spatial autocorrelation (Legendre & Legendre, 1998; Diniz-Filho *et al.*, 2003). Determination coefficient values for all regressions between species richness and elevation were used only for comparative purposes, and tests for statistical significance were performed at a more conservative level of 1% (Thomson *et al.*, 1996).

To evaluate differences in species richness between seasons, we compared the species density between plots at the same bands and in the same mountains through a paired Student's *t*-test. As we sampled two plots per band in the summer season, two independent paired Student's *t*-tests were performed. We applied square-root transformation for species number and log + 1 transformation for specimen abundance to remove heteroscedasticity for all analyses using plots as sample units.

RESULTS

Harvestman richness along altitudinal gradients

We collected 846 adult harvestmen belonging to 38 species and two families (five Sclerosomatidae and 33 Gonyleptidae). Harvestman species richness per mountain was 27, 26 and 19 for Cuscuzeiro, Corcovado and Capricórnio, respectively. Species richness decreased with elevation on all three mountains, but with marked differences between the mountains (Fig. 1a–c; Table 1). Species richness in Cuscuzeiro Mountain was characterized by a lower elevation plateau to 450 m with an accentuated decrease above this altitude. Corcovado Mountain showed a less distinct plateau in species richness and a smooth decrease above 250 m. In Capricórnio Mountain, species richness showed a smooth decrease along the whole gradient, with a weak increase in richness at 750 m. The general inverse relationship between species richness and elevation was not altered at the regional scale (Fig. 1d; Table 1). The recorded species richness is between the upper and lower 95% values predicted by the mid-domain effect at all elevational bands above 250 m in Corcovado and Capricórnio mountains. In Cuscuzeiro Mountain, the recorded species richness is only between the 95% confidence limits of species richness predicted by the mid-domain effect between 450 and 550 m bands. The species richness predicted by the mid-domain effect had a low and non-significant fit with the observed species-richness pattern for the three mountains and for the regional pattern (Cuscuzeiro: $r^2 = 0.055$, $P = 0.49$; Corcovado: $r^2 = 0.015$, $P = 0.72$; Capricórnio: $r^2 = 0.016$, $P = 0.73$; regional: $r^2 = 0.043$, $P = 0.54$).

Table 1 Simple linear regression between harvestman species richness per elevational band, and elevation of each band at each mountain and for combined bands in all three mountains studied

Mountain	a	b	r^2	d.f.	F	P
Cuscuzeiro	19.62	−0.0162	0.804	1–9	36.89	0.0002
Corcovado	12.93	−0.0093	0.899	1–9	80.32	<0.0001
Capricórnio	11.34	−0.0070	0.703	1–8	18.95	0.0024
Regional	26.37	−0.0167	0.812	1–8	35.21	0.0003

a, Intercept; *b*, regression coefficient; r^2, determination coefficient.

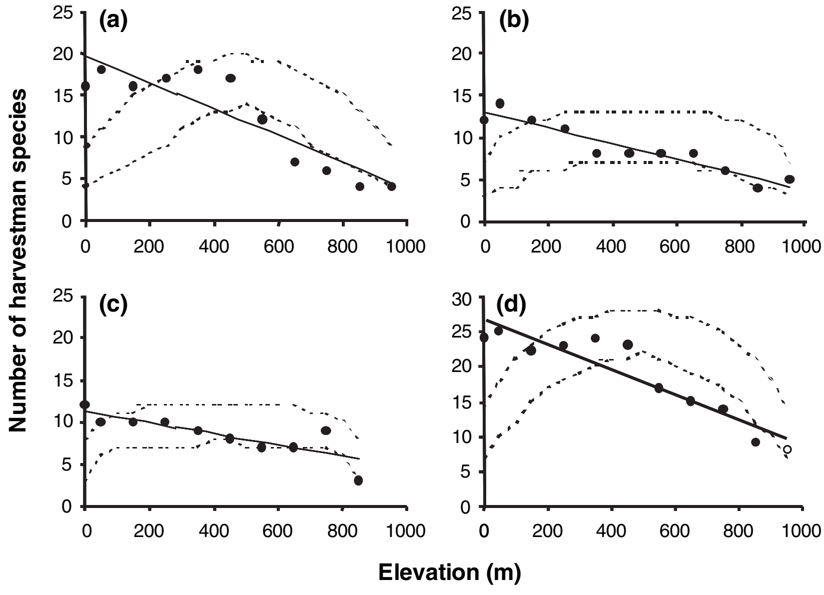

Figure 1 Relationship between elevation and number of harvestman species in three Brazilian Atlantic Forest mountains: (a) Cuscuzeiro Mountain; (b) Corcovado Mountain; (c) Capricórnio Mountain; and (d) regional pattern. The open circle for regional pattern at 950 m represents only two mountains and was not included in the analysis. Dotted lines enclose 95% prediction curves sampled without replacement using empirical range sizes and simulated mid-points; solid lines are least-squares linear regression lines.

Rapoport effect

Elevational ranges for all species at each mountain are shown in Fig. 2. As predicted by the Rapoport effect, species with higher elevational midpoints tended to have broader elevational ranges (Fig. 3a–c; Table 2). The regional analysis of the Rapoport effect is in accordance with the pattern observed for each mountain (Fig. 3d; Table 2).

