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# Partitioning the impact of abiotic factors and spatial patterns on species richness and community structure of ground ant assemblages in four Bornean rainforests

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Contrasting theories have been proposed to explain the structure of ecological communities. Here, we studied the impact of environmental factors and spatial patterns on ground-foraging ant communities in four different forest types of Gunung Mulu National Park in Sarawak, Borneo, Malaysia. Forest types differed in their environmental parameters and were inhabited by distinct ant communities, with various indicator species characteristic for single forest types. Three environmental parameters, soil volume, number of trees and amount of leaf litter, had the most influence on ant communities. Spatial patterns were correlated with environmental parameters and also influenced ant communities. Environmental parameters influenced community composition only moderately ($r^2 = 0.14$), but had a high impact on species richness ($r^2 = 0.44$). Spatial patterns explained only a small fraction of the total variance in species patterns, while much of the residual space in the ordination space of ant community patterns remained unexplained. We conclude that environmental parameters shape the number of niches within a tropical soil habitat, but identities of species that occupy those niches are accounted for by other factors like competition, traits and neutral processes that may further reduce unexplained variance in species ordination.

Main questions in community ecology are how species are recruited from a pool of regional species to form local communities and whether the structure of local communities differs from null expectations (Gotelli and McCabe 2002).

The large number of species in tropical ecosystems seems to be in conflict with traditional niche theories and the mechanisms that sustain these highly diverse communities need to be explained. Insects are the most species-rich eukaryotic animal taxa (Basset 2001); among them, ants are the dominant group with a large diversification in the tropical rain forests around the globe (Longino et al. 2002, Dunn et al. 2009). For some tropical ant communities, random species assembly has been reported from the diverse arboreal ant communities in the lower canopy layer of Bornean primary forests (Floren and Linsenmair 2005). In contrast, abiotic factors such as microclimate (Kaspari 1993), soil type (Bihn et al. 2008) and flooding (Vasconcelos et al. 2010) influence ant community patterns in the Neotropics. Spatial patterns are a further factor that might influence ant communities. Limited dispersal of gynes and habitat and environmental similarity of neighboring plots may cause positive spatial autocorrelation in ant communities and might also affect the statistical evaluation of community composition (Theunis et al. 2005, Legendre et al. 2009a).

The island of Borneo is especially rich in ant species, and has been the focus of several long-term studies on both arboreal (Floren et al. 2001), and leaf litter ants (Brühl et al. 2003). Tropical leaf litter communities appear to be structured by resource availability (Kaspari 1996b, Theunis et al. 2005). However, little is known about the mechanisms that generate and maintain such high levels of ant diversity of the tropical ground ant communities in primary forests. In this study we investigated the influence of environmental factors on the community composition of highly diverse ground ant communities in four contrasting types of natural primary forest in tropical Borneo. We quantified the influence of environmental parameters and distances between all the plots to assess their influence on the structure of tropical ant communities. In particular, we investigated the following predictions: 1) particular ant species are associated with particular habitats. 2) Environmental parameters govern the local composition of ant communities. 3) Spatial structure (distances between the plots) influences environmental parameters and ant communities.

## Materials and methods

### Study sites

The study was conducted in Gunung Mulu National Park (4°57′N, 114°47′E) in Sarawak (Malaysia) on Borneo between 5 April 2006 and 4 June 2008. The climate in the lowlands of this 528 $km^2$ large area is tropically wet with mean temperatures of ca 26°C and 4000–5000 mm rain $yr^{-1}$ (Sarawak Weather Service pers. comm.). The area of the Gunung Mulu National Park (Mulu NP) is covered with a diverse mosaic of tropical forests (Hazebroek and Morshidi 2001). We compared ground-foraging ant communities in the soil and leaf litter in four types of primary forests that co-occurred within a range of few kilometres. These sites were purposefully close to one another so as to minimize the effects of regional climate and biogeographic history. The four forest types are 1) alluvial forests (50 to 60 m a.s.l.) are inundated several times a year. The lower, more often flooded parts grow on gley soils from the Bijat-family, whereas the higher areas grow on podzolic or peaty soils (Proctor et al. 1983): alluvial forests in Mulu NP are rich in tree species and dominated by Leguminosae and to a lesser extend by Ebenaceae, Euphorbiaceae and Dipterocarpaceae. 2) Limestone forests (75–250 m a.s.l.) are found on steep terrain. Their shallow soils consist largely of mull humus (0–50 cm in depth), irregularly interrupted by acute limestone rocks. Dipterocarpaceae dominate these tree species-poor forests (Proctor et al. 1983). 3) Lowland mixed dipterocarp forest (200–300 m a.s.l.) grows on red-yellow podzolic soils with a substantial organic layer up to 15 cm. This species-rich forest type is dominated by Dipterocarpaceae that reach heights up to 57 m (Proctor et al. 1983). 4) Kerangas or heath forests (180–200 m a.s.l.) rise on terraces with sandy organic podsols. These forests are dominated by trees of the families Dipterocarpaceae, Guttiferaceae and Myrtaceae and have a medium richness of tree species (Proctor et al. 1983).

### Habitat description

In each of the four forest types, we established 20 evenly spaced plots along a 400-m transect (Fig. 1) by Winkler sampling according to the Ants of the Leaf Litter (ALL) protocol (Agosti et al. 2000), a conventional method sampling of ground ant communities. In both limestone and alluvial forest, we collected ten additional samples along a further 200-m transect (see Supplementary material Appendix S1 for a detailed description of sampling). As minimum requirement for independent leaf-litter samples Kaspari (1996a) and McGlynn (2006) propose distances of at least 5 m between the single plots. According to Agosti et al. (2000), we used transects with a distance of at least 20 m between plots. Despite of this large distance, we cannot exclude completely the potential for pseudoreplication since the largest ant species might have foraging ranges that exceed the distance between the plots.

