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Anthropogenic disturbance changes the structure of arboreal
tropical ant communities.

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Abstract

We investigated the influence of anthropogenic disturbance on the structure of arboreal Formicidae communities in SE-Asian lowland forests. Included were a primary forest and three disturbed forests which had been cut for crop planting and abandoned 5, 15, and 40 years after agricultural use for natural regeneration. Ant communities of at least 10 individuals of one tree species were sampled from each forest type by fogging. Diversity and community structure differed clearly among forest types. During the course of forest regeneration ant communities became more and more similar to those of the primary forest. A surrogate analysis shows that ant communities of the primary forest cannot be distinguished from randomly composed communities. This is in contrast to the theoretical expectations according to which ant communities should be structured by interspecific competition that lead to a large degree of predictability. However, a deterministic pattern of ant communities is found in the disturbed forest. This indicates that human disturbance not only changes the faunistic composition of ant communities but could also change the dynamics of the whole system. The transition from stochastic to deterministic communities might be of general importance for understanding the mechanisms structuring communities in disturbed habitats. The question how anthropogenic disturbance changes the structure of communities and how they influence the functioning of ecosystems has become particularly topical because of environmental destruction which is proceeding globally with increasing speed (Turner and Corlett 1996, Didham et al. 1996, Wardle 1999). Natural ecosystems become to a large degree fragmented or completely converted into systems used by man and both is usually associated with a dramatic loss of species diversity (Wardle 1996, Bascompte and Solé 1996). This coincides with large changes in species abundances (e.g. Mason 1995, Davis and Sutton 1998, Lawton et al. 1998) and happens without knowing the consequences for the maintenance of ecosystem functioning and ecosystem services (Chapin et al. 1997, Schwartz et al. 2000). Human destruction is taking place in a particularly reckless way in the tropics in which the loss of biodiversity is at its greatest and where the effects are most severe.

Our newest results from investigating the influence of anthropogenic disturbance on arboreal arthropod communities in SE–Asian lowland forests indicate that disturbance does not only reduce biodiversity but also has drastic consequences for the mechanisms structuring these communities (Floren and Linsenmair 1999, 2000, in press). In this paper, we investigate this in detail for arboreal Formicidae communities along a disturbance gradient, which comprises a primary forest and three differently disturbed forest types. We have already shown that Formicidae are in particular suited for such an analysis because they are of moderate species richness and do not show any tree specific adaptations. No myrmecophytes (plants associated with ants) were investigated (Floren and Linsenmair 2000, in press). Furthermore, ants are nesting in the trees and thus form – different to other taxa (see Floren and Linsenmair 1998a, b, unpublished, Horstmann et al. 1999) – long lasting communities. This makes it possible to recognise alterations in community structure resulting from human forest use.

Here we ask, how the structure and species composition of ant communities differ in primary and disturbed forests and how human disturbance affects the mechanisms structuring these communities.

Material and methods

Study sites

Our project started 1992 in Kinabalu National Park, Sabah, Malaysia on Borneo (6°2.75'N, 116° 42.2'E) where a primary lowland rain forest, dominated by Dipterocarpaceae, occurs up to 700 meters above sea level. Since detailed information about the research areas, the tree species investigated, and the methodology have been published elsewhere (Floren and Linsenmair 1997, in press), we confine ourselves to the most necessary information. Arthropod communities of few tree species were sampled with an improved tree selective fogging method (see below). In 1997 we extended our investigations to include three forests of different disturbance level which were found at the margin of the National Park.

The forest types of the disturbance gradient

In the primary forest (abbreviated with P) we fogged 10 trees of *Aporosa lagenocarpa*, 5 *A. subcaudata* (Euphorbiaceae) and 4 *Xantophyllum affine* (Polygalaceae), all of which belong to the lower canopy stratum (average height of 23 meters). As the composition of arthropod communities between trees was very similar on the order level and no tree specific differences could be detected (Floren and Linsenmair 1997, 1998b, in press) the 19 trees were pooled and considered to be a representative overall sample of the mature forest. Three disturbed forests of 5, 15 and 40 years (abbreviated with SI, SII, SIII), which had all been cleared for agricultural use and then left for regeneration, were chosen for the comparative investigations. They were situated directly adjacent to one another and merged after a few kilometres into mature forest. Since none of the primary forest tree species occurred in the disturbed forests, as also the pioneer trees of SI were not found in SII and SIII, we had to select two other tree species (for a comprehensive discussion of the selection of study trees see Floren and Linsenmair in press). In SI, the undergrowth was formed by dense grasses and bushes and only pioneer trees were growing which reached an average height of eight meters. Ten tree individuals of a yet to be identified Euphorbiaceae were chosen for the comparison. SII was clearly more species rich in trees, which formed a loose canopy layer at about 20