The alternative analysis of the Rapoport effect through the specimen method showed that species with higher specimen mean elevation had greater elevational ranges (Fig. 4; Table 3). As seen in Fig. 2, species with broader elevational ranges are not from higher elevations. Only one species with an elevational range > 800 m had its abundance peak higher than 650 m (Fig. 2).

The comparison between the midpoint method and specimen method regression graphics showed few differences for Corcovado and Capricórnio mountains, and clear changes in species mean elevation for Cuscuzeiro Mountain and for the regional pattern (Figs 3 & 4). The specimen method resulted in a more widely distributed set of values around the regression lines than the midpoint method. Consequently, the *P* values for the regression coefficients in the specimen method are higher than that recorded for the midpoint method (Fig. 4).

Harvestman occurrence at fine spatial scale

An initial analysis through Spearman's rank correlation showed that only temperature and humidity presented significant correlations with species number and specimen abundance per plot (Figs 5 & 6; Table 4). Moreover, the correlations shown in Table 4 suggest that the relationships of elevation, temperature and humidity with harvestman richness and abundance changed between the two seasons. Elevation and humidity had stronger correlations with richness and abundance in the winter, whereas temperature showed higher correlations with richness and abundance when we combined the data from the two seasons. Multiple regressions explained 59% of the variance in species richness per plot ($\sqrt{}$species richness = −1.744 − 0.0011 elevation + 0.0897 temperature + 0.0212 humidity; $F_{[3,91]} = 42.99$; $P < 0.001$); and 61% of the variance in specimen abundance (log specimen abundance + 1 = −1.166 − 0.0005 elevation + 0.0549 temperature + 0.0111 humidity; $F_{[3,91]} = 49.11$; $P < 0.001$). The values of regression coefficients of each independent variable in the above equations represent the absolute effects of these variables on harvestman richness (square root-transformed) and harvestman abundance (log + 1-transformed). The comparative effects of elevation, temperature and humidity on the dependent variables are shown by their standardized values (Tables 5 & 6).

The negative effect of low temperature and humidity on harvestman occurrence is observed between seasons. In summer, harvestmen were collected throughout the entire elevational range, but in winter individuals were not found above 750 m (Fig. 7). Furthermore, the regional number of harvestman species was lower in winter plots when compared with the same sampling effort for summer plots (Fig. 7; paired *t*-test: $P < 0.0001$ for the two comparisons between winter and summer plots).

DISCUSSION

Harvestman distribution and the Rapoport effect

There have been few detailed studies on arachnid species distribution along elevational gradients (Otto & Svensson, 1982; Bosmans *et al.*, 1986), and the reported patterns are often based on anecdotal observations or general leaf litter invertebrate surveys (Leakey & Proctor, 1987; Atkin & Proctor, 1988; McCoy, 1990; Olson, 1994). Recently, Chatzaki *et al.* (2005) provided the first detailed account of the distribution of gnaphosid spiders along an altitudinal gradient in Crete, Greece, and showed that the elevational range of species distribution increases with altitude (Chatzaki *et al.*, 2005). The only study dealing exclusively with harvestman distribution along altitudinal gradients has been undertaken in the Eastern Alps from 900 to 3300 m (Komposch & Gruber, 1999). Although the authors do not present any statistical analysis in the paper, we analysed the data from their Table 1 and also found a decrease in species richness along the elevational gradient. Moreover, species with higher-range midpoints tended to cover broader elevational range sizes. Although our study was conducted in a tropical area, and along a much narrower altitudinal range, the pattern of species distribution is quite similar to that reported for the temperate harvestman community, and provides empirical support for an elevational Rapoport effect. This effect has been documented previously for grasshoppers (Claridge & Singhrao, 1978), butterflies (Fleishman *et al.*, 1998), ants (Sanders *et al.*, 2003) and spiders (Chatzaki *et al.*, 2005), but this is the first demonstration for harvestmen.

Although several studies on the distribution of spider species along altitudinal gradients have shown that richness declines with altitude following a hump-shaped pattern (Otto & Svensson, 1982; Bosmans *et al.*, 1986; Chatzaki *et al.*, 2005), our results show that harvestmen from the Brazilian Atlantic Forest present low-elevation plateaux in diversity that decrease at higher elevations. At lower elevations, the inverse relationship between harvestman species richness and elevation does not conform to the species number predicted by the mid-domain effect based solely on geometric constraints assuming hard boundaries (McCain, 2004, 2005). The regional relationship between elevation and species richness is strongly influenced by the Cuscuzeiro Mountain pattern: a bimodal pattern with a secondary peak at mid-elevation. This secondary peak at 400 m in Cuscuzeiro Mountain could be explained both by the mid-domain effect (Colwell & Lees, 2000) and by interpolation of species occurrence at mid-elevations (Grytnes & Vetaas, 2002). According to Chatzaki *et al.* (2005), the great variety of results among studies on the distribution of species along altitudinal gradients suggests that there is probably not a

