Biodiversity and Conservation **12:** 1371–1389, 2003.

Size does matter – effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia

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Received 28 September 2001; accepted in revised form 22 July 2002

Key words: Biodiversity, Conservation, Formicidae, Isolation, Species loss

Abstract. Primary tropical lowland rainforest in Sabah, Malaysia, has been largely reduced to small to medium-sized, often isolated, forest islands surrounded by a highly altered agricultural landscape. The biodiversity patterns of leaf litter ant communities were monitored in two forest fragments of differing size as well as in a contiguous forest over the course of two years. Species number and diversity in the forest isolates was significantly lower, reaching only 47.5% of the species number collected in the contiguous forest. Species density was also lower, which had led to a thinning of the ant community in the fragments. Community composition was substantially altered in the forest remnants, and an increase of tramp species with smaller fragment size was detected. These results were unexpected and alarming, as the medium-sized forest is with its 42.9 km^2 a comparatively large primary forest fragment for Sabah.

Introduction

The most species-rich terrestrial ecosystems, tropical rainforests, are disappearing from the surface of the earth at a fast rate. Their valuable timber is targeted by logging operations, leaving forests with an open canopy and highly altered stand structure. Not only is the tropical rainforest affected by disturbances due to timber harvesting, it is also becoming increasingly fragmented because of conversion of the landscape into agricultural plantations and pastures. This process often starts with selective logging within a matrix of natural forest, then increasingly intensive agricultural landscapes develop, finally leaving only isolated islands of residual forest (Seidler and Bawa 2001). A key study has found that by 1988, the part of the Amazon forest in Brazil that was fragmented or prone to edge effects was over 1.5 times larger than the area actually deforested (Skole and Tucker 1993). So far only few biodiversity studies have included the remaining systems of logged-over and regrowth secondary forests or forest fragments of various sizes in their inventory (Chazdon 1994), although these habitats will be the target areas in future conservation and management strategies.

The forests of Borneo are especially species-rich in their floral and faunal composition, comprising many endemic species (MacKinnon et al. 1996), with a recognised hotspot of biodiversity in Sabah, a federal state of Malaysia in the northwestern part of the island (Myers 1988; Wilson 1992; Kitching 2000). Although Sabah had about 45% (33486 km^2) of its land under natural forest in 1992, the forest cover has been disappearing at a fast rate since then (Chey et al. 1997). Today Sabah has almost depleted its primary forests outside the conservation areas because of the commercial value of its dipterocarp timber (Chung et al. 2000). Many logged-over and regenerating forests are threatened by conversion to other land uses because they are close to the agricultural frontier and easily accessible.

During the past decades, the tropical rainforest in Sabah has not only been subjected to selective logging at various intensities, but the establishment of oil palm plantations has led to clearing on a wide scale. Over 1 million ha of forest land has been converted into large-scale monocultures of oil palm, a major cash crop of great importance to the state economy. The remaining lowland primary forests only persist in the form of small forest isolates within a matrix of highly disturbed habitat. Most of these isolates are protected virgin jungle reserves (VJR) covering a total of 90386 ha. The average size of VJRs in Sabah is 1802 ha compared to 244 ha on the Malaysian Peninsula (Laidlaw 1996). There is uncertainty about the condition of most of these forest reserves, though it is known that some of the smaller VJRs have been illegally logged or affected by extensive anthropogenic forest fires in the 1997–1998 ENSO event.

According to the theory of island biogeography (MacArthur and Wilson 1967), species richness in habitat fragments is a function of island size and degree of isolation. Conclusions about the effects of fragmentation on tropical rainforest fauna have so far mostly been based on observational studies on butterflies (e.g. Shahabuddin and Terborgh 1999; Thomas 2000), birds (e.g. Stouffer and Bierregaard 1995; Jullien and Thiollay 1996; Arango-Velez and Kattan 1997; Cooper and Francis 1998) and mammals (e.g. Laidlaw 1996, 2000; Chiarello 2000). The only study of fragmented landscapes – the Biological Dynamics Forest Fragments Project (BDFFP) in the tropical rainforests of Brazil – has so far provided us with most of what we know about the reaction of tropical forests to fragmentation, despite its limited information about replicates, size of fragments and matrix composition (Bierregaard et al. 1992; Laurance and Bierregaard 1996). Due to the differences in the ecosystem characteristics of tropical forests, the results from Brazil are not easily transferable to Southeast Asian rainforests (Linsenmair 1997).