meters height. The grass and shrub cover was replaced by a dense growth of tree saplings. Since only two of the pioneer trees of SI were found as old trees in SII, we concentrated on the most common tree. This was *Vitex pinnata* (Verbenaceae), of which we fogged 11 individuals. In SIII, *Vitex pinnata* became rarer and the trees found were older than in SII. Ten individuals of this species were fogged. On the ground, the growth of tree saplings was thinner and distinctly more rotting trees were found than in the previous forest types. All secondary forest types had only a single canopy layer which was never closed. The multilayered forest structure, which is characteristic in the mature forest, was always lacking. In all forests, only trees growing under similar habitat conditions were chosen for the foggings. This concerned, for example, edaphic conditions, crown cover by lianas, or the phenology of the trees (compare Floren and Linsenmair 1998b).

Investigations were carried out with only few tree species in order to keep tree taxonomic effects on ant community composition as low as possible (see also discussion). This approach was given priority over a completely random selection of trees within each forest type which would not circumvent tree taxonomical effects. The number of tree species even in the 5 year-old forest was estimated to be around 50 (Biun pers. com.). Therefore, assessing within stage variation in ant community composition would have made it necessary to sample at least several individuals from each randomly chosen tree species, resulting in a much larger number of trees.

The fogging method

In the primary forest, the crowns of the relatively small trees that we studied were covered with a 100m² cotton roof in order to keep away intoxicated arthropods from higher canopy strata from the collecting funnels. Fogging was carried out early in the following morning when there was no wind. Natural pyrethrum, diluted in a highly refined white oil, was used as insecticide which is highly specific to arthropods and completely biodegraded within hours. From each tree 80–90% of the crown projecting area on the ground was covered with funnels which guaranteed that most arthropods were caught. All arthropods that fell into the funnels within two hours after fogging were collected and considered in the evaluation. For more information concerning the sampling process see Floren and Linsenmair (1997) and Adis et al. (1999). Voucher specimens of ants are deposited in the collection of A.Fl.

Data analysis

Rarefaction statistics

Since rarefaction statistics does not depend on sample size, it can be used to directly compare ant diversity between forest types (Hurlbert 1971). For that purpose, the ant specimens of all trees fogged within each forest type were pooled. Ant diversity was then expressed as the number of expected species ($E(q)$) within a subsample (q) of n specimens. The size of the subsample used for comparing forest types was equivalent to the largest possible subsample (q) the forest types had in common. That was the number of ants of the five year-old forest type (4143 individuals). Therefore, in this case, the number of expected ant species corresponded with the real number of ant species.

Also the Shinozaki curve is derived from rarefaction statistics which refers to presence absence data (Shinozaki 1963). For increasing subsample size, the result is a species accumulation curve. It gives information about species richness, species turn-over between communities (beta-diversity), and the sampling effort (see Floren and Linsenmair 1997).

The correlation matrices

The correlation coefficient is a direct and widely used measure of association between continuous as well as discrete variables. We have calculated the correlations between ant community compositions of all 50 trees fogged. The observed frequencies were combined in a matrix, in which A_{ij} is the abundance of species i on tree j ($i = 1, \dots, 158, j = 1, \dots, 50$). Rare ant species, those found with less than 5 individuals, were excluded from the analysis because we did not know whether they really belonged to the arboreal community (see Table 1). This reduced the number of ant species in the evaluation from 273 to 158. Besides abundances, we also analysed a binary matrix B_{ij} , which recorded whether species i occurred on tree j (maintaining the same restriction that only species with at least 5 individuals were considered). The columns of matrices A and B characterise individual trees. The correlation coefficient r was used as a measure of similarity of species and abundance composition among two column-vectors (i.e. two trees). Results are given as a symmetric correlation matrix which is displayed in Fig. 2.

The surrogate analysis

In order to test whether the ant communities of the trees of a forest type show a deterministic (predictable) or a stochastic (unpredictable) structure, we carried out a surrogate analysis. Usually statistical tests are based on the theoretical knowledge of the distribution of the test quantity under the null hypothesis. In our case, this knowledge is lacking because the data are not normally distributed. Therefore, we determined the distribution of the correlations (our test quantity) with the help of computer generated data, which correspond in their decisive characteristics with the original data. This procedure is called a surrogate analysis (see Kantz and Schreiber 1997). It allows us to decide whether the mean of the correlation coefficients between trees of a forest type differs significantly from the mean of randomly generated communities. The surrogate matrices were generated by random shuffling of data in the rows of the original matrix, therefore keeping the frequency distribution of each species constant. However, surrogate matrices differed with respect to species number and species abundance on trees and thus represent computer generated forests of randomly assembled ant communities. For each of the computer generated forests the mean value of the correlation coefficient between various trees was noted and from 500 realisations we were able to obtain the distribution of this test quantity. In particular, we found that 500 realisations were sufficient to obtain a smooth distribution curve and that a larger number did not change this result. The analysis was performed separately for the primary and the disturbed forest (i.e. with submatrices $A_{i,1-19}$, $A_{i,20-50}$ and the respective submatrices of B). In order to test whether community composition (of species abundances or species presence) was predictable or random, the mean correlation value for different trees as obtained from the original matrices was compared with the distribution obtained from the surrogate data. In the case, that the empirical value was larger than 95% of the surrogate values, the hypothesis of a random composition of ant communities was rejected.