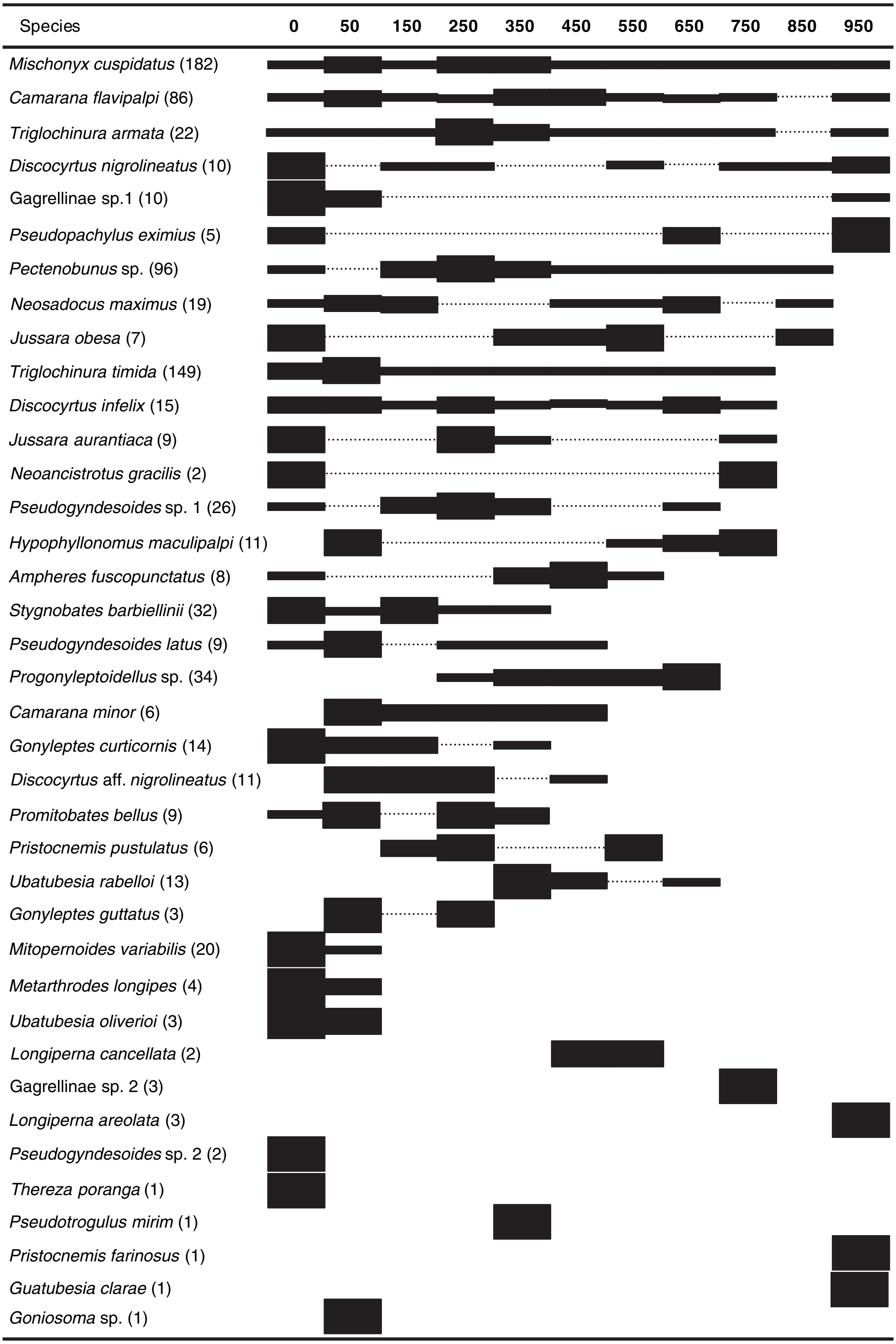

Figure 2 Combined elevational ranges of harvestman species in three mountains in Brazilian Atlantic Forest. Number in parentheses after each species indicates total number of individuals captured. Width of bars represents four abundance classes based on the proportion of individuals of a species recorded in each band in relation to the total number of individuals of the same species recorded in all bands. Ranges of abundance from thinnest to thickest bar are: (1) 0–12.5; (2) 12.5–25; (3) 25–50; (4) 50–100%. Dotted lines represent interpolation of species occurrence. Species are sorted from high to low according to range size and total abundance.