Mounted voucher specimens of all species are kept in the ''AntBase.Net Collection'' of the Univ. of Ulm (ABNC), with Automontage photographs of most species being available via <www.antbase.net>. Identification of the ant genera was done with Bolton (1995). Details of species identification (55% of all species have been identified to species level) and results from the diversity study are described elsewhere (Mezger and Pfeiffer unpubl.). To describe each habitat, we measured 24 environmental parameters (Table 1). Eighteen of these parameters were quantified on a local level (one measurement per sample site). To measure understory vegetation complexity rather than vegetation coverage as expressed by traditional geobotanical methods (Mueller-Dombois and Ellenberg 1974), we developed a measurement scheme in which all plants in each of the plots were assigned a specific number of points according to the mean three-dimensional size of the respective plant types (seedling: 0.25 points, tree sapling: 1 to 4 points according to size, herbs and ferns: 1 point, small trees: 5 points and climbers: 1.5 points).

Living and dead trees were counted in a circle of 5 m around the sample site. To estimate canopy openness, we took a photograph (Coolpix 5900 compact camera, focal range 38 mm wide angle) of the canopy above the sample area and analysed it with Gap Light Analyzer software (Frazer et al. 1999). Top-soil samples were taken to analyse pH-values (Machery-Nagel test strips: accuracy 0.5 degrees). We calculated the mean carbon/nitrogen ratio for each plot from analyses of the nutrient concentration of leaf litter and top-soil (isotope mass spectrometer Delta Plus with Conflo III interface from Finnigan MAT; a NA1110 element analyser from CE-Instruments).

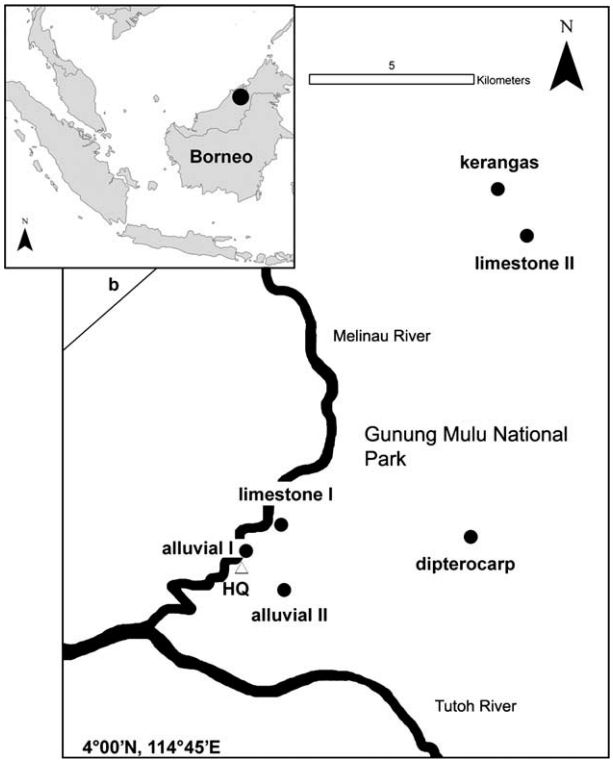


Figure 1. Location of the six transects in Gunung Mulu National Park. The position of the National Park's headquarter (HQ) is marked. This National Park is situated at the border (b) between Brunei (on the map to the north) and Malaysia. The coordinates on the map are those of the lower corner on the left. The inserted map shows the position of this National Park on Borneo.

Table 1. List of all environmental parameters, all being used for further analyses, except for "altitude", which covaried with other parameters. P-values indicate whether a significant difference occurred between the respective parameters within forest types (Kruskal-Wallace ANOVA). Regional parameters could not be tested. Parameters marked with 1 to 4 are those parameters that were unified by calculating a PCA.

| Parameter | Unit | Alluvial | Dipterocarp | Limestone | Kerangas | Average | p |
|---|---|---|---|---|---|---|---|
| Local parameters | | | | | | | |
| Canopy openness | % | 10.09±2.51 | 11.88±2.10 | 11.13±3.21 | 11.37±2.85 | 11.1±2.8 | n.s. |
| Vegetation density | points | 17.2±13.5 | 6.2±4.8 | 13.0±7.3 | 5.7±4.9 | 11.7±10.0 | 0.001 |
| Living trees | numbers | 9.6±2.4 | 11.6±3.0 | 6.9±1.8 | 12.1±3.7 | 9.6±3.3 | 0 |
| Dead trees | numbers | 1.0±0.7 | 0.9±0.6 | 1.0±0.7 | 1.2±0.7 | 1.0±0.7 | n.s. |
| Stones (at the surface)[1] | % | 1.3±4.0 | 0.1±0.5 | 14.9±10.0 | 0.4±1.2 | 5.0±8.8 | 0 |
| Rocks under top-soil[1] | % | 0.2±0.9 | 0.0±0.0 | 96.7±18.3 | 0.0±0.0 | 29.6±45.8 | 0.001 |
| Slope angle | ° | 3.5±4.3 | 17.0±14.6 | 20.3±12.8 | 21.1±21.0 | 14.6±15.2 | 0 |
| Leaf litter coverage | % | 91.2±8.5 | 94.8±9.7 | 91.7±11.2 | 82.5±10.9 | 90.5±10.7 | n.s. |
| Leaf litter thickness | cm | 1.7±0.8 | 2.8±1.3 | 3.5±1.4 | 1.9±1.0 | 2.5±1.4 | 0.001 |
| Dead wood <5 cm | numbers | 5.8±6.3 | 6.9±6.1 | 9.7±5.9 | 7.9±4.6 | 7.6±6.0 | n.s. |
| Small twigs | numbers | 15.8±6.8 | 15.2±3.6 | 14.9±7.3 | 13.1±5.1 | 14.9±6.1 | n.s. |
| Carbon/nitrogen ratio | | 17.1±4.4 | 24.1±1.0 | 21.7±1.7 | 26.7±1.2 | 21.7±4.4 | 0.001 |
| pH-value | | 4.3±0.2 | 3.5±0.2 | 5.5±0.7 | 3.2±0.1 | 4.3±0.9 | 0.001 |
| Depth of top-soil[2] | cm | 4.2±1.1 | 6.1±2.8 | 5.3±2.3 | 8.3±2.5 | 5.7±2.6 | 0 |
| Soil volume[2] | classes | 2.7±1.1 | 2.8±0.7 | 2.1±1.3 | 4.1±1.2 | 2.8±1.3 | 0 |
| Surface roots[3] | numbers | 0.3±0.6 | 0.2±0.6 | 1.1±1.4 | 1.3±1.1 | 0.7±1.1 | 0.003 |
| Root penetration[3] | classes | 2.1±0.8 | 2.3±0.9 | 3.4±0.7 | 3.5±0.4 | 2.8±1.0 | 0 |
| Number of invertebrates | numbers | 130±49 | 149±27 | 181±9 | 158±46 | 158±47 | 0 |
| Regional parameters | | | | | | | |
| Altitude (m) | m | 52 | 249 | 192 | 190 | 161±81 | * |
| Temperature top-soil[4] | °C | 24.03 | 23.85 | 23.89 | 23.55 | 23.86±0.16 | * |
| Phosphate (total) | mg $kg^{-1}$ | 258 | 320 | 446 | 267 | 330±81 | * |
| Leaf litter decay rate[4] | % | 28.0 | 23.9 | 25.4 | 26.7 | 26.1±1.5 | * |
| Microbial activity[4] | mpnx106 $g^{-1}$ | 1335 | 223 | 2998 | 1000 | 1555±1040 | * |
| Temperature above leaf litter[4] | °C | 24.8 | 23.6 | 24.48 | 24.1 | 24.33±0.44 | * |

