

An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo

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Abstract. This study investigated factors responsible for the decline of ant species richness with increasing elevation in an evergreen tropical rain forest on Mount Kinabalu. From 580 m to 1520 m a.s.l. we studied the ant community as well as biotic and abiotic factors in parallel on the ground and in the lower vegetation with various methods. We collected a total of 376 ant morphospecies, belonging to 65 genera and 8 subfamilies. The decline of ant species richness was significantly correlated with the decline in temperature but the pattern of decline differed between the two strata. In contrast the ant nest density remained the same on the ground and in the lower vegetation up to 1000 m, but then dropped significantly. As the main nesting resource (dead wood) remained rather constant over the elevation gradient, the most plausible explanation is a direct impact of temperature. In addition, the increasing compaction of the soil and increased depth of the humus layer also restricts nesting on the ground at the highest elevations. A case study of the ground ant *Diacamma* sp. along the elevation gradient indicated scarcity of food as another important factor in the ground layer uphill.

Keywords: elevational gradient, ants, Malaysia, Kinabalu, species richness, temperature, tropical diversity

INTRODUCTION

To identify the factors involved in the maintenance or change of species richness with time and space is a prerequisite for reaching an understanding of community dynamics and comprehending the consequences of diversity changes. Within tropical rain forests there are many natural gradients along which species richness may change. Extensive tropical mountain slopes offer

the opportunity to investigate especially pronounced climate gradients. While species richness of most animal and plant taxa seems to decline with increasing elevation (Janzen 1976, reviewed in Rahbeck 1995), species number and biomass of certain groups of Arachnida, Crustacea, Myriapoda, Lepidoptera and Coleoptera can increase and may reach their maximum in tropical montane zones (Holloway 1970; Collins 1980; Olson 1994; Nor 2001; Brehm & Fiedler 2003).

The decline in tropical ant species richness and biomass with increasing elevation is extraordinarily distinct wherever it has been studied in the tropics (Collins 1980; Olson 1994; Samson *et al.* 1997; Fisher 1998; Brühl *et al.* 1999). Furthermore ants are especially suited to such a gradient study since (1) they represent a keystone group in tropical lowland forests (Fittkau & Klinge 1973; Stork 1988; Tobin 1991), (2) they are taxonomically one of the best-investigated invertebrate groups, and (3) even a single worker of a species can be attributed to a certain area and altitude as their mode of life requires a narrow site fidelity (Hölldobler & Wilson 1990).

Until now only speculative explanations have been given for the steep decline of ant species richness with increasing elevation and the general restriction of ants to rather low altitudinal zones in the tropics remained enigmatic. Of the many hypotheses to explain this elevational gradient in richness we address some of the most probable here. (1) Janzen's (1967) hypothesis is based on the fact that in the tropics daily temperature differences are, in contrast to temperate regions, greater than annual temperature differences. This leads to rather uniform temperatures year-round at a given altitude and to fast changes in average as well as minimum and maximum temperatures along an altitudinal gradient. Janzen (1967) hypothesised that this condition favours adaptations to narrow temperature ranges, resulting in high species turnover and an early attainment of uninhabitable zones with increasing altitude due to temperature conditions. (2) Brown (1973) observed that the upper altitudinal distribution boundaries of ants are generally lower in tropical regions compared to temperate regions. He assumed the lack of sufficient direct 'warming solar radiation' in the tropics, as a result of the permanent fog and cloud belt in mountain rainforests, to be the decisive factor for this phenomenon. (3) Olson (1994) and Brühl *et al.* (1999) discussed increasing humidity, and decreasing temperature and availability of nutrition, as being responsible for the decrease of ant species richness with increasing altitude. (4) Fisher (1998) considered the decrease of primary productivity with increasing altitude to be the cause for ant species decline.

We aimed at contributing to the clarification of the factors underlying the decline of tropical ant species richness with increasing elevation. By investigating biotic and abiotic factors as well as ant species' distribution in ground stratum (GS) and on lower vegetation (LV) in parallel along the elevational gradient we applied a novel approach. As these strata typically differ in their biotic and abiotic properties as well as in the taxonomic composition of ants (Hölldobler & Wilson 1990; Baron-Urbani *et al.* 1992; Brühl *et al.* 1998; Malsch *et al.* 2003), we expected to find patterns indicative of relevant factors for the observed decline.

MATERIALS AND METHODS

To assess ant community patterns, we collected ants at different elevations and recorded nest densities. As possible factors influencing ants along the elevational gradient, we recorded a number of abiotic and biotic parameters in the GS as well as in the LV (including temperature, humidity, nest site availability and vegetation structure).

Study site

In the Mt. Kinabalu National Park (Sabah, Borneo, Malaysia) all investigations were restricted to one mountainside, the 'East Ridge' near Poring Hot Springs (6°02'N, 116°42'E). Rainy seasons in this area usually occur between December and February and between July and September (Kitayama *et al.* 1999). In 1996 (January to April) we collected data in the forest at 580 m, 830 m, 1140 m, 1340 m, and 1520 m a.s.l. These altitude points comprise a spectrum from lowland to lower montane forest with a transition zone from about 900 m (Hotta 1974, Menzel 1988, this study) to 1200 m a.s.l. (Kitayama 1992). With respect to vascular plants the transition zone is the most species-rich elevation band at Mt. Kinabalu (Grytnes & Beaman 2006).

Since we found a steep species decline at lower elevations (see Results), we restricted further investigations (April to July in 1997, 1998 and 1999 respectively) to the lowland forest and transition zone, collecting data at 600 m, 720 m, 850 m, 1000 m and 1140 m a.s.l. Due to the steepness of the study

sites it was impossible to establish all sampling plots exactly according to an identical pattern at the respective elevation. To remain in the same habitat type the spatial design had to be modified in regard to topography, resulting in a deviation in elevation of up to 30 m.

Abiotic and biotic factors

Within both strata temperature was measured with TinyTalk II temperature loggers (Gemini Data Loggers (UK) Ltd., Orion Group). They registered 48 data points in each 24 hours over a total of 10 months between 1996 and 1998. Two loggers were installed at each altitude point: one within each stratum (Table 1). Similarly TinyTalk II humidity loggers registered relative humidity for a total of 6 months in 1997 and 1998 (Table 1), outside the El Nino period (December 1997 to April 1998). We consider that our data are representative of non El Nino years.

Further data collection (e.g. plot characterisation, ant sampling, nest density, nest site characteristics) is described below for each stratum separately:

1) Ground stratum

The ground stratum (GS) comprised dead wood, the leaf-litter layer, the humus layer plus the top 20

cm of mineral soil; dead wood was divided according to diameter into 'twigs' (< 0.5 cm) and 'sticks' (> 0.5 cm to < 5 cm). Square GS plots (0.5 x 0.5 m = 0.25 m²) were chosen according to the following criteria: (1) leaf-litter coverage > 75%; (2) canopy cover > 60%; (3) no permanent water-logging; (4) only sparse growth of herbs; and (5) no large (> 5 cm wide) pieces of wood. The plots were spaced at least 5 m apart.