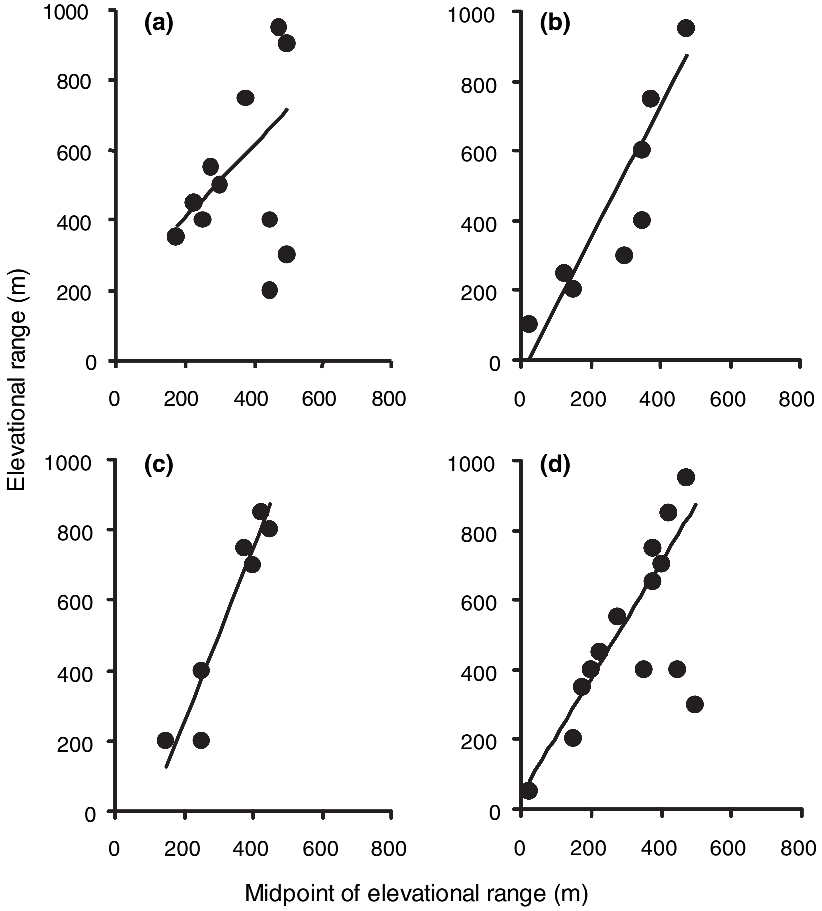

Figure 3 Midpoint plots of the Rapoport effect in three Brazilian Atlantic Forest mountains. (a) Cuscuzeiro Mountain; (b) Corcovado Mountain; (c) Capricórnio Mountain; (d) regional pattern. Lines are least-squares linear regression lines.

Table 2 Simple linear regression between midpoint and elevational range size for harvestman species at each mountain and for the three mountains combined

Mountain	*a*	*b*	r^2	d.f.	*F*	*P*
Cuscuzeiro	200.82	1.03	0.280	1–16	6.23	0.0239
Corcovado	−41.47	1.93	0.866	1–10	64.57	<0.0001
Capricórnio	−244.91	2.49	0.904	1–7	65.87	<0.0001
Regional	46.15	1.65	0.685	1–25	54.33	<0.0001

a, Intercept; *b*, regression coefficient; r^2, determination coefficient.

single model to describe how animals react to the change in altitude, even under similar environmental conditions.

Harvestman richness at elevations below 50–150 m is higher than that predicted by the mid-domain effect. The higher species richness at lower elevations in the neotropical elevational gradients studied here was, in part, due to stronger upper limits when compared with the lower limits in the ranges of species (Fig. 2). These stronger upper limits created an asymmetrical species distribution along the gradient, so that higher elevational bands (above 450 m) generally presented subsets of species recorded from lower elevations. The effect of available area on decrease in species number along the elevational gradient seems weak because those species that were present at higher elevations cover a larger total area of habitat than species restricted to lower elevations (Jones *et al.*, 2003). Thus the Rapoport effect observed in our study cannot be explained by an artefact of uniform sampling effort for all elevational bands, as suggested by Colwell & Hurtt (1994). In fact, there is a set of species that have never been collected above 350 m: *Gonyleptes curticornis*, *Gonyleptes guttatus*, *Mitopernoides variabilis*, *Promitobates bellus*, *Thereza poranga* and *Ubatubesia oliverioi* (Kury, 2003). Although we do not have samples for the total elevational range in one mountain (Cuscuzeiro), extensive data from the literature show that only one of the recorded species in this study, *Longiperna areolata*, is found exclusively at higher elevations (Kury, 2003). Therefore we believe that the small number of high-elevation specialists may be an additional cause of decreasing harvestman richness at higher elevations, and that the pattern from 0 to 950 m adequately reflects trends at the highest elevations.

Although we found a pattern in species range distribution, as predicted by the elevational Rapoport effect (Stevens, 1992), the process proposed by Stevens (1989, 1992) to explain the Rapoport effect (the Rapoport rescue effect) is not in accordance with our data. As described by Brown & Kodric-Brown (1977), the rescue effect suggests a tendency for a continual influx of individuals of species outside their optimum distribution to sites where they are unable to