Results

Composition of ant communities

In total 273 species of Formicidae were identified, 195 (71.4%) in the primary forest¹ and another 78 (28.6%) species which were found exclusively in the secondary forest. Total number of species of all disturbed forest types was 136. Of all 273 species, only 15 (5.5%) occurred in all forest types, 4 (1.5%) were restricted to SI, 11 species (4.0%) to SII and 43 (15.7%) to SIII. The changes among forest types are in particular obvious when focusing on the 87 more common ant species listed in the Appendix table. Of these, 44 species had their abundance maximum in the primary forest and 28 were exclusively found here. From all secondary forest ant species, 21 species did not occur in the primary forest and 20 species seemed to profit distinctly from the disturbance (these were species, which were already found in the primary forest and which increased in abundance at least 100%).

Table 1 shows, that diversity of ant communities converged on the conditions of the primary forest with increasing time of forest regeneration. This can be seen, for example, in the increasing total number of ant species as well as in the continuously increasing proportion of primary forest species (see also Floren and Linsenmair in press). Although a differing number of trees (between 10 and 19) were fogged per forest type, this picture remains very clear after standardising the samples with the rarefaction method and, thus, is no effect of variable sample size. The differences between forest types can be described on the species level as follows (compare the Appendix table): In comparison to the primary forest, the greatest loss of species occurred in the Formicinae genera *Camponotus* and *Polyrhachis*, the Dolichoderinae genus *Dolichoderus*, and in the Myrmicinae genus *Crematogaster*. In the five year-old forest (SI), three species were numerically dominant, *Crematogaster* #43, *Camponotus* #282 and *Tetraponera difficilis*, of which *Crematogaster* occurred only on two trees, while the latter ones appeared regularly also in a subdominant position in the ant communities.

Only *Crematogaster* #43 was also found with 279 individuals in a single primary forest tree. In the fifteen year-old forest (SII), the abundances of all these three dominants increased and *Camponotus* #282 became the most characteristic species, dominating 8 of the 11 trees. Although *Crematogaster* #43 was found only in a single community in the highest rank position, this species occurred regularly in subdominant position and reached its abundance maximum in SII. With *Crematogaster* #44 and #224, two new dominants appeared. In total, 16 species reached their abundance maximum in SII. In the oldest secondary forest (SIII), seven numerically dominant species were found, of which *Camponotus* #282, #153 and *Crematogaster* #224 have already been found dominant in SI and SII. New dominants were *Crematogaster* #46 and #223, *Philidris* #94, which reached their highest numbers in SIII, and *Dolichoderus* #23. *Dolichoderus*, a regularly occurring dominant in the mature forest, appeared in greater abundance only in SIII. Many characteristic species of SI and SII decreased in abundance or disappeared, as for example *Cladomyrma* #278, the *Crematogaster*-species #43, #44, and #313, or *Camponotus* #285, of which the latter two were restricted to SII.

1) Compared to Floren and Linsenmair 2000, the number of primary forest ant species was corrected from 194 to 195.

Fig. 1 shows Shinozaki accumulation curves of the expected new species per forest type. In comparison to the primary forest (P) we detected 15 new species in SI. Combining P and SI, 20 species were found for the first time in SII. Compared to P, SI, and SII, another 43 species occurred for the first time in SIII. While the flat curves of SI and SII demonstrate that hardly any additional species would occur in further samples, the ten fogged trees in SIII were not sufficient to represent the local ant species pool and much more sampling is required in the primary forest (P). The steepness of the curve calculated for all forests and ants demonstrates the high regional diversity of the ant fauna, which is still far from reaching species saturation with the 50 trees fogged.

The correlation matrices

The ant communities of the primary forest and of the secondary forest clearly separate in the correlation matrices (Fig. 2). While the primary forest communities correlated only slightly with each other, we can observe a tendency to greater correlations in the disturbed forest types. SI and SII can hardly be distinguished from each other, while the 40 year-old forest (SIII) is clearly separated. Whether the differences between primary and secondary forest are statistically significant, was tested with the help of a surrogate analysis (see below). Separation of forest types is obvious both in species composition (Fig. 2a) as well as in species abundances (Fig. 2b), although the species abundance distribution shows a greater variation. An example are the trees 42, 43, and 44, of the 40 year-old forest type SIII that were dominated by the Dolichoderinae *Philidris* #94 which, however, had no uniform influence on the species composition of these communities. A characteristic aspect of this analysis is the rareness of negatively correlated ant communities in the primary as well as in the disturbed forests. Only three pairs of trees in the mature forest show a slight negative correlation while these were 30 pairs of trees in the secondary forests ($r < -0.04$).