Investigations conducted were:

- 'ant diversity assessment' between 580 m and 1520 m in 1996: at each altitude point 4 x 4 m² (each 4 m² sample comprising 16 x 0.25 m² plots) samples of the GS (excluding top soil) were extracted using the Winkler method (Besuchet *et al.* 1987; Agosti *et al.* 2000);
- 'nest collection' between 600 m and 1140 m in 1997 and 1998: at all elevations 4 m² (16 x 0.25 m² plots) of the GS were inspected carefully for nests. Nest characteristics (e.g. position, size, material) were recorded;
- 'potential nesting space assessment' between 600 m and 1140 m in 1997 and 1998: during 'nest collection' (see b) we recorded different parameters of possible nest sites: dead wood (e.g. number of pieces; classification into five classes of hollowness and strength); leaf litter (e.g. volume;

Table 1. Position of temperature and humidity loggers at Poring Hot Springs, Sabah, Borneo (* = only temperature logger; a.s. = above top soil; i.s. = in the top soil; months are given in numbers, e.g. 1 - 4 = January - April).

	1996		1997		1998		
	2 cm a.s.*	2 m a.s.*	2 cm a.s.	2 m a.s.	2 cm a.s.	2 m a.s.	2 cm i.s.*
580 m	1 - 4	1 - 4	5 - 7	5 - 7	5 - 7	5 - 6	6 - 7
650 m							
720 m			5 - 7	5 - 7	5 - 7	5 - 6	6 - 7
830 m	1 - 4	1 - 4	5 - 7	5 - 7	5 - 7	5 - 6	6 - 7
950 m							
1000 m			5 - 7	5 - 7	5 - 7	5 - 6	6 - 7
1140 m	1 - 4	1 - 4	5 - 7	5 - 7	5 - 7	5 - 6	6 - 7
1340 m	1 - 4	1 - 4					
1520 m	1 - 4	1 - 4					

- height); humus layer (e.g. depth; rooting) and topsoil (e.g. solidity; constitution) (for details see Malsch 2002);
- d) ‘*Diacamma* study’ in 1998 and 1999 (at 650 m, 830 m and 950 m): to investigate changes in nesting and foraging behaviour with increasing altitude for a given species the ground ant *Diacamma* sp.1 was chosen as an example. This species was well suited to study due to its large worker size (ca. 0.8 – 1 cm), small colony size (<500 workers), simple ground nests and ubiquity on the ground across a broad altitudinal range (ca. 500 – 1050 m). Prey intake per unit time was recorded by observing nests with a comparable level of nest activity (defined by five to six active workers within 1 m radius around the nest entrance). Prey was collected from 36 ± 1 workers per elevation point and the total foraging time was measured. At each altitude point 25-30 *Diacamma* sp.1 nests were mapped.

2) Lower vegetation

For ant collection on Lower Vegetation (LV) all plants were inspected up to 3 m above the ground (including taller trees and lianas). Ant sampling was conducted in continuous transects of 1 m x 1 m quadrats, which ran parallel to each other along the contour line. Transect length and spacing varied with the chosen method (see a - d). All transects had to meet the following habitat criteria: (1) canopy cover > 60%; (2) relatively homogeneous plant growth (no gaps, no thickets); and (3) no recent damage, e.g. due to large animals’ activity or fallen larger branches.

Investigations conducted were:

- a) ‘altitudinal diversity assessment’ between 580 m and 1520 m in 1996: for each elevation ants were collected on about 400 plants (plus the remaining plants to complete the last quadrat). At each elevation nine to 11 transects (length = 5 m, spacing > 5 m) were checked for ants depending on plant density;
- b) ‘quantitative plant assessment’: during ‘altitudinal diversity assessment’ the number of plants within the transects were recorded and classified by absolute plant height and stem diameter;
- c) ‘nest collection’ between 600 m and 1140 m in 1997 and 1998: an additional 900 plants per elevation were checked carefully for ant nests (plant height > 50 cm; ant nests occurred only very rarely on plants < 50 cm). Depending on plant density nests were collected along six to nine transects of 10 m length (spacing > 3 m);
- d) ‘potential nesting space assessment’ between 600 m and 1140 m in 1997 and 1998: during ‘nest collection’ potential nesting sites (dead wood) were recorded and categorised as in the GS (see above).

It was not possible to record the abundance of ants in LV in a fully standardised manner.

Other methods applied and mentioned in the total species list for the sake of completeness (see Electronic Appendix) are not described here, since they are not relevant for the focus of the paper. They will be presented in future articles.

Taxonomy

All ant specimens were identified to genus (Bolton 1994) and sorted to morphospecies (hereafter ‘species’). For body-size comparisons the mean length of the alitrunk of each species was determined. In the case of dimorphic species we measured the alitrunk of the more abundant minor workers and in polymorphic species we used the most frequently sampled worker caste. Voucher specimens are deposited at the University of Würzburg, Germany, at the collection of Kinabalu Headquarters of Sabah Parks, Malaysia and at Borneensis, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah.

RESULTS

Temperature

At the East Ridge the mean temperature lapse-rate of the total data set was $0.61 \pm 0.03^\circ\text{C}$ per 100 m increase in altitude in GS and $0.60 \pm 0.04^\circ\text{C}$ per 100 m in LV. However, on a finer spatial scale the temperature data showed differing curves with

increasing altitude: while mean temperature decreased steadily on the ground, it followed a more stepwise course in the LV (Fig. 1). The mean temperature maxima and minima in the LV (Fig. 2). temperature decline differed over time due to seasonal influences (Fig. 1), as did the mean temperature maxima and minima in the LV (Fig. 2).

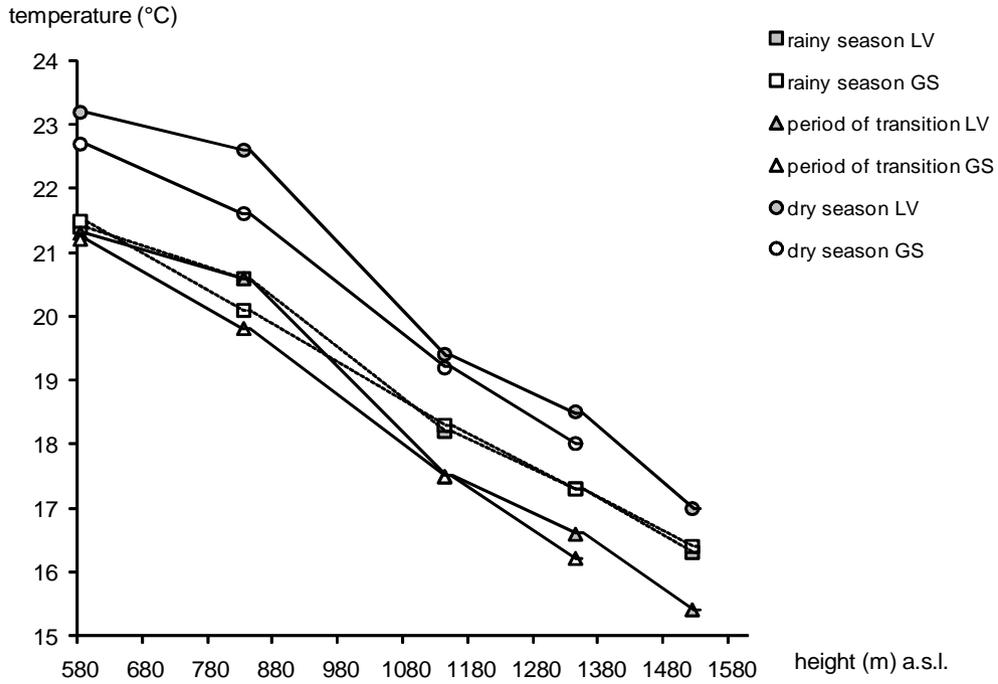


Fig. 1. Decrease of mean temperature 2 cm above the ground (GS) and at 2 m height in the lower vegetation (LV) during the rainy season, a period of transition and the dry season along the East Ridge (580 m to 1340 m a.s.l.), Poring Hot Springs, Sabah, Borneo.