Studies on Malaysian forest fragmentation and its effects on fauna or flora are scarce (Laidlaw 1996, 2000) and do not exist for Sabah, despite the recent large-scale landscape alterations described above. This study describes the results of an analysis of the leaf litter ant fauna of primary rainforest fragments of various sizes in comparison with a contiguous rainforest.

Leaf litter ants are considered to be useful indicators of ecosystem disturbance in various habitats (Majer et al. 1984; Agosti et al. 2000) and they have been found to show congruent patterns in their responses to environmental change with other taxa (Lawton et al. 1998; Alonso 2000). As a rule, 45–50% of all macro invertebrates in the leaf litter of a tropical rainforest are ants (Adis et al. 1989) and there is high local diversity: 139 species were collected in only 60 m^2 of leaf litter in a tropical rainforest in Sabah (Brühl et al. 1998). Due to their effects on soil structure and

Table 1. Description of study sites: number of plots and samples, distances between sites, sampling date. Each year, all plots were sampled between January and April.

Forest	Type	Plots	Sampled in	Number of samples (m^2)	Distances (km)	Danum Valley	Sepilok Forest	Kebun Cina
Danum Valley	Large	L1 L2	1998, 1999 1998	180	Danum Valley	–	100	100
Sepilok Forest	Medium	M1 M2	1998, 1999 1999	180	Sepilok Forest			15
Kebun Cina	Small	S1	2000	60	Kebun Cina			

processes which affect the flow of energy and material in ecosystems and provide habitats for other species, ants have been described as ecosystem engineers (Folgarait 1998). Worldwide, they possibly turn and enrich more soil than earthworms (Wilson 2000), thereby promoting the mineralisation of nutrients (Gunadi and Verhoef 1993) and furthering microbial activity in the soil (Dauber and Wolters 2000). In tropical rain forests, ground-dwelling ants are especially important as invertebrate predators, exerting a structuring influence on the entire arthropod community (Carroll and Janzen 1973; Hölldobler and Wilson 1990).

Methods

Study sites

Danum Valley Conservation Area (large)

The Danum Valley Conservation Area covers 438 km^2 of dipterocarp lowland forest of the *Parashorea malaanonan* Type A (Marsh and Greer 1992). The area is surrounded by logged-over forest in varying degrees of disturbance. The forest around the Danum Valley Field Center (DVFC) is dominated by *Parashorea malaanonan* and *P. tomentella* (white Seraja group) together with *Shorea johorensis* and other *Rubroshorea* sp. (red Seraja group) with a very distinguished high proportion of Euphorbiaceae and Meliaceae (Newbery et al. 1992).

The mean annual rainfall calculated over 13 years (1986–1998) stands at 2662 mm, making the area drier than most northern parts of Sabah east of the Crocker Range (Chappell 2000). Two research plots were established around the DVFC (4°57.7′ N, 117°48.2′ E): L1 and L2 (L stands for large; see Table 1).

Sepilok Forest Reserve (medium)

The Sepilok Forest Reserve (5°54′ N, 118°04′ E), a lowland rainforest reserve of 42.9 km^2, is situated 24 km west of Sandakan on the east coast of Sabah. Sepilok is dominated by a mixed dipterocarp lowland forest of the *Parashorea tomentella-Eusideroxylon zwagleri* type, with interspersed keranga forest on sandstone ridges. The reserve is surrounded by various types of plantations (fruit trees, old rubber and oil palm plantations) to the east, north and west and by mangrove forests and the sea to the south (Fox 1969, 1973). The mean annual rainfall measured at Sandakan Airport (1951–1998) was 3017.4 mm. Two research plots were established: M1 and M2 (M = medium).