The surrogate analysis

The primary and secondary forest ant communities can be clearly separated from each other by their structure and species composition. This is illustrated by the surrogate analysis – for species presence/absence in a community as well as for abundance distribution of species. Figure 3 shows that the primary forest communities can not be distinguished from randomly composed communities – the mean correlation value of the original matrix (of the fogged trees) is not significantly different from the mean of the correlation coefficients of the surrogate communities (for species presence/absence, $r = 0.183$, $p = 0.51$ and for species abundance, $r = 0.173$, $p = 0.87$). In contrast to this, the communities of the disturbed forests show a clear deterministic pattern – here, the mean correlation value of the original matrix differs in a highly significant way from the mean correlation coefficient of the surrogate communities (for species presence/absence, $r = 0.280$ and species abundance, $r = 0.256$, each $P = 1.00$). One might argue, that the hypothesis ant communities of the disturbed forests are randomly composed, had to be rejected simply because there were many more trees of the disturbed forest considered (31 trees) than of the primary forest (19 trees). We therefore carried out the same analysis with the first 19 trees of the disturbed forests in order to make the results comparable. We focused on SI and SII because the 40 year-old forest SIII clearly distinguishes from the younger forest types (Table 1, Fig. 1 and Fig. 2). However, after standardising the sample size, the ant communities showed a clearly deterministic structure (for species presence/absence, $r = 0.357$, $p = 0.96$ and for species abundance, $r = 0.411$, $p = 1.0$).

Discussion

As a result of the clearing of a primary forest for agricultural use, its arthropod communities are completely destroyed. If such areas are abandoned and left to natural succession, also arthropod communities show a succession in respect to the composition on the order level, diversity, and community structure (Floren and Linsenmair 1999, in press). These processes can be followed particularly well on arboreal ant communities, because they are nesting in the trees. In the five year–old forest only rudimentary ant communities had been formed in comparison to the primary forest. After 15 years and in particular after 40 years, each forest type had changed to a distinctly more diverse forest, which correlated with an increasing degree of complexity of ant communities on the alpha and beta–diversity level (see also Floren and Linsenmair in press).

For every forest type we were able to identify characteristic ant species, which reached their abundance maximum here. In comparison to the primary forest, however, only 20 of the 195 species profited clearly from the disturbances. How far these species, as for example *Crematogaster* #43, *Camponotus* #282 or *Tetraponera difficilis*, are suitable as disturbance indicators (e.g. Andersen 1990, Folgarait 1998) will have to be critically tested by detailed autecological investigations. The large amount of species discovered for the first time in the secondary forests (47% of all 136 species) points to a considerably unsampled regional diversity of the ant fauna.

The structural changes of Formicidae communities

Beside the faunistic aspects, our results demonstrate the strong structural changes in ant communities after anthropogenic conversion of primary forest into agriculturally used land. Species composition of ant communities in the primary forest could not be distinguished from randomly generated communities, a pattern that holds true also for larger sample sizes than the 19 fogged trees. For example, pre–sorting of 32 foggings on 13 tree species did not produce a distinct deviation from this result (Floren unpublished) and ant communities of mature forest trees which were re–fogged after a three year time of re–colonisation showed a similar random arrangement in species as the original communities (Floren and Linsenmair 2000). In contrast, we observed a clear deterministic community structure in the highly disturbed secondary forests SI and SII. Usually, the emergence of a deterministic community structure is seen as a consequence of interspecific competition (for references see Walter 1988, Hölldobler and Wilson 1990, Floren and Linsenmair 2000). According to this presumption, dominant, aggressive species should mutually exclude each other and should be associated with a defined set of subdominant species. As a consequence, an ant mosaic should form, as it has been discovered, above all, in plantations and strongly disturbed forests (e.g. Leston 1973, Room 1975, Majer 1993). However, even in SI and SII no ant mosaic could be detected. Compared to the primary forest, diversity in disturbed forests was distinctly lower, but the fewer remaining species occurred in high numbers on almost all trees. Apart from that, our data demonstrate that ant communities of the 40 year–old forest SIII were already so different on the alpha– and beta–diversity level that they had to be treated separately. Furthermore, we must take into account that all forest types investigated by us were in immediate vicinity of each other, so that colonisation from the primary forest was possible.