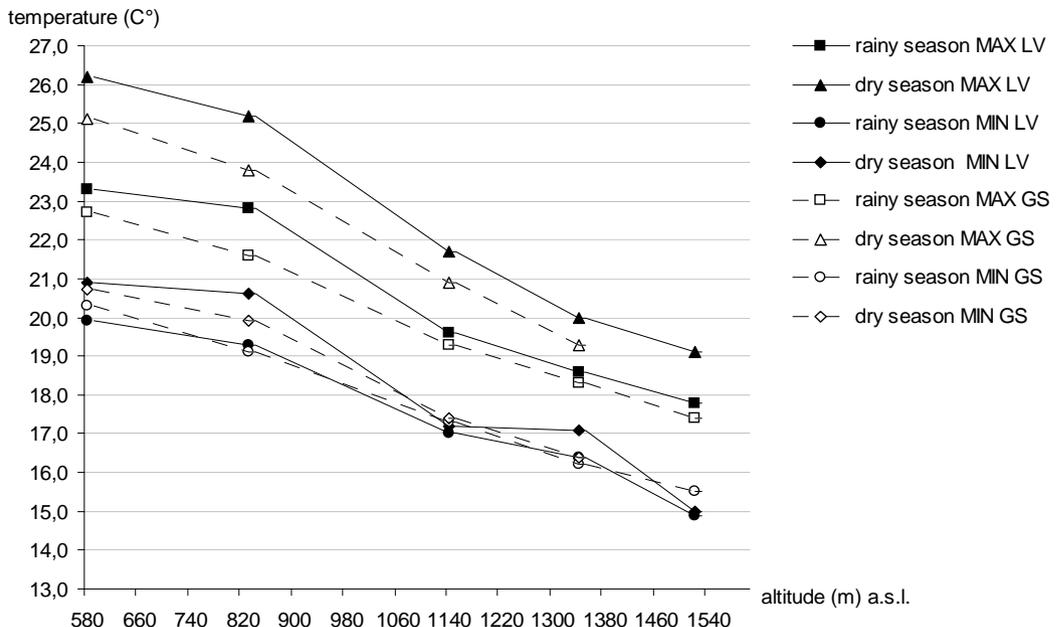


Fig. 2. Decrease of mean MAX and MIN temperatures in 2 m height in the lower vegetation (LV) and on the ground stratum (GS) during rainy season and dry season along the East Ridge (580 m to 1340 m a.s.l.), Poring Hot Springs, Sabah, Borneo.

In both strata and all seasons the variation in daily temperature diminished with increasing altitude, but this effect was less pronounced during the rainy season: for example the mean daily MIN/MAX temperature difference in the GS was about 2.5 °C at 580 m and 2°C at 1140 m; during the dry season the difference was about 5–6°C at 580 m and about 4°C at 1140 m.

Humidity

Although the relative humidity was expected to increase with decreasing temperature we could not detect any trend along the gradient within the lowland forest (580 m - 1140 m a.s.l.). In May and June 1997 the relative humidity oscillated between 90% and 100% in the GS and between 80% and 90% in the LV. During June and July 1998 a reduction in mean humidity of c.10% was observed in both strata.

However, from about 900 m there was a distinct increase in the frequency of fog, accompanied by a strong increase in moss

abundance. At 1520 m mosses and epiphytes covered the trees densely from ground to tree crown. Here clouds could remain all day, especially during the rainy season.

Ant species composition and diversity

Including all methods and ad-lib ok sampling we collected 37,997 ant specimens representing 376 species from 65 genera and 10 subfamilies in total (see Electronic Appendix).

The standardised ‘altitudinal diversity assessment’ (580–1520 m) within the two strata revealed 277 species in 56 genera and 8 subfamilies. It revealed a distinctly different composition of subfamilies for the two strata (Table 2). The species similarity between the ant communities of each pair of altitude points was expressed as the Sørensen Index (Magurran 1988; Table 3). The ground ant assemblages shared about half of their species with the neighbouring altitude point (respective distance c. 200–300 m) up to 1340 m. The species similarity drops, however, to 19-31%

Table 2. The taxonomic composition of the ant communities on the ground (GS) and in the lower vegetation (LV) at Poring Hot Springs, Sabah, Borneo. Of each subfamily the species number (n) and proportion (%) is given.

Ant subfamily	Species (n) GS	Species (%) GS	Species (n) LV	Species (%) LV
Myrmicinae (M)	117	55.5	29	37.2
Formicinae (F)	26	12.3	21	26.9
Ponerinae (P)	51	24.2	3	3.85
Dolichoderinae (D)	12	5.7	22	28.2
Cerapachyinae (C)	5	2.3	3	3.85
Σ	211	100	78	100

Table 3. Taxonomic similarity (%) of the ant communities in the ground stratum (GS) and the lower vegetation (LV) at different heights along the East-Ridge, Poring Hot Springs, Sabah, Borneo.

GS	580 m	830 m	1140 m	1340 m	1520 m	LV	580 m	830 m	1140 m	1340 m	1520 m
580 m	-	53.3	30.9	16.0	7.1	580 m	-	39.4	22.2	16.0	0.0
830 m		-	45.8	25.0	8.4	830 m		-	29.1	19.6	0.0
1140 m			-	45.1	19.4	1140 m			-	41.2	9.1
1340 m				-	32.7	1340 m				-	11.1
1520 m					-	1520 m					-

when comparing the community of one altitude point with that of the second-closest point (distance c. 400–500 m). The species turnover in the LV tended to be stronger than on the ground. In both strata the species turnover between 1340 m and 1520 m was proportionately the highest, but note that we collected only three species in the LV at 1520 m.

Of only 13 ant species found in both strata, each was collected at only a single altitude point. However, the number of ant species found in both strata increased slightly up the slope: one at 580 m, three at 830 m, five at 1140 m and four at 1340 m (none at 1520 m). Hence, species similarity between strata increased with elevation: 1.3% of all species at 580 m, 5.0% at 830 m, 13.2% at 1140 m and 20.5% at 1340 m.