Temperature and decay rates were obtained for each study plot on a regional basis. Temperature loggers (iButtons DS 1921G-F5, Maxim) were placed 5 cm deep into the soil and measured the temperature every 40 min for a period of 5 months. We measured air temperature 10 cm above the litter layer surface (ONS-H08 loggers, Synotech) and collected data every 20 min for 6 months.

For quantifying litter decay rates, we used 20 mesh bags filled with a mixture of leaf litter of all forest types (Bockock and Gilbert 1957). They remained for 4 months on the forest floor of the plots before we collected and weighed them again (AS 153 Adventurer: accuracy: 1 mg). Each bag was filled with 9 to 12 g thermally dried leaf litter (representative mixture from all four forest types). Phosphate concentration and numbers of microbes in the soil were analyzed from soil samples (n = 4) in a commercial lab in Malaysia. As continuous canopy cover made it impossible to locate site positions directly by GPS (Garmin GPS 12 XL), we mapped nearby positions and located original positions and altitudes from satellite maps in Google Earth 4.3.

To reduce co-linearity of the vectors, we combined similar environmental parameters by use of PCA (principal component analyses, Table 1), thus combining the 24 raw parameters to a final of 18 parameters used in further analyses. For statistical evaluation, all data except PCA scores were *Z*-transformed.

## Indicator species

Indicator species indicate the distinctness of environmental conditions and are thus particular to certain habitat conditions (Lindenmayer et al. 1999). To find characteristic species of the forest types, we conducted an indicator species analyses after Dufrêne and Legendre (1997) with PC-ORD. Their method calculates indicator values (from 0 to 100) for each species by combining the relative abundance (numbers of species occurrences in a certain forest type) of a certain species with its relative frequency of occurrence in the various transects. These values are tested for statistical significance against randomly generated indicator values calculated from randomly created species distributions (Monte Carlo, 1000 permutations). For each of these indicator species, we calculated a logistic regression (estimation method: quasi Newton) with the indicator species' species scores that had been calculated with R-function wascores (for details see below) with the nine environmental parameters that proved to be significant in the final model of the partial bioenv-calculation (see below).

## Analysing the impact of space and environment

We used constrained and unconstrained ordination techniques to assess different aspects of the community (McCune and Grace 2002). Unconstrained ordination, e.g. non-metric multidimensional scaling (NMDS), takes most of the variance inherent in the species matrix into account and environmental interpretation is performed after analysis. NMDS is especially suited for the analysis of ecological data, as it allows non-normally distributed and ranked variables and was used in our study to evaluate the impact of single environmental parameters on ant community composition.

Constrained ordination methods, e.g. redundancy analysis (RDA), do not try to display all variation in the data, but only the part that can be explained by the used constraints, and thus need a strong a priori hypothesis regarding spacial and environmental factors (Oksanen et al. 2008). We used RDA-based methods for the evaluation of spatial vs environmental processes on ant communities (Legendre et al. 2005). Estimation of sample coverage by comparing actual species richness with estimated species richness (by estimators Jacknife 1 and Jacknife 2, choosen according to the method of Brose and Martinez 2004) showed that the studied forests were well sampled (Mezger and Pfeiffer unpubl.): for the whole community 79.2% and for the single forest types 70.4–74.4% of all species estimated to live in the plots occurred in our samples. Therefore the samples of all forest types were considered to be suitable for a community analyses. From the species matrix, we conducted NMDS with R-package vegan (Oksanen et al. 2008, R Development Core Team 2009) to explore differences between the different forest types. These analyses were done with Wisconsin double standardizations, the Bray-Curtis index as distance measurement, several random start positions and a maximum number of 1000 iterations. Species scores that show the position of single species within the ordination configuration of the NMDS were calculated as weighted averages from the species matrix by using R-function wascores. We estimated the proportion of community variation explained by each axis with the PCORD package (McCune and Grace 2002). The stress was given at a scale from zero to 100 with zero being the state where the models fits best to the data.

### Evaluation the influence of space and environmental parameters

We tested for spatial autocorrelation of the environmental parameters by calculating Moran's I from the distance matrix with the Geary-Moran function of the R package ade4 (Chessel et al. 2004, R Development Core Team 2009). In order to explore the spatial relations between the plots we computed principal coordinates of neighbour matrices (PCNM) from the geographical distance matrix with R package PCNM (Legendre et al. 2009b). PCNM eigenfunctions represent a spectral decomposition of the spatial relationships among the sample plots; they describe all spatial scales that can be accommodated in the sampling design (Dray et al. 2006).