Kebun Cina Forest Reserve (small)

Kebun Cina Forest Reserve (Malay for 'Chinese gardens', 5°52′ N, 118°05′ E) is situated 3 km west of Sandakan harbour. The reserve is 1.46 km^2 in size and covered with *Parashorea tomentella-Eusideroxylon zwagleri* primary forest typical of the Sandakan area. The geology, soils and climate are also comparable to Sepilok Forest, which is at a distance of about 15 km. The reserve is surrounded by houses to the north and east and old rubber plantations to the west and south. No detailed information about the history of the forest fragment and time since isolation is available, although the rubber trees are at least 30 years old. The only transect line followed the main trail (Plot S1; S = small).

The distances between the study sites and year of sampling of the various plots are given in Table 1. The sampling took place between January and April every year. The borders of the plots were at least 500 m from the forest edge to avoid edge effects.

Sampling

The collection of leaf litter ants took place at six separate sampling sites along a transect line with a distance of 100 m between the centres of the sampling sites. This sampling design proved to be highly efficient in terms of effort, with ca. 70% of the estimated species pool collected (Brühl 2001). Around the centre of each sampling site, 10 1-m^2 samples of leaf litter were collected in one go, situated at least 3 m apart from each other. Three meters is a distance which exceeds the foraging range of most litter-inhabiting ants (personal observation; Kaspari 1993). The litter was sifted using a sieve with 1 × 1 cm mesh size. Litter is defined as the layer of leaves and detritus which can readily be scraped away from the more compact soil. Sampling was undertaken at least two days after heavy rains, thus ensuring that small arthropods would not stick to the water film on leaves and could reliably be extracted using the method. Sifting was conducted between 9.00 A.M. and 14.00 P.M. The litter samples were left for extraction in a mini Winkler apparatus in a shady place for three days (for more details, see Bestelmayer et al. 2000).

Sample processing

The resulting ant samples were presorted in alcohol to genus level under a dissecting microscope and then mounted on cardboard pins, following the convention of Bolton (1994). Genus identification was performed again, this time on the mounted specimen using the key of Bolton (1994). Finally, morphospecies were designated based on external morphological characters of the worker class using a Leica MZ 8

(16 × 14) and wherever possible valid species names were assigned with the help of experts. The processes of sorting, mounting and first identifications are excellently described by Lattke (2000). For the genus *Pheidole* we included additional characters of the major workers for morphospecies designation following Eguchi (2001).

For the analysis of the leaf litter ant communities of the various forests, only species that could be quantitatively collected by the Winkler method and species typical of the leaf litter stratum were included. Large species (>15 mm) which would not fit through the 4 mm mesh bag of the Winkler apparatus and could therefore not be collected systematically were excluded from the analysis. Information on the stratification of ants was available from previous studies on ants in Sabah (Brühl et al. 1998). Some ant species typical of deep soil (species of the genera *Protanilla* and *Aenictus*) or vegetation and canopy (*Camponotus*, *Polyrhachis*, *Dolichoderus*, *Echinopla* species and some species of *Cataulacus* and *Cerapachys)* occasionally encountered in the samples were consequently excluded from the analysis.

Data entry

The presence and absence of ant species in the samples was noted in a data matrix. We did not include data relating to abundance, as ants are social organisms and the presence of many individuals may be simply due to collecting a nest or a column of foragers. The presence–absence approach is preferred, as some analyses assume that within a spatially and temporally defined community, all individuals have an equal probability of being sampled, which is not the case for the highly aggregated ants (Folgarait 1998; Longino 2000). To get an estimate of the relative abundance of a species we therefore collected many samples and used the incidence in samples as the measure of abundance: a common ant species is present in most of the 60 samples of a forest plot, whereas a rare species is only found in fewer than five samples.

Statistical analysis

Only high sampling with the species accumulation curve reaching an asymptote and the species richness estimators following this pattern will yield a reliable estimate of the total species richness of a community (Soberon and Llorente 1993). It is therefore very important that sampling be thorough and large sample sizes collected (Peterson and Slade 1998; Longino 2000). Species accumulation curves and estimators were calculated using the computer package EstimateS 5.0 (Colwell 1997), randomising the data 100 times. We calculated six estimators of species richness, as so far no best performing estimator exists (for a detailed description of the mathematical background or applied examples, see Colwell and Coddington 1994; Coddington et al. 1996; Colwell 1997; Dobyns 1997; Butler and Chazdon 1998).