Species decline

We found significant differences in the pattern of decline of ant species richness on the ground and in the lower vegetation (Fig. 3). While the GS species number decreased quite steadily up to 1340 m (580 m = 118 sp., 830 m = 89 spp., 1140 m = 61 spp., 1340 m = 25 spp., and 1520 m = 23 spp.),

the curve of the species number in the LV shows a more step-wise decline (580 m = 35 spp., 830 m = 31 spp., 1140 m = 15 spp., 1340 m = 14 spp., and 1520 m = 3 spp.). This difference is rather distinct: while the ground species number decreased significantly between 580 m and 830 m (Chi square test with Bonferroni correction on this and the following results, $\chi^2 = 4.06$, $P < 0.05$) as well as between 1140 m and 1340 m (Chi square test, $\chi^2 = 15.1$, $P < 0.001$), the species number in the LV did not differ significantly in any adjacent-altitude comparison. The opposite situation is obvious between 1340 m and 1520 m: the species number in the LV decreased significantly (Chi square test, $\chi^2 = 7.12$, $P < 0.01$), but stayed nearly the same on the ground (Chi square test, $\chi^2 = 0.08$, $P = 0.77$). Only the decline between 830 m and 1140 m is significant in both strata (Chi square tests, GS: $\chi^2 = 5.23$, $P < 0.05$, LV: $\chi^2 = 5.57$, $P < 0.05$).

On the ground we also compared the decline of ant species number and ant abundance (Table 4). For this comparison we estimated the total number of individuals and the total number of species at each altitude respectively gained by the Winkler method. The abundance declined much faster than the number of species: at 580 m

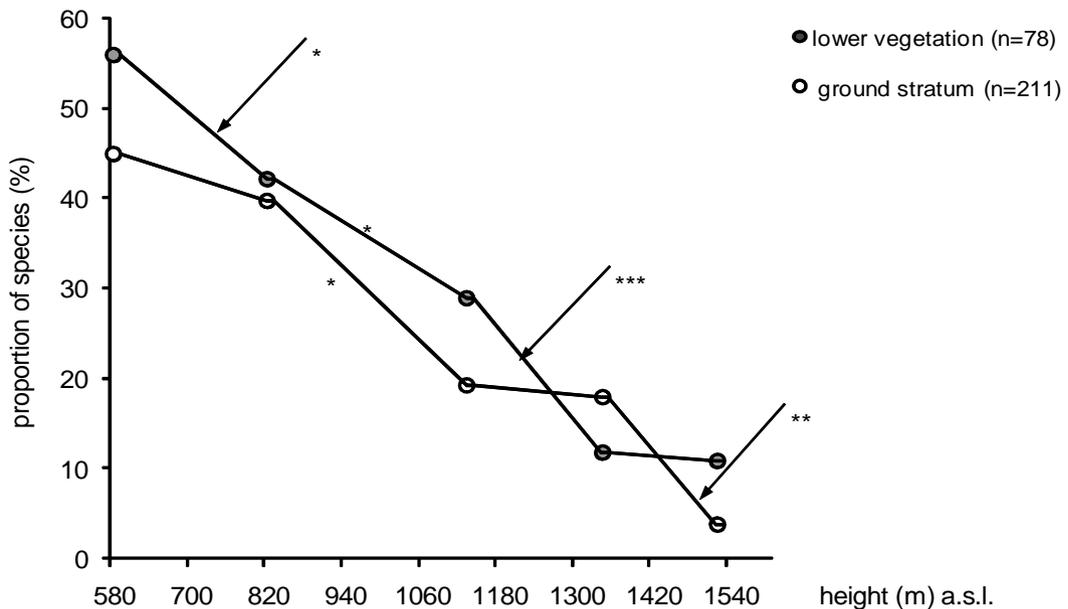


Fig. 3. Ant species decline (proportion of total species number (%)) on the ground and in the lower vegetation along the altitudinal gradient on the East Ridge (580 m to 1520 m a.s.l.), Poring Hot Springs, Sabah, Borneo. For each stratum, each difference in species number (n) between neighbouring altitudes was tested for significance (\pm : * = 0.05, ** = 0.01, *** = 0.001). The data points are connected to highlight the different mode of decline in the two strata.

Table 4. Decrease in species richness (proportion (%) of total species number, $n = 317$) and abundance (proportion (%) of total abundance, $n = 4919$) of ground ants along the East-Ridge, Poring Hot Springs, Sabah, Borneo.

	580 m	830 m	1140 m	1340 m	1520 m
Ant individuals (n / %)	2538 / 51.6	1501 / 30.5	438 / 8.9	258 / 5.2	184 / 3.7
Ant species (n / %)	118 / 37.2	89 / 28.1	62 / 19.6	25 / 7.9	23 / 7.3

37.2% of the total number of species was recorded, and 51.6% of the total number of individuals, while at 1140 m we found 19.6% of the total number of species and only 8.9% of the total number of individuals.

This steep decline in ground-ant abundance seems to influence the intra-site beta diversity. When comparing the samples within each altitude point, similarity decreases among the lowland forest samples: 580 m = Sorensen Index $57.1 \pm 2.7\%$, 830 m = $26.7 \pm 6.1\%$ and 1140 m = $20.4 \pm 7.7\%$ (montane forest: 1340 m = $43.5 \pm 5.2\%$ and 1520 m = $47.1 \pm 11.5\%$).

Temperature and species decline

Within both strata temperature and species richness were closely correlated, but between the strata the pattern differed slightly (Figure 4): in the GS the decline of temperature and species richness runs straight downwards (linear regression, $r^2 = 0.975$, $P < 0.02$, $F = 119$), while in the LV both parameters decline in a more stepwise manner (linear regression, $r^2 = 0.985$, $P < 0.01$, $F = 194$).