Although we are aware that our analysis is based on ant communities of three tree species, our results indicate that changes in ant communities were independent from the tree species fogged and mainly caused by the disturbance regime: 1. There are no hints that Formicidae showed any specific preferences to the trees investigated, as it, for example, should be expected for herbivores. Particularly we did not include myrmecophytes in the analysis. 2. Similar changes between primary and disturbed forests on the community level were found in other arthropod taxa currently under investigation (Coleoptera, Orthoptera, parasitic Hymenoptera and Diptera). If tree specific effects would be of great importance, then one would definitely not expect them to be the same in all taxa, including herbivores as well as predators. 3. Communities changed continuously in diversity and structure with increasing time of forest succession. However, these changes did not correspond to the particular occurrence of tree species in the forest types: the same tree species were fogged in SII and SIII, however, ant communities are quite different. In contrast, SI and SII have more similar ant communities, despite different tree species were sampled. Moreover, SIII showed an overlap in ant composition with the primary forest, although tree species were different. These observations contradict the assumption of relevant tree specific influences, even if we cannot completely exclude that some part of the variability in species composition might be due to taxonomic effects.

The importance of anthropogenic disturbances for the mechanisms structuring arthropod communities.

The transition from stochastic to deterministic communities described here might be a general principle which has been neglected in the discussion of the mechanisms structuring communities. According to our findings, human disturbances in highly diverse tropical ecosystems cause not only faunistic changes that mostly lead to a reduction of diversity (Turner 1996, Wardle 1996, Bascompte and Solé 1996) but change the dynamics of the whole system. Ant communities of disturbed forests, for example, corresponded to a large degree with predictions of the niche theory: They were saturated and only few species dominated the communities, resulting in a deterministic community structure (see also Floren and Linsenmair in press). Such a pattern, which is usually interpreted as a consequence of a resource dividing mechanism, was never observed in the primary forest. Here, a yet unknown number of species manages to coexist, probably because deterministic structuring has been replaced by stochastic processes. For example, decisive to the structure of a community might be the arrival of a species at an available resource at the most favourable time. Whether the species is successfully integrated in the community might then depend on the combined influence of all established members of the particular community. Such a mechanism of community assemblage would greatly depend on the initial conditions and could explain the coexistence of many communities in equilibrium. In correspondence with our results, communities could not be distinguished from randomly assembled ones, even if the actual community structure would be the result of a deterministic structuring mechanism (Floren and Linsenmair 2000). The reasons, that cause the change to a deterministic community structure in the disturbed forests are currently investigated. Essential are probably the greatly reduced number of species in the structurally much more simple disturbed forests, in which the distribution of food and nesting resources can change distinctly, therewith significantly influencing the structure of ant communities (Jackson 1984, Hölldobler and Wilson 1990).

If this hypothesis is true than it might be applicable also to the ecosystems of the temperate latitudes. For this reason, we are carrying out comparable studies in forests of Central Europe.

If our hypothesis could be confirmed, it would mean that the deterministic approach of the niche theory would refer mainly to anthropogenically disturbed ecosystems, and would not be of the general importance ascribed for the ecosystems of temperate latitudes.