For a first assessment of the correlation of environmental data with ant community structure, we performed a symmetric Procrustes rotation with the two NMDS of the ant data and the environmental data (Legendre and Legendre 1998, R package vegan). To describe and interpret the major environmental gradients in our data in detail, we used the envfit-function of R package vegan to fit single environmental parameters to the NMDS.

We used different approaches to include spatial patterns into our analyses. Our first aim was to assess the pure impact of the environmental data, while removing spatial effects. Therefore we checked for cross-product correlation between the complete distance matrices of species (Bray-Curtis distance), environmental parameters (Euclidean distances) and spatial distances (aerial distances) and compared the results of Mantel tests and partial Mantel tests that remove the effect of spatial correlation on the relationship of environmental data and species composition (Legendre and Legendre 1998). For these calculations we used R-package vegan and calculated significances by randomisation to account for the non-normal distribution patterns of the vectors (1000 permutations).

For a ranking of the influence of the single 18 environmental parameters on ant community patterns, we applied the partial bioenv function (R package vegan (Oksanen et al. 2008, R Development Core Team 2009)) that extracts spatial effects while finding the best subset of environmental variables, so that the Euclidean distances of scaled environmental variables have the maximum (rank) correlation with the community dissimilarity matrix (Clarke and Ainsworth 1993).

In constrained analyses, we used RDA to partition the variance in the ant community data, and in species richness and abundance patterns, into a pure spatial, pure environmental and spatially structured environmental fraction (R package vegan, functions varpart and rda, Oksanen et al. 2008). For this purpose we took Hellinger transformed community data, all environmental parameters and – as spatial descriptors – the PCNM eigenvectors with positive eigenvalues (Peres-Neto et al. 2006). Significance of the model was calculated by analyses of variance (ANOVAs) with 2000 permutations. Negative $r^2$ values may arise because of the process of adjustment (Oksanen et al. 2008).

## Results

### Ants, space and environmental parameters

We found a total of 206 ant species in the four forest types. We detected 96 species in alluvial forest, 110 species in limestone forest, 89 species in dipterocarp forest, and 68 species in the kerangas forest. The most species-rich genus was *Pheidole* with 24 species, followed by *Strumigenys* with 23 species; on the other hand, we discovered 23 ant genera with only one species. The five most common genera in all forest types were *Pheidole*, *Carebara*, *Hypoponera*, *Strumigenys* and *Monomorium*; we found species of these genera in at least 75% of our samples. More detailed information on species diversity will be given elsewhere (Mezger and Pfeiffer unpubl.). Forest types differed significantly in 13 out of 18 environmental parameters, thus corroborating the ecological differences between these habitats (Table 1, Kruskal-Wallis ANOVA, $p < 0.0001$).

The results of the Mantel tests indicated that species composition was influenced both by environmental parameters ($r = 0.42$ ($r^2 = 0.18$), $p < 0.01$) and spatial patterns ($r = 0.32$ ($r^2 = 0.10$), $p < 0.01$). The matrix of environmental factors was significantly influenced by spatial patterns ($r = 0.37$ ($r^2 = 0.14$), $p < 0.01$) (Table 2). Moran's I indicated significant negative spatial autocorrelation for 10 environmental parameters at the regional "forest type" scale (included all samples) and for three parameters on the local scale (Supplementary material Table S1), thus reflecting the

Table 2. Mantel analysis of the relationship between matrices representing ant community, spatial pattern and a set those of nine environmental parameters selected by the final model (for a list of these parameters, see Table 4). Above diagonals: simple Mantel statistics; below: partial Mantel statistics controlling for the effect of the matrix of environmental parameters. Bold numbers indicate statistical significance ($p < 0.01$ after Bonferroni correction).

| | Ants | Space | Environment |
|---|---|---|---|
| Ants | | **0.3194** | **0.4189** |
| Space | **0.1968** | | **0.3654** |
| Environment | **0.3425** | **0.2692** | |

mosaic structure of highly contrasting, neighbouring environmental patterns in Gunung Mulu NP.

### Indicator species

Of the 206 ant species, 53 were characterised as indicator species (Dufrêne and Legendre 1997) for one of the four forest types (Table 3), 35 of the indicator species belong to the subfamily Myrmicinae. We detected 6 to 21 indicator species per forest type. All these indicator species were tested by logistic regression. We found that the occurrence patterns of 36 indicator species in our plots could be significantly explained by the nine most important environmental parameters of the final model of the partial bioenv calculation (Table 3).

### Community analysis

The final configuration of the NMDS (stress 20.72) was obtained after 440 tries and explained 68.1% of the variance in species composition with three axes (distance measure: Bray-Curtis, axis 1: $r^2 = 0.35$, axis 2: $r^2 = 0.21$, axis 3: $r^2 = 0.12$). The correlation coefficient with the original data matrix was found to be 0.63 ($p < 0.001$). Plot scores of all three axes differed significantly between the four forest types (ANOVA, axis 1: $F_{3,96} = 29.6$, $p < 0.0001$, axis 2: $F_{3,96} = 52.1$, $p < 0.0001$, axis 3: $F_{3,96} = 6.8$, $p < 0.0004$).

As revealed by symmetric Procrustes rotation, NMDSs of ant community and environment structure as measured by the 18 variables correlated strongly ($r = 0.62$, $r^2 = 0.39$, $p < 0.001$). When we fitted single environmental vectors to the NMDS scores, we obtained the highest correlation coefficients for PCA decay, PCA stone and phosphate (Fig. 2); however, after accounting for the influence of spatial correlation by partial Mantel tests, the highest correlation coefficients were found for PCA top-soil, living trees and PCA roots (Table 4).

In order to rank environmental parameters, while at the same time extracting the partition of variation that was attributable to spatial autocorrelation of the data, we evaluated 18 of these parameters with the partial bioenv procedure, which subtracts the variance of the spatial matrix. The function compared 524 287 possible subsets and detected a subset of nine environmental parameters that correlated best with ant community data: PCA top-soil, living trees, leaf litter coverage, vegetation density, carbon/nitrogen content, PCA roots, PCA stone, PCA decay, and dead trees produced a combined a combined r of 0.353 ($r^2 = 0.12$) (Table 4). When we checked the validity of the calculation by a set of Mantel and partial Mantel analysis according to Legendre and Legendre (1998), we found that an extraction of spatial variation reduced the Mantel r of the respective nine environmental parameters from 0.42 to 0.34, and the explained variance $r^2$ from 0.18 to 0.12 ($p < 0.01$, Table 4).