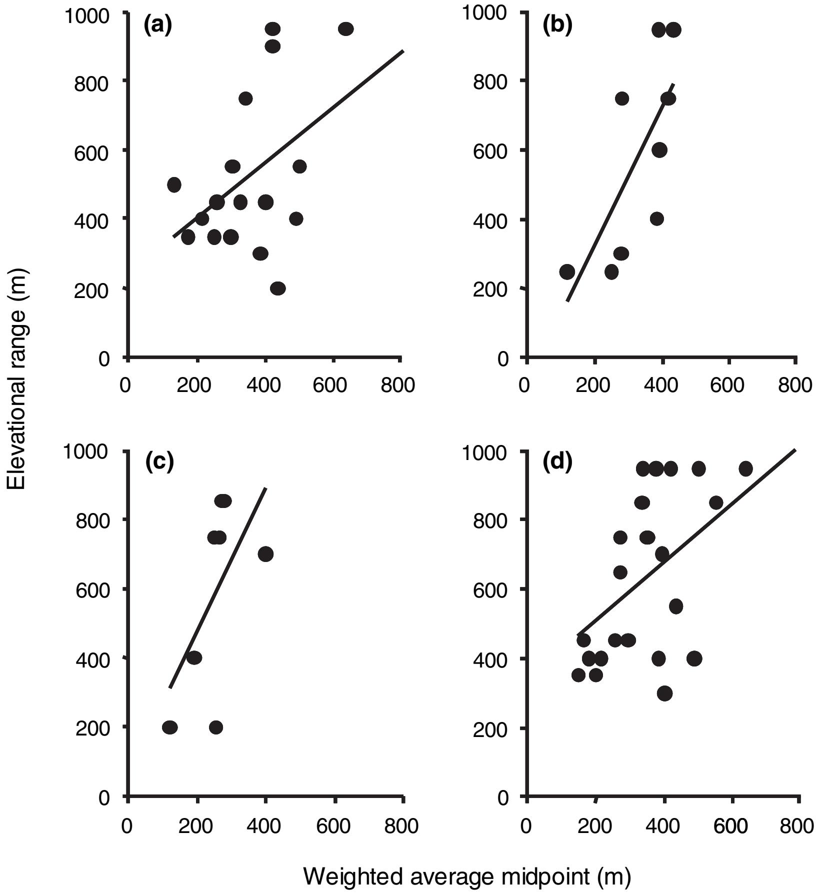

Figure 4 Specimen mean elevation plots of the Rapoport effect in three Brazilian Atlantic Forest mountains. (a) Cuscuzeiro Mountain; (b) Corcovado Mountain; (c) Capricórnio Mountain; (d) regional pattern. Lines are least-squares linear regression lines.

Table 3 Simple linear regression between weighted average midpoint and elevational range size for harvestman species at each elevational gradient and for all gradients combined

Mountain	*a*	*b*	r^2	d.f.	*F*	*P*
Cuscuzeiro	236.80	0.81	0.332	1–14	7.94	0.0124
Corcovado	−58.76	1.97	0.654	1–9	17.04	0.0026
Capricórnio	58.15	2.09	0.356	1–6	3.32	0.1182
Regional	333.22	0.85	0.335	1–22	11.09	0.0030

a, Intercept; *b*, regression coefficient; r^2, determination coefficient.

maintain themselves. In this way it is possible to prevent the disappearance of those species in the so-called sink habitats (*sensu* Pulliam, 1988). The difference in our data when compared with the hypothesis proposed by Stevens (1992) is that harvestman species covering broader elevational ranges present higher abundances at lower elevations, indicating that their optimum elevations are below the middle of the range. In this way there is little support for a rescue effect from higher to lower elevations. Similar results were found for ground spiders along altitudinal gradients in Crete, in which the great majority of species are constrained by their upper elevational limits (Chatzaki *et al.*, 2005). Like the harvestman assemblage studied here, on the Cretan summits there are highly tolerant lowland spider species and a few isolated residents of the high mountains (Chatzaki *et al.*, 2005).

In order to explain the patterns of elevational species distribution observed for both neotropical harvestmen and Cretan spiders, an alternative rescue effect is proposed here. Figure 8 shows the directions of three putative rescue effects in elevational gradients: (a) a non-directional rescue effect; (b) a rescue effect from higher to lower elevations (cf. Stevens, 1992); and (c) a rescue effect from lower to higher elevations. Although the general pattern of species richness along an elevational range may depend on the empirical ranges of each species, as well as their lower and upper limits, the non-directional model is expected to generate a peak at mid-elevations according to the mid-domain effect (Lomolino, 2001; Grytnes & Vetaas, 2002; Grytnes, 2003; Fig. 8a). On the other hand, both Stevens's model and our alternative rescue effect are expected to generate a decrease in species richness at higher elevations (Fig. 8). The main difference between them, however, is that Stevens's model predicts a peak in species richness at lower elevations due to asymmetrical inflation in species richness from higher to lower elevations (Fig. 8b), whereas our model predicts a decrease in species richness at higher elevations due to differential upper limits of species with source populations below mid-elevations (Fig. 8c). In fact, our data show that species with an optimum between 100 and 500 m may disperse to the upper-elevation belt, but generally do not make viable populations there. Consequently, differences in elevational range size should occur due to

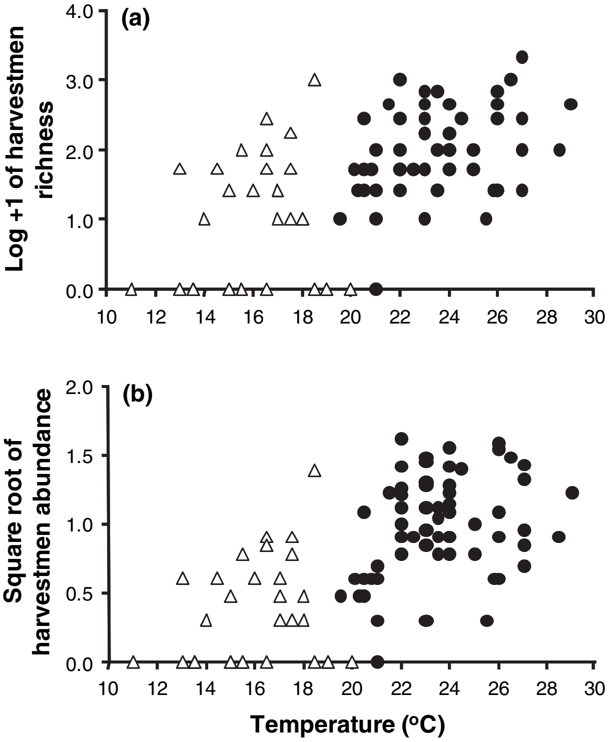

Figure 5 Relationships between (a) harvestman species richness and temperature, and (b) harvestman abundance and temperature along three mountains in the Brazilian Atlantic Forest. Black circles, summer plots; white triangles, winter plots.

differences in tolerance to changes in temperature and humidity among species with similar optimal elevations. Therefore this alternative rescue effect does not invalidate the influence of physiological factors, such as the differences in tolerance to changes in abiotic conditions among species (mainly temperature and humidity), as explanations for a Rapoport effect along elevational gradients.