To compare community diversities, we calculated the Renyi family for ranking of α-diversities (Legendre and Legendre 1998; Rennolls and Laumonier 2000). By

Table 2. Observed ant species numbers in the forest plots calculated by different species richness estimators (rounded). The sampling efficiency (percentage value of observed divided by estimated species) is given in brackets. Lowest and highest estimates of sampling efficiency are given in bold.

Forest	Plots	Species number	ICE	Chao2	Jack1	Jack2	Bootstrap	MMMean	Mean
Danum Valley	L1-98	105	126 (83.1)	133 (78.9)	132 (79.8)	145 (72.3)	117 (89.7)	118 (88.9)	129 (81.7)
	L1-99	97	116 (83.8)	112 (86.8)	120 (81.1)	125 (77.8)	108 (89.5)	114 (85.4)	116 (83.9)
	L2-98	100	133 (74.9)	141 (70.5)	132 (75.5)	152 (65.8)	114 (87.4)	114 (87.4)	131 (76.1)
Sepilok Forest	M1-98	49	77 (63.6)	**97** (**50.5**)	70 (69.0)	87 (56.3)	58 (84.4)	68 (72.0)	76 (64.1)
	M1-99	61	98 (62.2)	105 (58.0)	89 (68.5)	107 (57.0)	73 (83.5)	76 (80.2)	91 (66.9)
	M2-99	39	49 (79.5)	46 (84.7)	50 (78.0)	52 (75.0)	44 (88.6)	48 (81.3)	48 (80.9)
Kebun Cina	S1-00	45	65 (69.2)	71 (63.3)	61 (73.7)	71 (63.3)	52 (86.5)	**49** (**91.8**)	61 (73.1)

varying the scale parameter α, the resulting Renyi index $H(\alpha)$ generates a range of diversity measures including Shannon–Wiener's H' and Simpson's D. If a community displays higher values over the whole range it is more diverse; if the Renyi functions of two communities cross, they are non-comparable. The Renyi series was calculated using the Species Diversity and Richness 2.3 (Henderson and Seaby 1998) software package.

For the analysis of community composition, we followed the suggestions made by Faith et al. (1987) for species count data. The data were standardised by dividing each value by the maximum abundance for that species in the data set and the Steinhaus similarity measure was used (Legendre and Legendre 1998). The resulting matrix was subjected to multidimensional scaling (MDS) (Minchin 1987; Pfeifer et al. 1998). We used a stepwise approach in the reduction of dimensions (Legendre and Legendre 1998) in the available package in STATISTICA 5.5. (StatSoft 2000).

The general statistical tests follow Sokal and Rohlf (1981) and were calculated with STATISTICA 5.5. (StatSoft 2000).

Results

Number of species

A total of 187 species in 48 genera and five subfamilies were recorded in the 420 m^2 sampled. The highest species numbers per sampled 60 m^2 were reached in the large plots of Danum Valley (97, 100 and 105 species) and the lowest species number was recorded in a medium plot in Sepilok Forest (plot M2-99: 39 species) (Table 2).

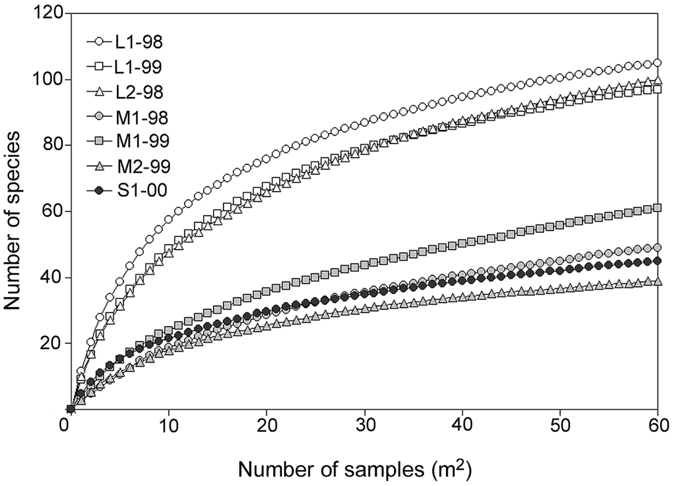

Figure 1. Randomised species accumulation curves of the ant communities of the forest plots in the different years (L = large, M = medium, S = small).