### Variance partitioning

We used canonical analysis with variance partitioning to compare the effects of environmental characteristics and spatial distribution on ant community structure as a whole and in different fractions. For all (sub-) data sets, some of the explained variation was obtained from the environmental parameters (Fig. 3, Supplementary material Table S1). For the whole ant community data, these parameters accounted for 14% of the $r^2$. However, this partition rose for smaller subsets of the ant community and explained 17% of the variation in the 60 most abundant species and 19% variation of the 20 most abundant species. Twenty percent of the variation in the distribution of the 53 indicator species could be interpreted by environmental variation. The influence of the environment on the distribution of species richness was especially high with 44% of the variation explained by environmental parameters (Fig. 3). Spatial distribution of the plots as given by the PCNM, explained $< 1\%$ in most of the cases but had a higher impact on the 20 most abundant species (1.3%) and on patterns of species richness (4.6%) (Supplementary material Table S2). Interaction of spatial and environmental data, made up to 7% of the explained variance (Fig. 3). Although the models of ant community patterns and species richness were all significant ($p < 0.01$), no significance was found for the explanation of the distribution of ant individuals.

## Discussion

Our results show that environmental parameters impact ant species richness mand that they have some influence on species composition of the single plots. Influences of the environment on community structure are highlighted by the large number of indicator species, which comprise more than a quarter of all species and are associated with only one forest type. The indicator species reflect the habitat differences which we have found between the four forest types; the different biotic and abiotic conditions of these forests are indicated by significant distinctions within 13 of the 18 final environmental parameters and within the NMDS scores of all three axes.

The strong dissimilarity of the forest types is reflected by the negative autocorrelation of environmental parameters at the regional scale. Positive autocorrelation results in an inflated rate of type 1 error and affects tests of significance, negative autocorrelation may produce the opposite effect, but actually has unforeseeable outcomes (P. Legendre pers. comm.). Although the order and impact of the single vectors differ between the spatial and non-spatial models,

Table 3. List of indicator ant species, their indicator values, statistical significance and results of logistic regression. Indicator values (IV) were calculated after Dufrêne and Legendre (1997) by using PC-ORD. These values were compared with Monte Carlo iterations for significance. Abbreviations for habitats: a = alluvial forest, l = limestone forest, d = dipterocarp forest, k = kerangas. The p-value of indicator species analyses is marked as ISA p-value, whereas the Chi-square and p-value of the logistic regression are marked with LR.