Our hypothesis that the Rapoport effect is a rescue effect from source populations at low and medium elevations to sink populations at high elevations would be applicable mainly for animal groups sensitive to low temperature and/or humidity, such as many ground arthropods, frogs and terrestrial gastropods. It may also apply for tropical and small-range elevational gradients, where variability in climatic factors is less accentuated than in temperate regions and broad elevational ranges.

Effects of humidity and temperature

In contrast to other arachnids, such as scorpions and some spiders, harvestmen are very susceptible to water loss, and the need for moist habitats is probably a significant ecological factor limiting the occurrence of most species of the order in xeric zones (Hillyard & Sankey, 1989). Our results show that temperature and humidity are strongly correlated with species density and specimen abundance at fine spatial scales. However, these relationships were detected only because we measured these variables in two distinct seasons, increasing the variability in the conditions measured. Thus in studies where environmental variables are measured for a single occasion or season, the lack or weakness of correlation with species density and abundance per sample unit may be a result of low variability in the environmental characteristics measured.

Studying the ecology of British harvestmen, Todd (1949) stated that temperature and humidity are the most important

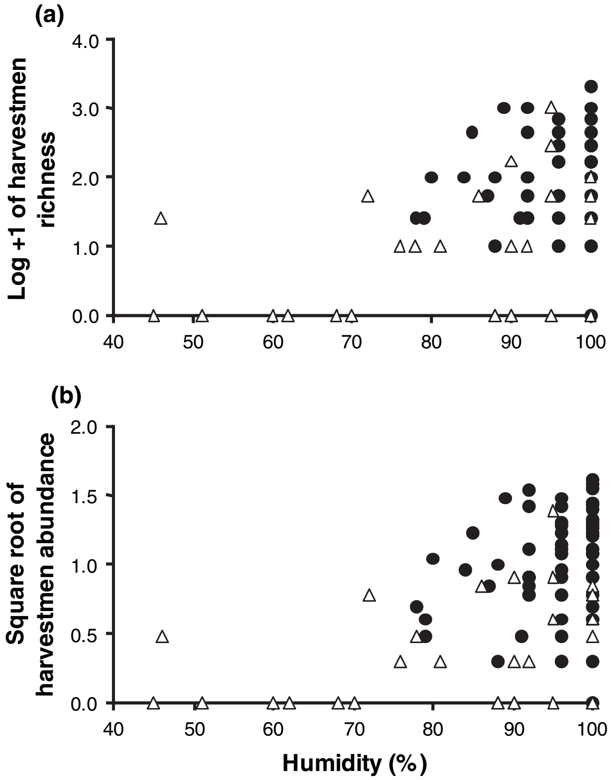

Figure 6 Relationships between (a) harvestman species richness and humidity, and (b) harvestman abundance and humidity along three mountains in the Brazilian Atlantic Forest. Black circles, summer plots; white triangles, winter plots.

Table 4 Spearman's rank correlation between local environmental features recorded at the moment of capture, and elevation, harvestman species number and harvestman abundance per plot

Season	Elevation	Temperature	Humidity	Leaf-litter depth
Species richness				
S + W	−0.540***	0.530***	0.332**	−0.089 n.s.
S	−0.571***	0.264*	0.140 n.s.	−0.152 n.s.
W	−0.760***	0.158 n.s.	0.352*	−0.033 n.s.
Specimen abundance				
S + W	−0.520***	0.612***	0.349***	−0.120 n.s.
S	−0.605***	0.308*	0.199 n.s.	−0.193 n.s.
W	−0.749***	0.195 n.s.	0.335 n.s.	−0.035 n.s.

S, summer plots; W, winter plots; S + W, all plots. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; n.s., not significant.

Table 5 Multiple regression between harvestman species number per plot (square root-transformed) and three independent variables: elevation, temperature and humidity

Independent variable	b	r^2	$F_{[1,91]}$	P
Elevation	−0.0011 (−0.3653)	0.103 (0.217)	25.219	<0.0001
Temperature	0.0897 (0.4195)	0.155 (0.264)	32.613	<0.0001
Humidity	0.0212 (0.2862)	0.077 (0.152)	16.348	0.0001

b, Regression coefficient, with standardized regression coefficients in parentheses; r^2, coefficient of determination, with adjusted coefficient of determination for the two other independent variables in parentheses.