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References

- Adis, J., Basset, Y., Floren, A., Hammond, P. M. and Linsenmair, K. E. 1998. Canopy fogging of an overstorey tree – Recommendations for standardisation. – *Ecotropica* 4: 93 – 97.
- Andersen, A. N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems. a review and a recipe. – *Proc. Ecol. Soc. Aust.* 16: 347–357.
- Bascompte, J. and Solé, R. V. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. – *J. Anim. Ecol.* 65: 465–473.
- Chapin, F. S. et al. 1997. Biotic control over the functioning of ecosystems. – *Science* 277: 500– 503.
- Davis, A. J. and Sutton, S. L. 1998. The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. – *Diversity Distrib.* 4: 167–173.
- Didham, R. K., Ghazoul, J., Stork, N. E. and Davis, A. J. 1996. Insects in fragmented forests: a functional approach. – *Trends Ecol. Evol.* 11: 255–260.
- Floren, A. and Linsenmair, K. E. 1997 Diversity and recolonisation dynamics of selected arthropod groups on different tree species in a lowland rain forest in Sabah, Malaysia with special reference to Formicidae. – In: N. E. Stork, J. Adis and Didham, R. K. (eds), *Canopy Arthropods*. Chapman and Hall, London, pp. 344–382.
- 1998a. Non–equilibrium communities of Coleoptera in trees in a lowland rain forest of Borneo. – *Ecotropica* 4: 55–67.
- 1998b. Diversity and recolonisation of arboreal Formicidae and Coleoptera in a lowland rain forest in Sabah, Malaysia. – *Selbyana* 19: 155–161.
1999. Changes in arboreal arthropod communities along a disturbance gradient. – *Selbyana* 20(2): 284–289.
- 2000. Do ant mosaics exist in pristine lowland rain forest? – *Oecologia* 123: 129–137.
- 2000. The influence of anthropogenic disturbances on the structure of arboreal arthropod communities. – *Plant Ecology*, in press.
- Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. – *Biodiv. Conserv.* 7: 1221–1244.
- Hölldobler, B. and Wilson, E. O. 1990. *The ants*. – Harvard Univ. Press.
- Horstmann, K., Floren, A. and Linsenmair, K. E. 1999. High species–richness of Ichneumonidae from the canopy of a Malaysian rain forest. – *Ecotropica* 5: 1–12.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. – *Ecology* 52: 577–586.
- Jackson, D. A. 1984. Ant distribution patterns in a Cameroonian cocoa plantation: investigation of the ant mosaic hypothesis. – *Oecologia* 62: 318–324.
- Kantz, H. and Schreiber, T. 1997. *Nonlinear time series analysis*. – Cambridge Univ. Press.
- Lawton, J. H. et al. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. – *Nature* 391: 72–75.
- Leston, D. 1973. Ants and tropical tree crops. *Proc. Royal Entomol. Soc.* , Ser C: 39: 6–1.
- Mason, D. 1996. Responses of Venezuelan understorey birds to selective logging, enrichment strips, and vine cutting. – *Biotropica* 28: 296–309.
- Majer, J. D. 1993. Comparison of the arboreal ant mosaic in Gahna, Brazil, Papua New Guinea and Australia – its structure and influence on arthropod diversity. – In: Salle, J. L. and Gauld, J. D. (eds), *Hymenoptera and Biodiversity*. CAB International, pp. 115–141.
- Room, P. M. 1975. Relative distributions of ant species in cocoa plantations in Papua New Guinea. – *J. Appl. Ecol.* 12: 47–61.
- Schwartz, M. W., Brigham, C. A., Hoeksema, J. D., Lyons, K. G., Mills, M. H, and van Mantgem, P. J. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. – *Oecologia* 122: 297–305.

- Shinozaki, K. 1963. Note on the species–area curve. Proc. of the 1th Ann. Meet. Ecol. Soc. Japan, Tokyo.
- Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. – J. Appl. Ecol. 33: 200–209.
- Turner, I. M. and Corlett, R. T. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. – Trends Ecol. Evol. 11: 330–333.
- Wardle, D. A. 1999. Biodiversity, ecosystems and interactions that transcend the interface. – Trends Ecol. Evol. 14: 125–127.
- Walter, G. H. 1988. Competitive exclusion, coexistence and community structure. – Acta Biotheor. 37: 281–313.

Table 1. Changes in species diversity of ant communities among forest types. P: primary forest, SI: 5 year–old forest, SII: 15 year–old forest, SIII: 40 year–old forest. RAF–value: Rarefaction value calculated on a subsample of $m = 4143$ ant individuals. Species with at least 5 ind.: number of species per forest type considered in the evaluation

Forest type	Fogged trees	Total number of species	RAF–value (m=4143)	Species with At least 5 ind.	% primary forest species
P	19	195	103.8	111	100 %
SI	10	34	34	23	9.7 %
SII	11	67	52.5	42	19.5 %
SIII	10	116	82.6	68	27.7 %

Table 2. (Appendix table): Changes in abundances of ant species between forest types. P: primary forest, SI: 5 year–old forest, SII: 15 year–old forest, SIII: 40 year–old forest.

Sp. number per genera	P	SI	SII	SIII
	Abundance			
<i>Camponotus</i> #115	786	0	0	0
<i>Camponotus</i> #74	405	0	0	600
<i>Camponotus</i> #1	324	0	0	0
<i>Camponotus</i> #2	193	0	0	0
<i>Camponotus</i> #73	159	0	0	0
<i>Camponotus</i> #24	156	85	342	453
<i>Camponotus</i> #135	125	0	0	0
<i>Camponotus</i> #91	88	0	0	0
<i>Camponotus</i> #25	58	0	0	0
<i>Camponotus striata</i> #132	56	0	0	0
<i>Camponotus</i> #17	28	14	389	42
<i>Camponotus</i> #144	9	0	28	105
<i>Camponotus</i> #176	5	51	151	170
<i>Camponotus</i> #153	3	177	5	209
<i>Camponotus</i> #282	0	821	6151	2274
<i>Camponotus</i> #283	0	0	69	0
<i>Camponotus</i> #285	0	0	380	0
<i>Camponotus</i> #75	0	0	126	0
<i>Camponotus</i> 326	0	0	1	61
<i>Polyrhachis</i> #6	533	14	7	2
<i>Polyrhachis</i> # 171	242	0	0	0
<i>Polyrhachis</i> #7	137	9	437	316