| Species | Subfamily | Main habitat | Indicator value (IV) | IV randomised | SD (IV randomised) | ISA p-value | LR $Chi^2$ | LR p-value |
|---|---|---|---|---|---|---|---|---|
| *Technomyrmex kraepelini* | Dolichoderinae | l | 23.3 | 6 | 2.98 | 0.0012 | 22.886 | 0.00647 |
| *Technomyrmex modiglianii* | Dolichoderinae | k | 15 | 4.4 | 2.65 | 0.0158 | 19.526 | 0.0211 |
| *Brachymyrmex* sp. 1 | Formicinae | k | 13.3 | 5.7 | 2.82 | 0.0366 | 39.134 | 0.00001 |
| *Paratrechina* sp. 1 | Formicinae | l | 31.2 | 18.8 | 3.09 | 0.001 | 22.658 | 0.00703 |
| *Pseudolasius* sp. 1 | Formicinae | k | 31.2 | 8.2 | 3.16 | 0.0002 | 35.821 | 0.00004 |
| *Pseudolasius* sp. 4 | Formicinae | d | 20 | 4.9 | 2.75 | 0.0034 | 21.064 | 0.01239 |
| *Leptanilla* sp. 3 | Leptanillinae | a | 13.3 | 4.9 | 2.81 | 0.0202 | 20.93 | 0.01298 |
| *Acanthomyrmex ferox* | Myrmicinae | l | 46.1 | 9.7 | 3.3 | 0.0002 | 31.744 | 0.00022 |
| *Crematogaster* sp. 1 | Myrmicinae | d | 34.4 | 17.7 | 3.31 | 0.0006 | 31.716 | 0.00022 |
| *Crematogaster* sp. 2 | Myrmicinae | l | 23.7 | 6.8 | 3.03 | 0.0008 | 35.331 | 0.00005 |
| *Eurhopalothrix elke* | Myrmicinae | d | 15 | 4.4 | 2.57 | 0.0124 | 5.807 | 0.75902 |
| *Eurhopalothrix jennya* | Myrmicinae | l | 25.7 | 7.1 | 3.02 | 0.0008 | 26.4 | 0.00176 |
| *Eurhopalothrix omnivora* | Myrmicinae | d | 15 | 7.2 | 3.11 | 0.026 | 11.893 | 0.21945 |
| *Lophomyrmex bedoti* | Myrmicinae | l | 29.2 | 14.4 | 3.37 | 0.0022 | 14.488 | 0.10604 |
| *Monomorium* sp. 1 | Myrmicinae | l | 35.5 | 22.5 | 2.64 | 0.0002 | 43.321 | 0.00001 |
| *Myrmecina* sp. 1 | Myrmicinae | a | 19.6 | 8.9 | 3.28 | 0.009 | 25.58 | 0.0024 |
| *Myrmecina* sp. 2 | Myrmicinae | d | 17.9 | 9.5 | 3.24 | 0.0166 | 4.399 | 0.88322 |
| *Carebara* sp. 1 | Myrmicinae | a | 28.7 | 16.3 | 3.32 | 0.0046 | 18.5 | 0.02982 |
| *Carebara* sp. 2 | Myrmicinae | l | 33 | 18.5 | 3.26 | 0.0016 | 19.207 | 0.02352 |
| *Carebara* sp. 3 | Myrmicinae | k | 28.8 | 12.3 | 3.51 | 0.001 | 39.151 | 0.00001 |
| *Carebara* sp. 4 | Myrmicinae | d | 39.2 | 7.5 | 3.03 | 0.0002 | 8.341 | 0.50022 |
| *Pheidole annexus* | Myrmicinae | l | 23.5 | 7.5 | 3.08 | 0.003 | 29.801 | 0.00048 |
| *Pheidole aristotelis* | Myrmicinae | l | 18.8 | 10.2 | 3.24 | 0.0302 | 4.158 | 0.90069 |
| *Pheidole gombakensis* | Myrmicinae | l | 20.2 | 9.8 | 3.32 | 0.0184 | 15.109 | 0.08805 |
| *Pheidole parvicorpus* | Myrmicinae | k | 50 | 7.2 | 3.1 | 0.0002 | 42.58 | 0.00001 |
| *Pheidole rugifera* | Myrmicinae | d | 28.3 | 6.8 | 3.1 | 0.0006 | 19.299 | 0.02279 |
| *Pheidole sauberi* | Myrmicinae | l | 13.9 | 5.7 | 2.92 | 0.0396 | 16.905 | 0.05027 |
| *Pheidole* sp. near *aristotelis* | Myrmicinae | l | 20 | 5.6 | 2.75 | 0.0022 | 30.867 | 0.00031 |
| *Pheidole upeniki* | Myrmicinae | a | 14.2 | 7.6 | 3.11 | 0.0284 | 11.567 | 0.23885 |
| *Pheidologeton affinis* | Myrmicinae | a | 24 | 10.2 | 3.32 | 0.0038 | 19.103 | 0.02436 |
| *Pristomyrmex rigidus* | Myrmicinae | l | 16.7 | 5.3 | 2.83 | 0.0132 | 20.273 | 0.01632 |
| *Proatta butteli* | Myrmicinae | l | 51.4 | 10.5 | 3.36 | 0.0002 | 40.432 | 0.00001 |
| *Recurvidris browni* | Myrmicinae | a | 60 | 9.8 | 3.28 | 0.0002 | 37.168 | 0.00002 |
| *Strumigenys aechme* | Myrmicinae | l | 17.8 | 7.5 | 3.05 | 0.0172 | 14.059 | 0.12031 |
| *Strumigenys kapryx* | Myrmicinae | a | 16.7 | 5.3 | 2.75 | 0.0112 | 25.044 | 0.00293 |
| *Strumigenys koningsbergeri* | Myrmicinae | a | 15 | 6.4 | 3.07 | 0.0184 | 15.661 | 0.07435 |
| *Strumigenys signeae* | Myrmicinae | d | 19.7 | 6 | 2.9 | 0.0026 | 24.94 | 0.00305 |
| *Tetheamyrma subspongia* | Myrmicinae | l | 13.3 | 4.8 | 2.71 | 0.0168 | 13.434 | 0.144 |
| *Tetramorium (chepocha*-group) sp. | Myrmicinae | d | 23.1 | 12.3 | 3.51 | 0.0128 | 24.405 | 0.00371 |
| *Tetramorium* (*scabrosum*-group) sp. | Myrmicinae | k | 30 | 7.9 | 3.09 | 0.0006 | 14.352 | 0.11041 |
| *Tetramorium* sp. near *vertigum* | Myrmicinae | a | 18.8 | 10.2 | 3.29 | 0.031 | 12.153 | 0.2487 |
| *Vollenhovia* sp. 1 | Myrmicinae | d | 41.7 | 8.2 | 3.22 | 0.0002 | 16.488 | 0.0574 |
| *Hypoponera* sp. 1 | Ponerinae | a | 26.9 | 8.6 | 3.24 | 0.0012 | 22.222 | 0.00822 |
| *Hypoponera* sp. 3 | Ponerinae | l | 26.8 | 12.2 | 3.35 | 0.002 | 28.702 | 0.00073 |
| *Hypoponera* sp. 4 | Ponerinae | l | 39.3 | 11.4 | 3.36 | 0.0002 | 30.481 | 0.00036 |
| *Hypoponera* sp. 10 | Ponerinae | a | 31.1 | 10.9 | 3.42 | 0.0008 | 20.214 | 0.01666 |
| *Hypoponera* sp. AL16B | Ponerinae | a | 32 | 20.9 | 2.93 | 0.0044 | 14.117 | 0.11827 |

Table 3. Continued.

| Species | Subfamily | Main habitat | Indicator value (IV) | IV randomised | SD (IV randomised) | ISA p-value | LR $Chi^2$ | LR p-value |
|---|---|---|---|---|---|---|---|---|
| *Anochetus* sp. near *graeffei* | Ponerinae | l | 17.4 | 8.6 | 3.26 | 0.0226 | 11.484 | 0.24401 |
| *Myopias* sp. 2 | Ponerinae | l | 16.7 | 5.2 | 2.68 | 0.01 | 17.796 | 0.03765 |
| *Pachycondyla* sp.1 | Ponerinae | d | 30 | 7.9 | 3.09 | 0.0002 | 13.863 | 0.12733 |
| *Pachycondyla* sp.9 | Ponerinae | d | 30.6 | 6.4 | 3.15 | 0.0002 | 17.612 | 0.03998 |
| *Pachycondyla pilidorsalis* | Ponerinae | d | 20.9 | 9.9 | 3.34 | 0.0134 | 24.677 | 0.00336 |
| *Probolomyrmex maryatiae* | Proceratinae | a | 16.7 | 5.4 | 2.83 | 0.0136 | 12.384 | 0.19257 |

we were able to identify the main parameters that affect ant community patterns. Three parameters were especially important for characterising the habitat and had most of the explanatory value in both of the models: PCA top-soil, leaf litter coverage and number of living trees (spatial: cumulative $R = 0.286$ ($r^2 = 0.08$) or non-spatial: $R = 0.370$ ($r^2 = 0.14$)).