Table 6 Multiple regression between harvestman specimen abundance per plot (log + 1-transformed) and three independent variables: elevation, temperature and humidity

Independent variable	b	r^2	$F_{[1,91]}$	P
Elevation	−0.0005 (−0.3380)	0.103 (0.207)	23.782	<0.0001
Temperature	0.0549 (0.4802)	0.203 (0.340)	46.952	<0.0001
Humidity	0.0110 (0.2783)	0.073 (0.157)	16.984	0.0001

b, Regression coefficient, with standardized regression coefficients in parentheses; r^2, coefficient of determination, with adjusted coefficient of determination for the two other independent variables in parentheses.

determinants of species distribution and habitat use. Indeed, the results of our multiple regression analysis showed that these two environmental factors are also important for harvestman distributions in tropical areas. Their effects on harvestman distributions could be either direct (as physiological constraints), or indirect (through prey depletion). However, since gonyleptid harvestmen are generalist feeders, which include fruits, fungi, dead and live prey in their diet (Gnaspini, 1996; Machado & Pizo, 2000), food availability probably does not affect their distribution to a great extent (Adams, 1984). Therefore physiological constraints may be the most important factor influencing harvestman distribution in our study sites. Temperature and humidity are also important determinants of harvestman phenology, influencing reproduction, egg development, growth rates, adult activity and mortality (Clingenpeel & Edgar, 1966; Curtis, 1978; Bachmann & Schaefer, 1983; Machado & Oliveira, 1998). A recent study on the population ecology of the gonyleptid harvestman *Mischonyx cuspidatus*, the most abundant species in our study sites, has shown that after winter there is a drastic decrease in population size, and fewer than 10% of individuals survive this period of stressful climatic conditions (Mestre & Pinto-da-Rocha, 2004). Similar results were obtained at the community level: during our winter samples no harvestman was found above 750 m, suggesting that the density of harvestmen is considerably reduced in highlands.

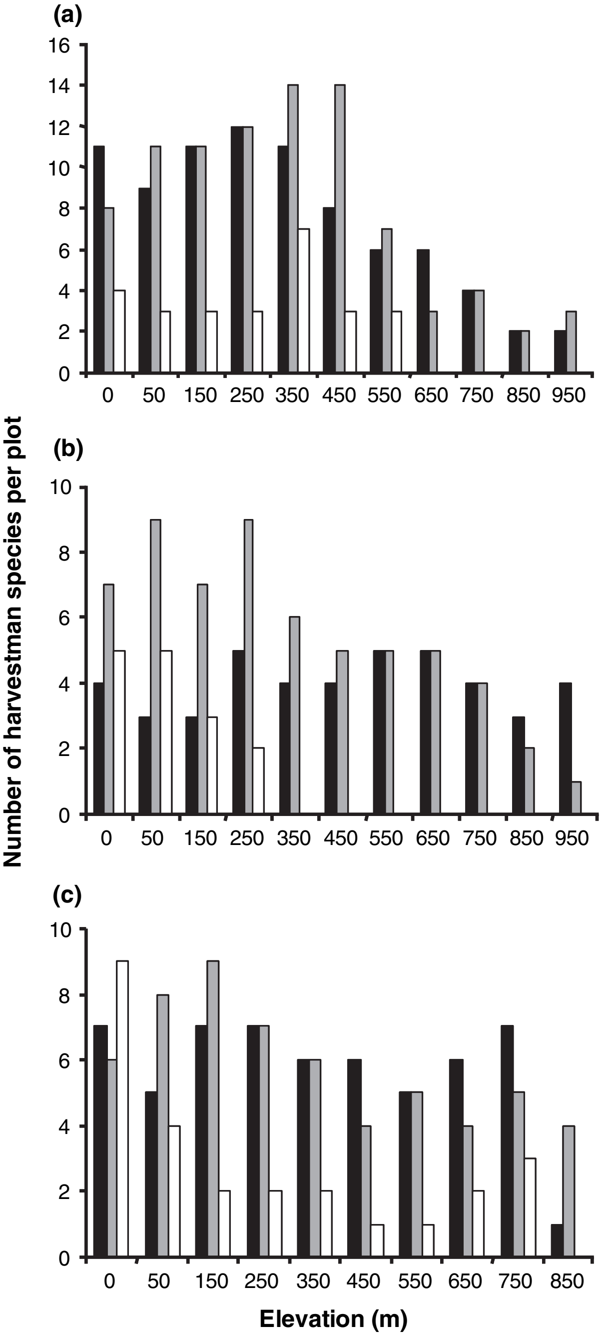

Figure 7 Harvestman species richness per plot in three mountains in the Brazilian Atlantic Forest: (a) Cuscuzeiro Mountain; (b) Corcovado Mountain; (c) Capricórnio Mountain. Black and grey bars, summer plots; white bars, winter plots.