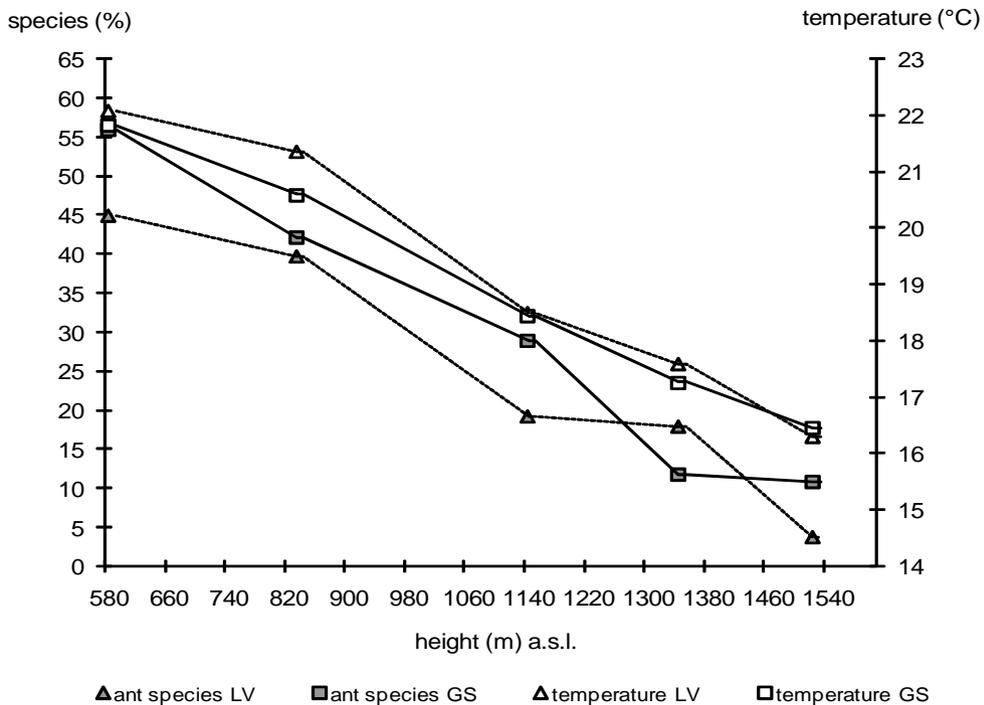


Fig. 4. Decline in ant species richness (proportion of total species number (%), left scale) and the mean temperature gradient over all seasons ($^{\circ}\text{C}$, right scale) in the ground stratum (GS) and in the lower vegetation (LV) along the East Ridge, Poring Hot Springs, Sabah, Borneo. The data points are connected to highlight the different mode of decline in the two strata.

Ant occurrence in the lower vegetation

The quantitative plant assessment revealed that 95% of LV plants ($n = 2038$) had a stem diameter of $d < 2$ cm and a height of $d < 5$ m. We distinguished a herb layer ($d < 0.5$ m, $n = 986$) and a shrub layer (0.51 to 5 m, $n = 1052$). The abundance of the two classes showed a strong negative correlation along the slope (Pearson correlation: $r = -0.989$, $P < 0.001$). While the abundance of herbs decreased significantly from 580 m to 1520 m (Chi square test, $\chi^2 = 14.3$, $P < 0.001$), the shrub layer increased correspondingly ($\chi^2 = 11.6$, $P < 0.001$). Moreover the plant density was significantly higher at 1340 m than at 1140 m (two-tailed t -test, $t = -2.56$, $P = 0.015$, Table 5).

Along the slope 222 out of 2038 plant individuals were visited by ants during sampling. The number of visited plants (Table 5) decreased distinctly from 580 m to 1140 m (Chi square test, $\chi^2 = 6.57$, $P = 0.01$ and from 1340 m to 1520 m (Chi square test, $\chi^2 = 31.7$, $P < 0.001$; Table 5). Ants were more frequent foraging on shrubs ($n = 162$, 74.3%) than on herbs ($n = 56$, 25.7%; $P < 0.001$).

At 580 m ants were regularly encountered on plants: at least on every 11th plant an ant was recorded (Table 5). This pattern changed uphill. Although we collected more ant individuals at 1340 m than at 1140 m, at 1340 m the variation in ant encounter rate was much broader. This might suggest a patchier ant distribution uphill.

Nesting space

A 'nest' was defined by the presence of a queen, brood and/or alates or by a minimum five workers in a cavity that we considered to represent a suitable nesting site. In cases where more than one nest of one species was found per 0.25 m² plot (GS) or per plant (LV), we assumed a polydomous nest structure and counted only one nest, since we wanted to use nest numbers as a proxy for colony numbers. However, we cannot exclude the possibility of having underestimated monodomous colonies.

GS: In total we found 179 nests of 67 species, from 25 genera and 6 subfamilies (Fig. 5). Four nest types were identified: nests in dead wood (DW; $n = 131$), nests in topsoil (TS; $n = 26$), nests in leaf litter (LL; $n = 12$) and nests within humus (HL; $n = 10$). Hence DW turned out to be the most important nesting space (73.2%). 75% of DW nests were situated in the humus layer.

Total nest density remained nearly the same between 600 m (11.5 ± 1.2 nests m⁻²) and 1000 m (10.3 ± 5.1 nests m⁻²), but decreased significantly between 1000 m and 1140 m (1.5 ± 0.6 nests m⁻²; $\chi^2 = 25.1$, $P < 0.001$). Though the number of nests remained constant between 600 m and 1000 m their spatial distribution changed considerably. While the number of nests in TS, LL and HL strongly decreased, nests in DW increased proportionately (600 m: 57.8%, at 1000 m: 84.6%; Fig. 5). At 1140 m

Table 5. Plant density (n / m²) and parameters of ant – plant interaction at the East-Ridge (580 m – 1520 m), Poring Hot Springs, Sabah, Borneo (* = evaluation of only four transects with ants - another six were without ants).

	580 m	830 m	1140 m	1340 m	1520 m*
Plant density (n / m ²)	7.7 ± 1.3	8.1 ± 2.1	7.7 ± 1.8	9.0 ± 2.1	9.3 ± 1.5
Plants (n) visited by ants	69	58	42	47	6
Range of examined plants (n) before encounter an ant	2.9 - 11	3.3 - 22.5	4.2 - 29	2.7 - 77	27 - 48
Mean of examined plants before encounter an ant	6.3	9.0	13.7	18.8	30.0

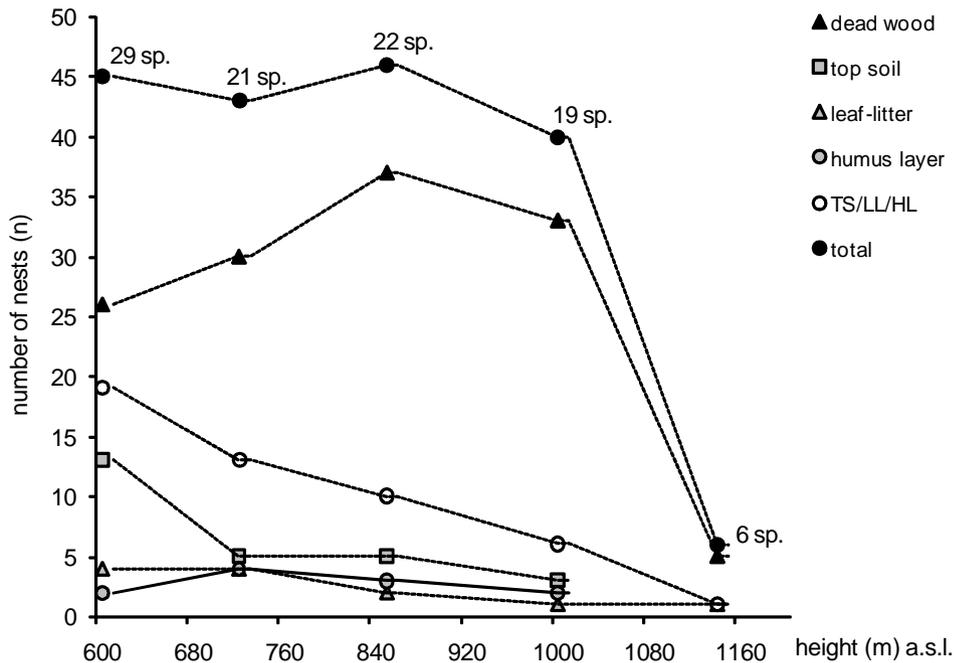


Fig. 5. Abundance (n) of ant nests in the ground stratum along the East Ridge, Poring Hot Springs, Sabah, Borneo (580 m - 1140 m a.s.l.): TS/LL/HL = total number of ant nests in top soil, leaf litter and humus layer; total = total ant nest number (graph) and respective total species number.

too the majority of ant nests were found in DW (83.3%). Since none of the species ($n = 67$) changed nesting preference along the altitudinal range of its distribution, the increasing relative abundance of small (in body size) and polydomous ant species are suggested to be responsible for the relative increase of nests in dead wood: at 600 m 25%, at 720 m 62% and at 850 m 82% of the nests were *Pheidole* or *Carebara* species with an alitrunk size of 0.5-0.6 mm.