<i>Polyrhachis</i> #88	133	0	0	0
<i>Polyrhachis</i> #112	125	0	0	0
<i>Polyrhachis</i> #173	70	0	0	0
<i>Polyrhachis</i> #10	65	17	13	21
<i>Polyrhachis</i> #103	9	0	0	91
<i>Polyrhachis</i> # 239	0	0	0	73
<i>Polyrhachis</i> #230	0	0	0	167
<i>Polyrhachis</i> #273	0	313	76	343
<i>Gesomyrmex</i> #95	13	0	33	57
<i>Gesomyrmex</i> #241	0	192	0	0
<i>Lepisota</i> #21	738	0	0	0
<i>Prenolepis</i> #108	3	304	77	98
<i>Echinopla</i> #72	70	0	0	0
<i>Paratrechina</i> #87	70	0	0	0
<i>Plagiolepis</i> #154	5802	0	14	0
<i>Cladomyrma</i> #278	0	0	406	91
<i>Dolichoderus</i> #23	7110	0	48	859
<i>Dolichoderus</i> #22	2694	0	0	0
<i>Dolichoderus</i> #267	2201	0	0	0
<i>Dolichoderus</i> #236	891	0	0	0
<i>Dolichoderus</i> #68	391	0	0	0
<i>Dolichoderus cuspidatus</i> #97	165	0	0	0
<i>Technomyrmex</i> #29	9280	0	0	63
<i>Technomyrmex</i> #27	1507	0	0	0
<i>Technomyrmex</i> #159	237	0	0	0
<i>Technomyrmex</i> #60	162	0	0	5
<i>Technomyrmex</i> #28	153	0	0	250
<i>Tapinoma</i> #61	58	58	4	392
<i>Tapinoma</i> #62	59	2	3	9
<i>Philidris</i> #94	76	0	0	2709
<i>Crematogaster</i> #155	4717	0	0	0
<i>Crematogaster</i> #83	2658	0	0	0
<i>Crematogaster</i> #116	467	0	0	32
<i>Crematogaster</i> #46	350	0	16	2843
<i>Crematogaster</i> #43	279	998	1867	34
<i>Crematogaster</i> #44	257	0	611	0
<i>Crematogaster</i> #105	161	8	61	34
<i>Crematogaster</i> #156	133	0	0	0
<i>Crematogaster</i> #45	51	0	0	0
<i>Crematogaster</i> #223	0	0	0	1400
<i>Crematogaster</i> #224	0	0	782	674
<i>Crematogaster</i> #312	0	95	0	0

<i>Crematogaster</i> #313	0	0	667	0
<i>Cataulacus</i> #36	98	0	83	62
<i>Cataulacus</i> #55	50	0	0	0
<i>Cataulacus</i> #20	3	0	0	60
<i>Cataulacus</i> #304	0	0	30	283
<i>Monomorium</i> #38	344	0	0	0
<i>Monomorium</i> #58	121	0	1	1
<i>Dilobocondyla</i> #211	1	0	11	90
<i>Oligimymex</i> #65	867	0	0	112
<i>Pheidole</i> #56	808	0	1	27
<i>Tetramorium laparum</i> #34	78	0	0	224
<i>Vollenhovia</i> #104	5	0	1	68
<i>Meranoplus</i> #77	6	0	0	233
<i>Tetraoponera attenuata</i> #92	735	31	586	653
<i>Tetraoponera</i> #48	71	0	0	2
<i>Tetraoponera</i> #47	59	0	3	10
<i>Tetraoponera pilosa</i> #147	1	49	75	50
<i>Tetraoponera difficilis</i> #258	0	793	925	492
<i>Tetraoponera</i> #119	0	24	34	173
<i>Tetraoponera</i> #301	0	0	89	7
<i>Tetraoponera</i> #324	0	8	2	65
<i>Tetraoponera</i> #303	0	0	54	0
<i>Diacamma</i> #291	0	0	0	172

Figure 1: Shinozaki curves: a) computed for all ant species of all forest types (circles), and b) cumulative curve for new species found in each forest type (diamonds). To give a clear picture, this curve begins with SI and not with the primary forest (P), which, however, was taken as the basis of the comparisons (see text).