The periodical change in distribution of species associated with seasonal climatic changes (upward expansion of range limits in the warm season followed by the downward contraction of ranges in winter) provides additional support for an alternative rescue effect to explain the Rapoport effect. According to Stevens (1992), high-elevation species would be expected to have wider tolerance to environmental changes

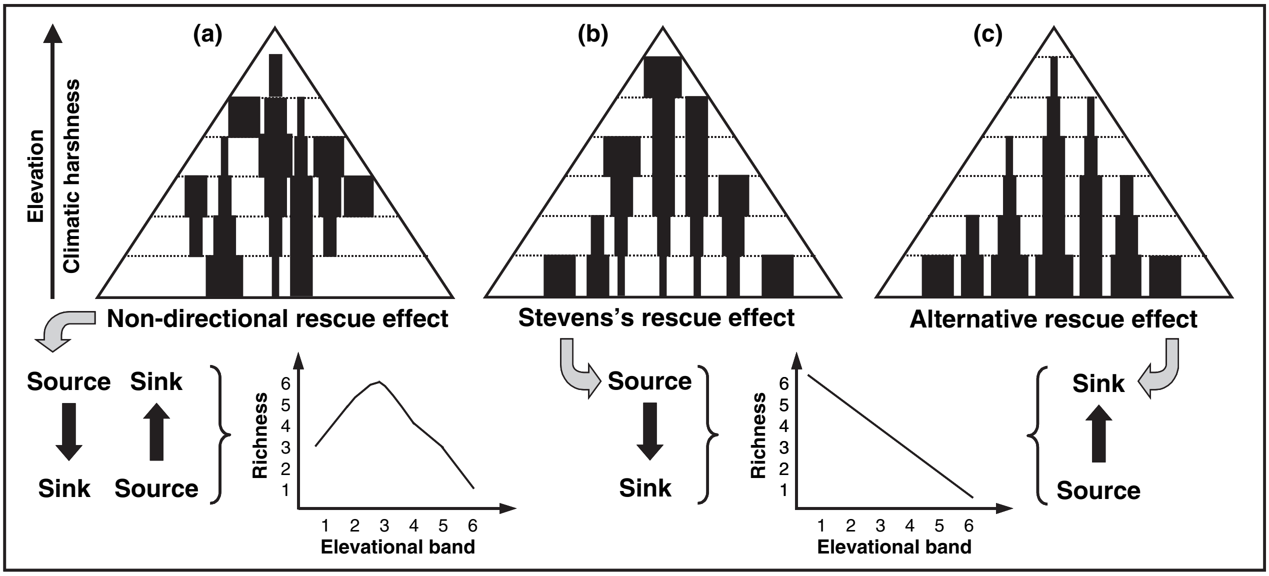

Figure 8 Schematic representation of three putative rescue effects in elevational gradients. Triangles, mountains divided into six elevation bands (dashed lines); vertical bars, elevational ranges of seven hypothetical species; width of bars indicates proportional abundance for each species in the band. Below the triangles is an indication of the main direction of each rescue effect and a graphic showing the relationship between elevation and richness for the different models. (a) A non-directional rescue effect, in which there are source populations both at higher and lower elevations. In this case the distribution of species along the elevational range generates a peak at mid-elevations in accordance with the mid-domain effect. (b) Stevens's rescue effect, in which source populations are those from higher elevations. (c) An alternative rescue effect, in which source populations are those from lower elevations. Both models (b) and (c) generate a pattern of decreasing species richness at higher elevations, but the underlying process is different. Stevens (1992) proposes an asymmetrical inflation in species richness from higher to lower elevations, whereas our alternative rescue effect proposes that decreasing species richness at higher elevations occurs due to differential upper limits of species with source populations below mid-elevations.

than low-elevation species. High-elevation species could, therefore, expand their lower limits of elevational range, whereas low-elevation species would be constrained by their upper elevational limits. Contrary to these predictions, climate harshness during the winter has a marked negative effect on high-elevation populations, so no harvestman species appear able to sustain dense populations in the highlands. In this way, individuals of species more abundant at low and medium elevations may be considered 'accidentals' that inflate the species counts of local assemblages at high elevations during the warmer months.

It is worth noting that the three mountains sampled are close to the sea (*c.* 15 km) and, like many other montane forests worldwide, the highlands are subject to fog deposition throughout the year (Hamilton *et al.*, 1995). The ecological importance of this extra moisture input on leaf litter fauna has rarely been investigated. Nevertheless, studies in several tropical cloud forests have demonstrated that the soil of the upper parts of the mountains is typically very wet (Bruijnzeel, 2001), which could attenuate the hydric stress for those organisms living in the leaf litter, including many arthropods. Data for ants do not corroborate this hypothesis, and show that the richness of species along an altitudinal transect in a montane cloud forest from Malaysia decreases with altitude (Brühl *et al.*, 1999). The authors argue that low temperatures associated with high humidity at higher altitudes could impose problems for ants by critically shortening foraging time. Our results also show no support for a positive effect of fog deposition on harvestman occurrence and, more importantly, provide empirical data demonstrating that the leaf-litter humidity in the upper parts of the montane cloud forests from south-eastern Brazil does not receive an extra input of moisture.

CONCLUSIONS

Our study shows that harvestmen, an important group of leaf-litter fauna, decline at higher elevations, in part due to a decline in temperature and humidity. Consequently, species distribution along the elevational gradient changes between seasons, and no harvestman species was found above 750 m during the dry and cold season despite the deposition of cloud water on vegetation in the highlands. We found support for an alternative process generating an elevational Rapoport effect. Our hypothesis is based on the two mechanisms proposed by Stevens's (1992) original hypothesis for an elevational Rapoport effect: differences in tolerance ranges to abiotic conditions; and a rescue effect at species level. However, contrary to Stevens's hypothesis, we suggest that the rescue effect operates from lower to higher elevations, and between species within similar optimal elevational ranges.

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