In our models, the quantitative measurements as described by PCA top-soil were the most important soil parameters, although soil qualities, e.g. PCA decay and pH value had also proven to be significant factors. The dependence of ants on the top-soil stratum has been demonstrated by Bihn et al. (2008) in a study in Brazil, where they recorded differing community structure in habitats with different soil types. The number of living trees around the plot was the second most important parameter in our spatial model and was negatively associated with species richness (regression, beta $= -0.44$, $r^2corr = 0.18$, $F(1,96) = 22.758$, $p < 0.00001$), because the numbers of trees were highest in the kerangas, the habitat with the most species- and individual-poor ant community (Mezger and Pfeiffer unpubl.). Wardle (2006) has shown that biotic interactions, e.g. those with vegetation, have a large impact on ground-living organisms, while Ribas and Schoereder (2007) stress the importance of structural heterogeneity of vegetation for ant diversity. Old growth forests with a few enormous trees could offer improved conditions for ants compared to forests with many smaller trees, as they provided valuable nesting and foraging places: larger amounts of leaf litter layer, dead wood and small twigs than forests with only smaller trees. The third factor in our model was leaf litter coverage, which was highly affected by the number and crown volume of trees, as well as by litter decay rates. The litter layer proved to be an important habitat for a large proportion of species. Although only 3% all species were restricted to the leaf litter and not found in the soil, the litter layer provided habitat of 68% of all species (Mezger and Pfeiffer unpubl.). Soil characteristics and leaf litter quality are correlated with one another: soil influences litter decay by moisture and the number of soil arthropods, whereas litter nutrients influence the nutrient content of the soil (Ribas and Schoereder 2007). Litter quantity impacts the distributions of ants (Dent et al. 2006, McGlynn et al. 2009).

The remaining parameters, like vegetation density, carbon/nitrogen content, PCA roots, PCA stones and PCA decay, explained only small amounts of variance in our model (spatial cumulative $R = 0.067$, ($R^2 = 0.004$)), although they might be of some importance for community composition. We showed this for temperature (measured on regional scale an essential part of PCA decay in the present study) in a further study, which proved the ecological importance of temperature on a very local scale for niche differentiation in leaf litter ants (Mezger and Pfeiffer 2010). When we tested a subset of 54 indicators species by logistic regression, we found that variation in the presence/absence of 36 could be explained by the nine parameters of our model. This result confirmed the importance of the environmental parameters for ant community composition. There might also be a potential to use these indicator species as bioindicators (sensu Andersen and Majer 2004) to characterise different types of primary forests.

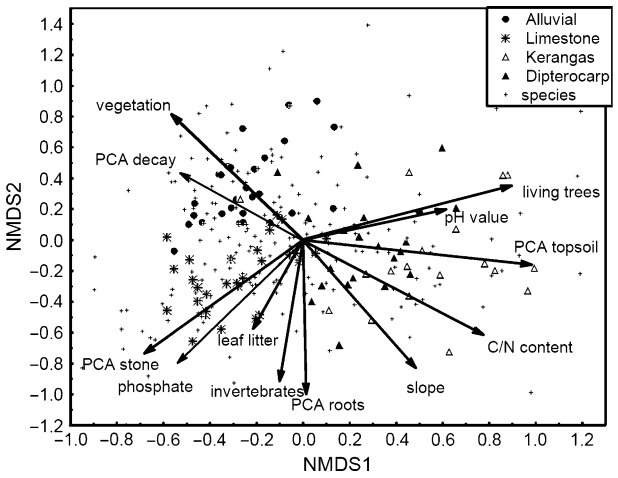


Figure 2. Environmental vectors of the twelve most important environmental parameters fitted onto the NMDS scores of the ant community by R-function envfit. Given are 100 sites scores of community, separately for the four forest types (open and closed circles and triangles) and species scores (crosses) of all 206 species for the first and second NMDS axes.

To assess the impact of niche processes and other spatial processes on community composition, species richness and abundance pattern, we used variance partitioning by RDA (Peres-Neto et al. 2006). This mathematical framework assesses the overall influence of various parameters and is thus helpful to unravel the processes that shape the variation of community composition (beta diversity) within a region (Laliberte et al. 2009, Legendre et al. 2009a). Provided that our 24 parameters quantified a large part of environmental variation this part of the variation can be attributed to niche processes. It was surprising that for the whole ant community pure environmental variation made only 13.6% of all variation (Supplementary material Table S1); however, similar results were recently obtained in a study on neotropical ant communities along the Amazon river, in which this fraction accounted for 15.2% of all variation (Vasconcelos et al. 2010). In contrast to this and other studies (Legendre et al. 2009a), the impact of spatial variation in Mulu NP was minimal, as all plots were situated in a patchy pattern within a distance of only few kilometers, while at the Amazon the plots followed an environmental gradient of 2000 km. So the impact of the spatially structured environmental variation in Mulu NP was low and reached not even for the indicator species 5%, while it made 6.6% for the neotropical ant community, in which the pure spatial variation was 9.4% (Vasconcelos et al. 2010). In the Mulu community the pure spatial fraction was the smallest, all values for community structure were below 2%, obviously due to the close spatial situation of all plots. The biological explanation for the pure spatial influence is the dispersal limitation of the gynes, which leads to low beta diversity between (and positive auto-correlation of) neighboring plots, as ant species are small and their alates are poor dispersers in many cases. However, as the "pure space" fraction may hide the effect of some unmeasured spatially structured environmental variables (Jones et al. 2008, Laliberte et al. 2009), the low impact of this fraction in the data from Mulu NP points also towards the high quality of our environmental data.

Total explained variation was rising for smaller subsets of more abundant species and highest for the indicator species, which were more affected by environmental variation than the whole ant community. However, total explained variation for the indicator species in Mulu NP was only 24%, while it made 31.2% for all of Amazonian ant communities – mainly due to stronger spatial effects.