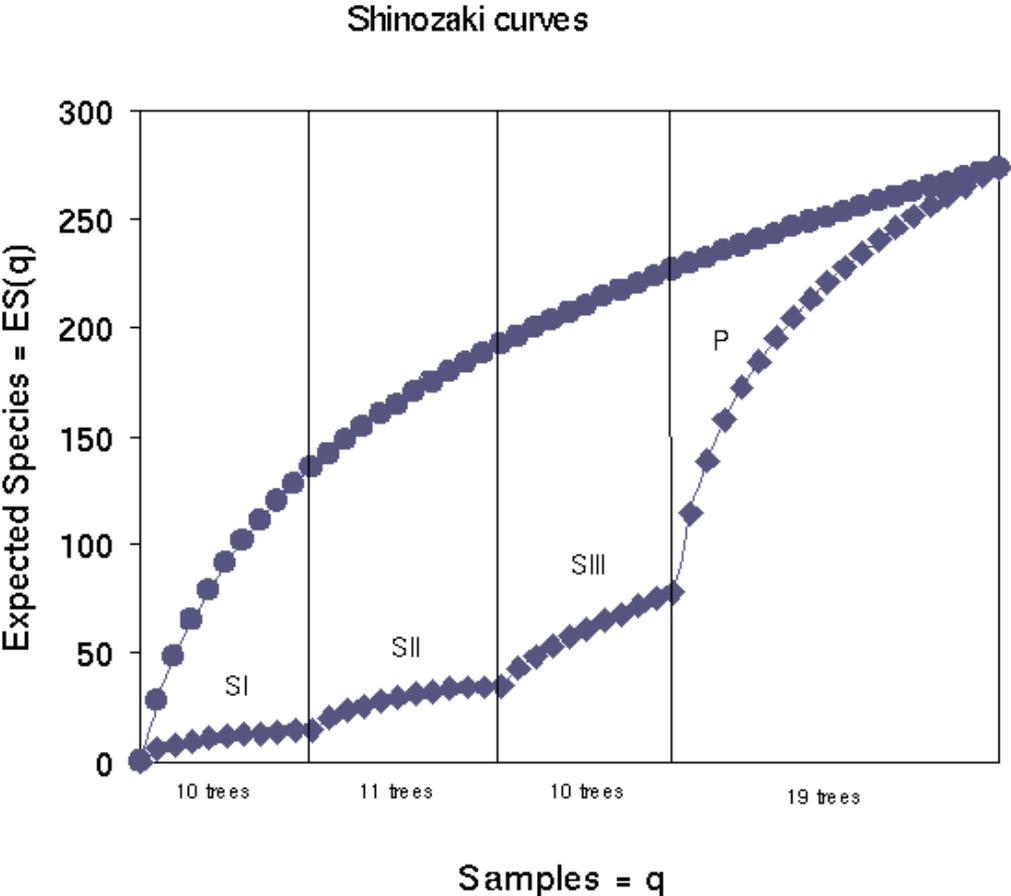


Figure 2: Correlation matrices of ant communities of all forest types. a) computed on the basis of species presence b) computed on the basis of species abundances. Tree numbers: 1 to 19 refer to the primary forest, 20 to 29 refer to SI, 30 to 40 refer to SII, 41 to 50 refer to SIII.

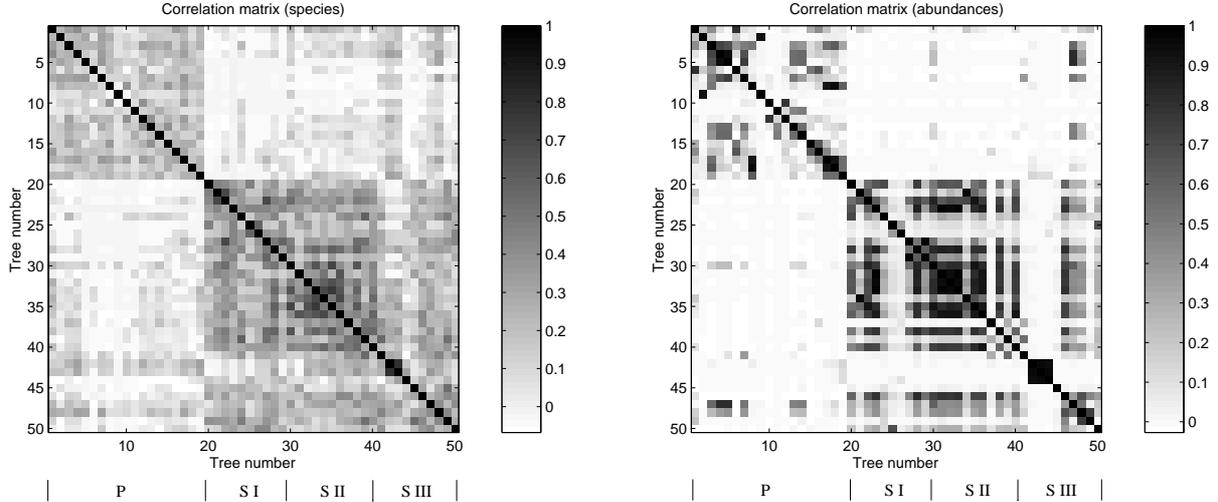


Figure 3: Results of the surrogate analysis for the primary and for the disturbed forest types. Dark columns: distribution of the mean correlation values of the primary surrogate forests, light columns: distribution of the mean correlation values of the disturbed surrogate forests. The mean correlation values of the original matrices are marked by open circles (primary forest) and diamonds (disturbed forests).