Sampling efficiency: species richness estimators and species accumulation curves

Estimated sampling efficiency (Table 2) was highest in S1-00 (MMMean estimator) and lowest in M1-98 (Chao2 estimator). Sampling efficiency was highest in the MMMean and Bootstrap estimators (generally over 80%) and reached lowest values in the Chao2 estimator that also yielded the highest variation between plots. The mean of the six estimators produced values of a sampling efficiency of between 64.1 and 83.9%.

The slopes of the species accumulation curves of the various plots were very similar (Figure 1). The increase in species in the last 10 samples was between three and six species. The species accumulation curves for plots in the large primary forest of Danum Valley increased more rapidly in the first 10 samples and were all situated above the curves of the plots in Sepilok Forest and Kebun Cina. The curve of the small plot (S1-00) was interspersed between the curves of the less species-rich medium plots.

Rank abundance curves

In Figure 2, species abundance is plotted against rank order for each plot. All rank

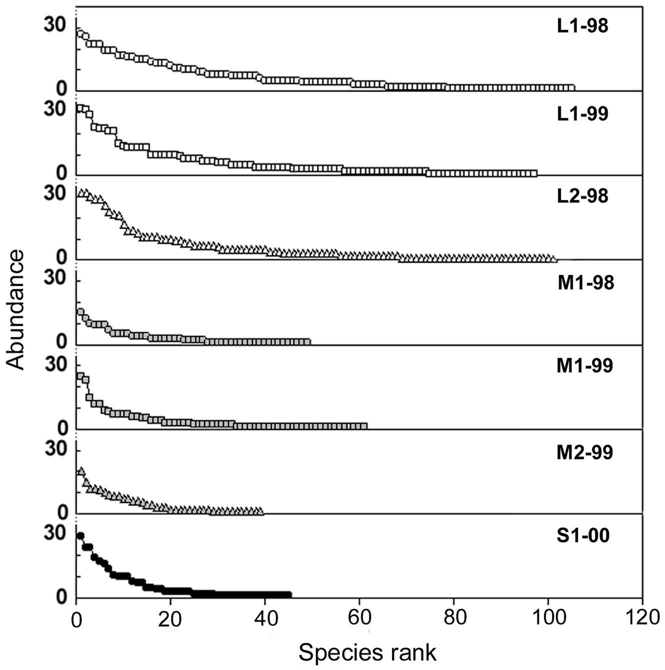

Figure 2. Rank abundance distributions of the ant communities in the various forest plots (L = large, M = medium, S = small). Species abundance is plotted against rank order for each plot (60 m^2 per plot).

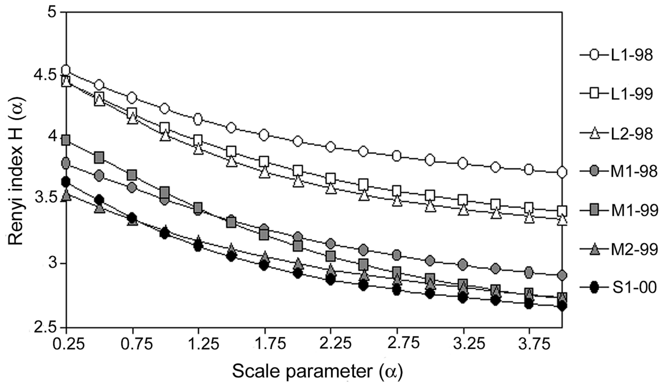

Figure 3. The Renyi family of the different forest plots. The Renyi index $H(\alpha)$ of the leaf litter ant communities of the different plots (L = large, M = medium, S = small) with varying scale parameter (α).