Interestingly, in both systems the explained variation was much higher for species richness, in Borneo 47.8% of all

Table 4. Correlation of environmental parameters with ant community patterns. Significant results ($p < 0.05$), which were all obtained by randomization (1000 runs), are presented in bold; stars give the reduced significant levels after false discovery rate correction. Given are 1) the ranks (in brackets) and the cumulative R of the simple bio-env function, 2) the correlation coefficients of fitted environmental vectors calculated with the envfit procedure of R, 3) the cumulative R of the partial bio-env function with extraction of the spatial distances, for the full significant model that included nine parameters and all combinations of a smaller number of parameters, 4) the results of partial Mantel correlations that extract spatial distances with the dissimilarity matrix, and – in the first column – the environmental parameters as listed in Table 1 ranked according to the results of the partial bio-env-procedure (fourth column), "X" in the last column indicates that assignation of a rank for seven allowed parameters gave results that differed from the ranking presented herein. Significance of the results of bioenv were tested by (partial) Mantel tests. The numbers in the names of the PCAs reflect to the combination of parameters given in Table 1.

| | envfit | Bioenv calculation (ranks) cumulative R | Partial Mantel correlation excluding spatial patterns | Partial bioenv calculation cumulative R |
|---|---|---|---|---|
| PCA top-soil (2) | **0.197***** | **(1) 0.27**** | **0.213**** | **0.201**** |
| Living trees | **0.308***** | **(3) 0.37**** | **0.177**** | **0.247**** |
| Leaf litter coverage | 0.068 | **(2) 0.33**** | **0.158**** | **0.286**** |
| Vegetation density | **0.244***** | **(6) 0.411**** | **0.118*** | **0.307**** |
| Carbon/nitrogen content | **0.387***** | **(4) 0.386**** | **0.144**** | **0.322**** |
| PCA roots (3) | **0.199***** | **(7) 0.418**** | **0.169**** | **0.328**** |
| PCA stone (1) | **0.453***** | **(8) 0.425**** | 0.068 | **X** |
| PCA decay (4) | **0.502***** | | **0.100**** | **0.350**** |
| Dead trees | 0.044 | | 0.062 | **0.353**** |
| Number of invertebrates | **0.127**** | | **0.146*** | – |
| Phosphate | **0.422***** | | **0.151*** | – |
| Slope angle | **0.219***** | | 0.041 | – |
| pH value | **0.328***** | **(5) 0.4**** | 0.007 | – |
| Leaf litter thickness | **0.132**** | | −0.046 | – |
| Canopy openness | 0.067 | | 0.013 | – |
| Dead wood <5 cm | 0.018 | | −0.045 | – |
| Small twigs | 0.027 | | −0.037 | – |

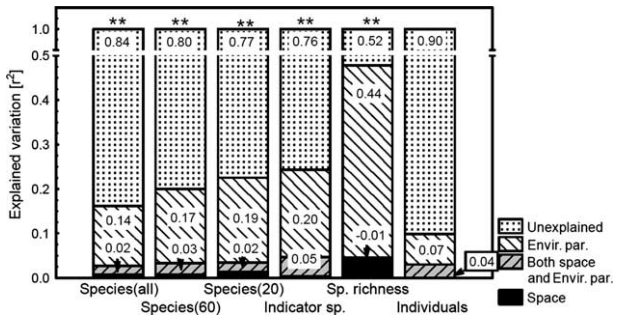


Figure 3. Variance partitioning of species composition, species richness and abundance of individuals of the ant community in Gunung Mulu NP. The figure presents the adjusted unique contribution ($r^2$) of spatial components (black), environmental components; envir. comp. (white-lined), interactions of spatial and environmental components (grey-lined), and the variation left unexplained (white-dotted), all calculated by RDA. Calculations were run for several subsets of the community: all 206 species, the 60 most abundant species, the 20 most abundant species, a set of 53 indicator species with significant habitat preferences, the patterns of species richness in the different plots, and the abundance of ant individuals among the plots. Labels show the exact $r^2$ values for all components except the spatial components (their values are given in Supplementary material Table S1). Tests of significance were possible only for fractions of spatial and environmental components, which explained the variation at a level of $p < 0.01$ for the marked models, but not for the number of individuals ($p = 0.11$).

variation in species richness could be explained, in the Amazonian forest it was 63.4%. Thus, the number of niches in tropical ant communities seemed to be largely determined by spatial and environmental parameters, whereas species identity seems to be assigned by other processes in most cases. If environmental parameters mainly defined the number of species that can exist in a certain place, but do not prescribe which species occupy these niches, the community may be structured to a large proportion by stochastic processes (Legendre et al. 2009a, b), meaning that species are allocated randomly from a pool of species with similar ecological traits. Such a mechanism would explain the persistence of ecologically similar species in the highly diverse tropical ecosystems. Thus functional redundancy may well depend on both niche and stochastic processes (Leibold and McPeek 2006). Stochastic processes are especially important in primary forest habitats, where they influence habitat patterns and community structure of ants in the lower canopy (Floren et al. 2001). The latter explanation has a theoretical connection to neutral theory (Hubbell 2001), which assumes that dynamics of populations are not habitat dependent and primarily driven by ecological drift and dispersal. Both effects come out in the unexplained variation, which was the largest fraction in our results, while dispersal has also a spatial signature (Legendre et al. 2009a, b). Thus in contrast to our hypothesis stochastic mechanisms, rather than environmental factors, seem to govern the assembly of ground ant communities in Mulu NP. As similar results have been found in different strata of Amazonian forest (Vasconcelos et al. 2010) and for the canopy layer in Borneo (Floren et al. 2001, Floren and Linsenmair 2005) a high impact of chance could be an intrinsic pattern of ant communities in tropical primary forests.

However, neutral processes are only one possibility to account for the residual fraction of unexplained variation. Non-spatially structured biological or environmental variation that was not measured in the field can also account for at least some part of it. Among those factors that may explain the residual variation are habitat disturbance (e.g. by frequent flooding in alluvial forest), competitive interactions (Pfeiffer et al. 2008), or selective hunting pressure by army ants (Hirosawa et al. 2000, Berghoff et al. 2003) that are with several subfamilies reported from the study area (Mezger and Pfeiffer unpubl.). On the other hand in certain habitats environmental filtering may select related species with similar traits, thus leading to a phylogenetic structuring (Vamosi et al. 2009), or several processes may occur at the same time with different parts of the community. Further analyses may uncover the identity of additional partitions of previously un-explained variance in species composition of tropical ground ant communities.

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