LV: In total we found 173 nests of 51 species, from 16 genera and 5 subfamilies (Fig. 6). Five nest types were distinguished: nests in dead wood (DW; $n = 119$), carton nests (CN; $n = 42$), nests in living wood (LW; $n = 8$), leaf nests (LN; $n = 3$) and silk nests (SN; $n = 1$). Again DW represented the most important nesting space (69%). CN were the second most abundant nest type (24%).

Between 600 m ($n = 44$) and 1000 m ($n = 37$) the nest number decreased marginally (mean up to 1000 m: one nest per $5.1 \pm 0.7 \text{ m}^2$), but significantly decreased from 1000 m to 1140 m ($n = 19$) (mean: one nest per 8.2 m^2 ; $\chi^2 = 5.79$, $P < 0.05$). All nest types occurred until 1140 m and

their distribution along the ridge showed no distinct pattern (Fig. 6). None of the species ($n = 51$) in the LV changed its nesting preference with changing altitude.

Potential nesting space

Potential nesting space was assessed on GS plots ($n = 16$) or along LV transects during nest collection. The depth of leaf-litter and humus layer were measured frequently ($n = 6$ per plot) and the mean value was noted for each plot ($n = 80$). Mean LL depth ($2.7 \pm 0.7 \text{ cm}$) and volume ($8.0 \pm 2.5 \text{ litre m}^{-2}$) showed no significant trend up the slope. The depth of the HL showed no change up to 850 m ($1.7 \pm 1.2 \text{ cm}$), but increased significantly to $4.6 \pm 4.0 \text{ cm}$ at 1000 m ($t = 2.62$, $P = 0.019$); two plots were not taken into account (out of $n = 16$) since their HL exceeded 20 cm depth and the total depth could not be determined. At 1140 m the HL exceeded a depth of 20 cm on six plots, and the remaining ten plots had a depth of $5.8 \pm 2.9 \text{ cm}$. Above 1140 m the HL steeply increased, reaching a mean depth of 40 cm at 1340 m (Kitayama 1992).

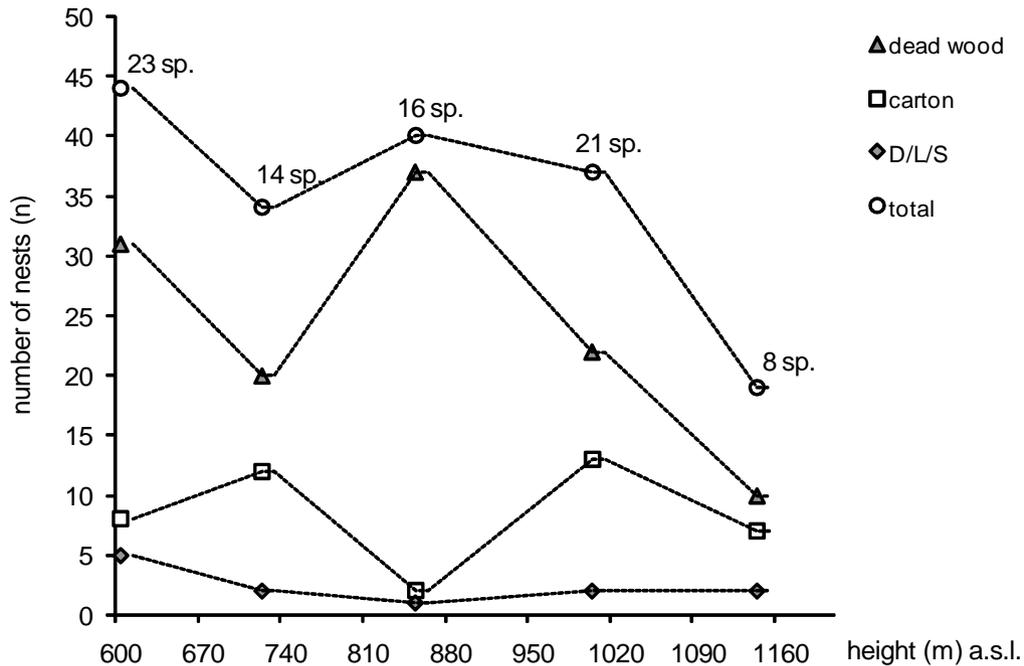


Fig. 6. Abundance (n) of nests in the lower vegetation along the East Ridge, Poring Hot Springs, Sabah, Borneo (580 m - 1140 m a.s.l.): D/L/S = comprises domatia, leaf nests and silk nests; total nest number (graph) and respective total species number.

Between 600 m and 850 m the solidity of the topsoil increased highly significantly (Chi square test, $\chi^2 = 16.8$, $P < 0.001$); at all plots at 850 m soil consisted of very hard clay. Uphill the solidity was reduced due to a higher content of sand. Uphill dead wood ($n = 4675$) showed no significant changes in quantity or quality in either strata. Twigs ($n = 4298$) were much more abundant than sticks ($n = 377$).

In the GS 39.7% ($n = 1854$) and in the LV 57.9% ($n = 841$) of total dead wood pieces were potentially suitable as nesting space for ants. Ants colonised sticks distinctly more often than twigs: 87.6% ($n = 114$) of the GS ant nests occurred in sticks (Chi square test, $\chi^2 = 74$, $P < 0.001$) as did

66.7% of the LV nests ($n = 84$; Chi square test, $\chi^2 = 14.0$, $P < 0.001$). Nearly every second or third stick harboured an ant nest (Table 6).

Diacamma study

Between 650 m and 950 m the mean *Diacamma* nest distance increased significantly (from 5.80 ± 1.40 m, $n = 87$, to 8.0 ± 1.80 m, $n = 71$; $t = -8.27$, $P < 0.001$).

The collected prey items (animal, plant, fungal and faecal items) indicated *Diacamma* sp. to be omnivorous. At each elevation about 60% of the collected faunal prey items (total $n = 20$ at 650 m, $n = 21$ at 830 m and $n = 20$ at 950 m) could

Table 6. Proportion (%) of suitable twigs (e" 0.5 cm to d" 5 cm) used as nesting space by ants in the ground stratum (GS) and in the lower vegetation (LV) along the East-Ridge (600 m – 1140 m), Poring Hot Springs, Sabah, Borneo.