abundance distributions followed the log series model and were therefore generally similar in appearance. The species on first ranks were collected in most samples (common species). The species forming the tail of the curve were only encountered in a few samples (rare species). Highest abundances for the most common species were obtained in Danum Valley (L2-98: 32 samples), though closely followed by the small plot (S1-00: 29 samples). In Sepilok, most common species show mean abundances of 20 samples (M1-98: 15, M1-99: 25, M2-99: 20) compared to Danum Valley with 28 samples (L1-98: 27, L1-99: 26, L2-98: 32). The rank abundance curves for the large plots display a longer tail because of a higher number of rare species. The number of uniques (species collected in only one sample) is slightly higher in the large plots (L1-98: 27 species, L1-99: 23, L2-98: 32) than in the medium or small plots (M1-98: 22, M1-99: 28, M2-99: 11, S1-00: 16). The plots in the various forests are even more distinct if the number of species collected below five samples (rare species) is taken into account: the large plots show similar high numbers of rare species (L1-98: 58, L1-99: 60, L2-98: 60), whereas the numbers were lower in the medium and small plots (M1-98: 38, M1-99: 46, M2-99: 25, S1-00: 29).

Renyi index

The Renyi index curves of the Danum Valley communities are positioned above those of the smaller forests for all scale parameters, with L1-98 being the most diverse community across the entire range of the scale parameter (Figure 3). The communities L1-99 and L2-98 of Danum Valley and M1-98 and M1-99 of Sepilok could not be ordered because the curves cross each other. The communities of M2-99 and S1-00 were also non-comparable. The community diversities in the small forest of Kebun Cina are lower across all scale parameters than in plots M1-98 and M1-99 of Sepilok Forest.

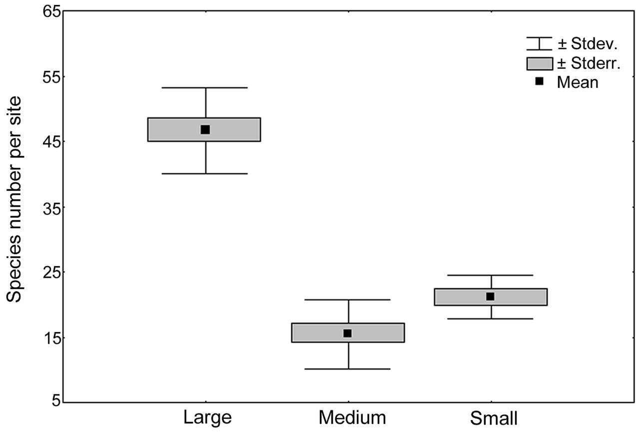

Figure 4. Species number per site (10 m^2) in the three different forests ($n = 12$ for large and medium, $n = 6$ for small).

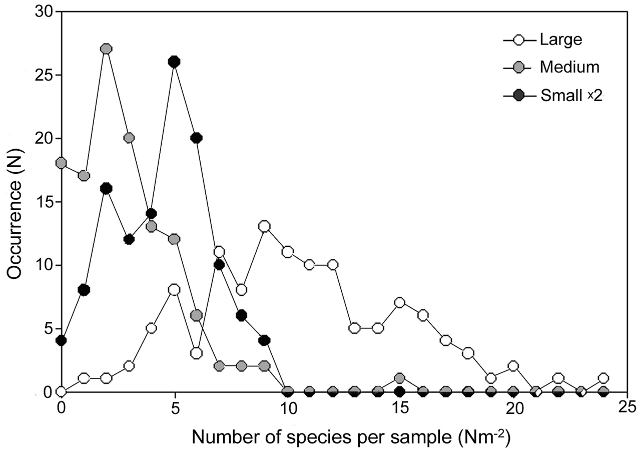

Figure 5. Species density distribution per m^2. The number of species occurring in the 1-m^2-unit samples in the different forest plots ($n = 120$, small corr. ×2).