	600 m	720 m	850 m	1000 m	1140 m
Twigs GS (%)	32.3	33.3	47.2	26.5	13.2
Twigs LV (%)	28.4	16.4	30.1	18.2	9.6

be identified to order or family level. Faunal prey comprised various arthropod taxa, but a preference for termites and ants was apparent. While at each of 650 m and 830 m five (25%) of the identified prey items were termites, at 950 m no termite was captured during the 12 hours of observation. The proportion of ant prey remained approximately the same (24% at 650 m, 20% at 830 m, 24% at 950 m).

At 850 m the 36 prey items were captured in 5 h. At 950 m significantly fewer prey items ($n = 15.5$ per 5 h; $\chi^2 = 8.16$; $P = 0.01$) were captured within the same time span.

DISCUSSION

Species decline

The basic approach in investigating the factors causing the decline in ant species richness with increasing elevation was to compare the mode of decrease in both the GS and LV stratum. We found significant differences in the decline of ant species richness on the ground and in the lower vegetation (Fig. 3). The two patterns agree with two other studies in this area (East-Ridge, Mt. Kinabalu): Brühl *et al.* (1999) recorded a steady decrease of ant species richness on the ground and U. Simon (Wuerzburg University, unpubl. data, pers. comm. 2000) a comparable stepwise decline within the tree canopy layer between 830 m and 1520 m. From the Philippines a different ant species richness decline in GS and LV was reported by Samson *et al.* (1997). Our study aimed at elucidating this different decline pattern in the two strata: are there different factors affecting ant species richness or do similar factors affect ants differently in each stratum?

Temperature

We recorded a much less uniform and steady decrease of temperature along the altitudinal gradient than expected: surprisingly we found a nearly stepwise decline of the mean temperature in the LV (Fig. 1), which seemed mainly to be caused by a decline in the mean minimum temperature (Fig. 2). The close correlation between falling average temperatures and declining ant species richness in both strata implicates temperature as the major causal factor for the decrease of ant species richness with increasing elevation. However, this close

correlation does not tell us whether lower temperatures affect the ant species' richness in a direct or an indirect way by modulating other vital parameters.

Many studies prove direct influences of temperature on ants. For example activity, brood development and nest location of ants are influenced by the microclimate (Bernstein 1979; Torres 1984; Hölldobler & Wilson 1990; Kaspari 1993; Roces & Nunez 1995). Temperature heavily and directly influences the growth rate of ant colonies (Porter 1988, Porter & Tschinkel 1993, Kaspari 2005). Consequently with increasing altitude a reduced growth rate would be expected, and this is supported by our results: between 580 m and 1140 m the total abundance of ant leaf-litter ants declined much more steeply than the corresponding number of species (Table 4), while nest density remained the same (Fig. 5) and within-altitude beta-diversity decreased. These abundance and density patterns point to a decrease of colony size, finally resulting in the disappearance of many species above a critical altitude, but our data are insufficient for statistical testing.

Ants are strongly thermophilic. Petal (1978) showed that none of 19 ant species from temperate and tropical regions had nest temperatures $< 19^\circ\text{C}$. Hölldobler & Wilson (1990, p. 370) generalise this pattern and state that ants 'function poorly below 20°C and not at all below 10°C ' with the exception of a very few cold-temperate species. By applying these taxon-specific temperature barriers to our data set, it can be shown that the steepest decline of ant species richness coincides with the maximum temperature permanently dropping under 20°C : in the GS between 1140 m and 1340 m and in the LV between 1340 m and 1520 m (Fig. 2).

Due to the relatively low daily and yearly temperature changes in tropical regions, tropical species at a given altitude live under constant conditions throughout the year. This prompted Janzen's (1967) presumption that tropical species have adapted to narrow temperature ranges restricting the species' distribution to a small altitudinal range. According to our data the daily temperature spectra of two altitude points separated by ≈ 500 m overlapped only marginally during the dry season in both strata. Between those altitudes the species turnover was $\approx 75\%$ (Table 3).

Foggy and cloudy conditions occurred more frequently with increasing altitude preventing any larger-scale heating up by direct radiation which otherwise could have temporarily overridden the tight coupling of temperature with altitude. An extrapolation of our data revealed a mean temperature of about 11.7°C at 2300 m with daily temperature changes probably less than at 1520 m ($\pm 1.5^\circ\text{C}$). Hence, at these altitudes the assumed lower temperature limit of 10°C (see above) is nearly reached, which might explain the upper limit of ant distribution at about 2300 m in the tropics.

In summary, direct temperature impact on ants seems to be a vital factor. Further results of our study, however, suggest additional factors to contribute to the steep reduction of ant species richness with increasing altitude.

Humidity

Foggy conditions increase with altitude above 900 m on Mt. Kinabalu until a broad cloud belt occurs regularly for most of the day between ca. 1800-2000 m and 2600 m (Burnham 1974; Frahm *et al.* 1996; Kitayama *et al.* 1999). In these conditions waterlogging of soils becomes increasingly frequent, negatively affecting foraging activities and nesting possibilities. However, since our humidity logger could not sufficiently resolve the range between 90% and 100% we cannot present quantitative data and conclusions remain speculative.

Nesting space

Within the lowland forest we recorded a constant nest density up to 1000 m a.s.l. within both strata, while the distribution of nest types changed up the slope with the first step from 580 m to 830 m. Since none of the ant species changed its nesting habits with increasing altitude this effect might be caused either by changing abiotic conditions or a reduction of certain types of nesting space.

While depth and volume of the leaf-litter layer did not differ within the lowland forest, solidity of the topsoil increased between 580 m and 850 m and depth of the humus layer increased above 850 m. These changes might be responsible for the decline of topsoil nests (Fig. 5).

Dead wood, especially small sticks, turned out to be the most important nesting space (Table 6), but no apparent changes in abundance, hollowness or strength up to 1140 m could be detected. Therefore the relative dominance of dead-wood nests might be caused by the dearth of other nesting resources and dead-wood specialists may increase their nest abundance.

A highly significant drop in ant nest abundance in dead wood occurred between 1000 m and 1140 m. Since neither quantity nor quality of this potential nesting space changed, factors other than nesting space must be relevant for the drop in nest numbers. We suspect a direct impact of temperature and humidity to be the main reason for this effect. About 75% of nests in dead wood were found in the humus layer, which seems to provide an especially balanced microclimate for ants. Along a vertical gradient of only about 6 cm (leaf-litter depth c. 2 cm plus humus layer depth c. 2 cm plus c. 2 cm into the topsoil) the daily temperature variation was reduced by more than 2°C ($\pm 1^\circ\text{C}$). At 2 cm soil depth the mean minimum temperature was about 1°C higher than 2 cm above the ground surface; this temperature difference is equivalent to a 200 m increase in altitude. Hence dead wood within the humus layer should be more attractive than within the leaf litter layer (where only 21% of the dead-wood nests were situated). Moreover nests within the humus layer are better protected from rain and desiccation than nests in the leaf litter. These comfortable conditions seem to apply to most arthropods: Fittkau & Klinge (1973) assume that half of the total animal biomass lives in the upper 10 cm of the ground stratum. At higher altitudes the situation worsens and most of the invertebrates are forced to live nearer the surface due to waterlogging (Collins 1980).

In our study about 81% of all collected dead-wood nests were soft and probably no longer watertight. The increasingly frequent and prolonged periods of wetness from about 900 m a.s.l. uphill might be causative of the drop in small dead-wood ant nests between 1000 m and 1140 m (Fig. 5).

In the lower vegetation the total nest number stayed nearly the same up to 1000 m, but was reduced at 1140 m. No distinct pattern of nest type distribution could be observed and hence no indication of nesting space restriction could be

identified. Also no changes in quantity or quality of dead wood occurred and no problems due to wetness can be assumed. The most plausible explanation for the drop in nest abundance between 1000 m and 1140 m in the LV is a direct impact of temperature and additionally an impact of food scarcity, associated with plant species turnover at the family level (for further details see below). However, within the lower montane forest (> 1200 m a.s.l.) humidity and scarcity of nesting space in the LV may become important, since tree crown volume becomes largely reduced. The ants from the canopy and from the lower vegetation may increasingly compete for living and nesting space.

Nutrition

The foraging behaviour of *Diacamma* sp. at different altitudes indicates the progressive scarcity of food in the GS uphill: the distances between the colonies increased significantly and the foraging efficiency decreased conspicuously. For the same number of prey items the capture time differed considerably. In part this might be traced back to the lower abundance of termites and ants – the preferred prey of *Diacamma* sp. at lower altitudes – with increasing altitude. Ants and termites have been found to comprise c. 68% (Fittkau & Klinge 1973) to 75% (Beck 1971) of the insect biomass within New World lowland tropical rain forests. With increasing altitude the abundance of ants (Table 4; Brühl *et al.* 1998) and the biomass of termites (Collins 1980; Jones 2000) decrease distinctly from lowland to montane forest.

Within the LV we have no concrete data about the distribution of the ant community's nutritional resources, but the results of the plant zonation and the ant diversity assessments facilitate some provisional conclusions. Ants foraging in the vegetation primarily feed on plant sap, either directly (e.g. at extrafloral nectaries, EFN) or indirectly (via trophobionts: Buckley 1982; Tobin 1991; Blüthgen *et al.* 2000). Elsewhere trophobionts have been found to be monopolised by a few dominant ant species (Blüthgen *et al.* 2000; Dejean *et al.* 2000) and hence may be of minor importance as a general food resource for most ant species in the LV. On the other hand EFN resources are available for many different ant species (Schemske 1982; Oliveira & Brandao 1991;

Blüthgen *et al.* 2000) and strong correlations have been found between plant sap excretions, ant abundance, and species richness on EFN plants (Bentley 1976; Keeler 1979; Blüthgen *et al.* 2000; Apple & Feener 2001). Therefore the EFN plant abundance and distribution is another possible influence on ant species richness along elevational gradients.

At the East Ridge an almost-total plant family turnover occurs between lowland forest and montane forest (Kitayama 1992). Nearly all plant families at the East Ridge that are known to have species with EFN (applying lists of EFN plants from Koptur 1992, Fiala & Linsenmair 1995) diminish from lowland to montane forest (starting at 900 m a.s.l.). From lowland to montane forest the abundance of ants on plants decreased significantly, except between 1140 m and 1340 m. Here a slight increase was recorded, which might be attributed to the simultaneous significant increase of plant density (Table 5) and to the species richness peak of vascular plants (Grytnes & Beaman 2006). Initial surveys from our team suggest very low abundance of EFN plants at higher altitudes at Mt. Kinabalu (unpubl. data, pers. obs. B. Fiala).

Hence, decreasing food supply seems to be another plausible factor for the decline in ant species richness with altitude, supported by the uphill increase in proportion of ant species foraging in both strata.

CONCLUSIONS

Our results demonstrate that the steep decline in ant species richness with increasing altitude is correlated with several factors: (1) temperature decrease, (2) high humidity (comprising the relative humidity of the air, fog, rain and water logging), (3) scarcity of nesting space and (4) scarcity of nutritional resources. The negative impact of each of these factors on ground and vegetation ants increases in a different manner along the altitudinal gradient (Fig. 7). Through the interplay of these factors, synergistic effects may arise leading to more severe living conditions. Overall we consider temperature to be the fundamental factor modulating other abiotic and biotic resources. However, only further experiments will reveal the definite evidence for which the present study provides the foundation.

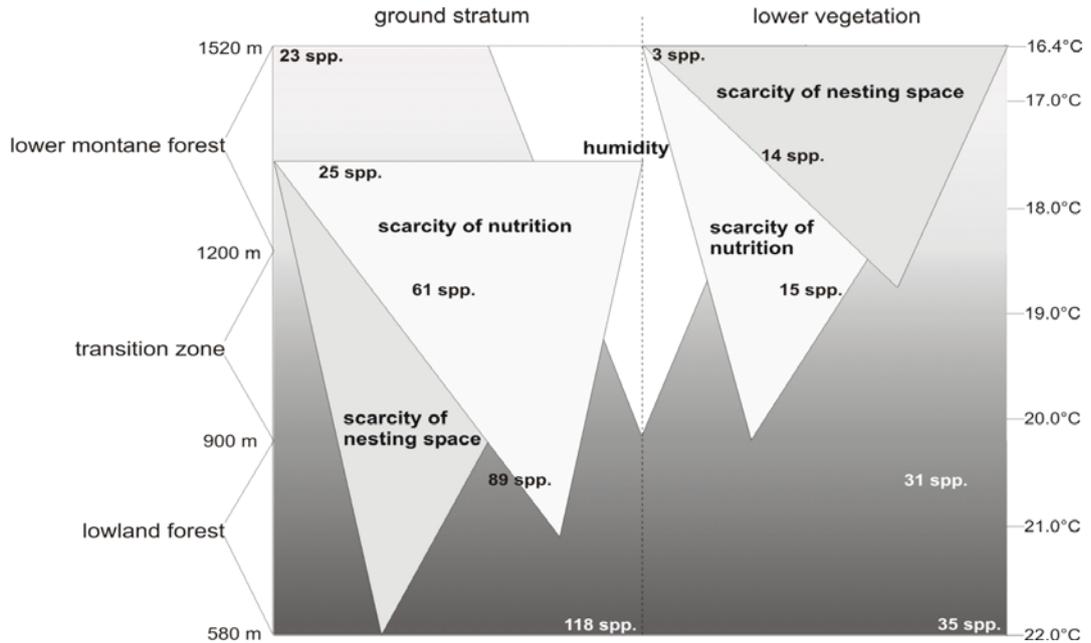


Fig. 7. Conceptual (qualitative) scheme of the most important factors influencing the ant species richness with increasing altitude (left scale) along the East Ridge (Mt. Kinabalu, Borneo) and visually summarises their impact separately for the ground stratum (left side) and the lower vegetation (right side): temperature (right scale and background) as fundamental, underlying factor modulating humidity, scarcity of nutrition and scarcity of nesting space directly or indirectly. Moreover the forest zones (left scale) and the numbers of ant species collected at certain altitudes (580 m, 830 m, 1140 m, 1340 m and 1520 m) in both strata are given.

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