Species number at the sampling sites (10 m^2*)*

To be able to do a comparison of the three forests at a lower spatial scale, the numbers of leaf litter ant species collected at individual sampling sites (10 m^2) were compared. The independent spatial samples (plots L1-98, L2-98, M1-98, M2-99) yielded 12 sites for Danum Valley and Sepilok Forest and six for Kebun Cina. An ANOVA revealed a statistically significant difference in species number per site between the three forests (df = 2, $F = 101.67$, $P \ll 0.001$; Figure 4). A Scheffe *post-hoc* test demonstrated highly significant values for the comparisons between

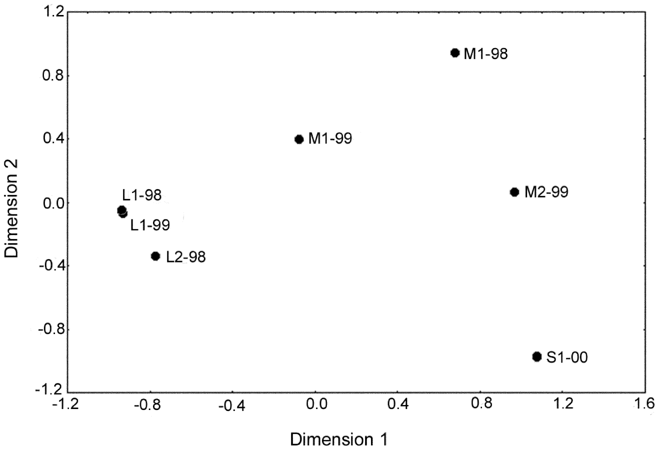

Figure 6. MDS based on the standardised Steinhaus index of the ant communities of the various forest plots (L = large, M = medium, S = small; two dimensions, stress: 0.03). The large plots are separated from the medium and small plots along dimension 1 (MANOVA, $P < 0.01$).

Danum Valley and the two other forests ($P \ll 0.001$). There was no statistically significant difference in the species numbers per site between Kebun Cina and Sepilok.

Species density distribution

The finest spatial resolution is represented by the number of ant species collected in 1 m^2 of leaf litter. For Danum Valley and Sepilok Forest only the spatial replicates were used and the Kebun Cina samples were corrected for sample size difference by multiplying by a factor 2. The shapes of the resulting species distributions of the three primary forests were different (Figure 5): the curve of Danum Valley was bell-shaped, whereas in Sepilok Forest and Kebun Cina Forest the distributions were skewed to the left. Ten species of leaf litter ants were collected in an average square meter in the large forest of Danum Valley; in the medium and small forests this value decreased to three and four species. In the large forest, ants were recorded in every sample; in the medium and small forests, 18 (of 180) and 4 (of 120) samples, respectively, were found without ants.

Community composition

MDS ordination of community similarity values produced the following picture (Figure 6): the large plots are generally situated adjacent to each other, especially the temporal replicates of consecutive years (L1-98 and L1-99). The temporal and spatial replicates in the medium plots of Sepilok Forest were positioned at a greater distance to each other. The position of the small plot of the Kebun Cina ant community is closer to Sepilok M2-99 than any other plot. The two dimensions explain 96.8% of the variation in the data, dimension 1: 87.8% and dimension 2: 9.0%. The Danum Valley plots are distinctly different from the plots in Sepilok and Kebun Cina along dimension 1 (MANOVA: $\mathrm{df}_{\mathrm{effect}} = 2$, $\mathrm{df}_{\mathrm{error}} = 4$, $F = 20.21$, $P < 0.01$; dimension 2 NS; Scheffe *post-hoc* test: differences between: Danum Valley–Sepilok: $P < 0.05$, Danum Valley–Kebun Cina: $P < 0.01$, Sepilok–Kebun Cina: NS).

Discussion

Sampling efficiency: species number, richness estimators and accumulation curves

The absolute measure of diversity – species number – decreased from an average of 101 species in the large forest plots to an average of 48 species per plot in the primary forest fragments (47.5%). Estimated species richness was closest to the observed species numbers in the large plots, producing high sampling efficiency values in the various estimators. The lowest values for sampling efficiency in the different estimators were obtained in plots M1-98 and M1-99 in Sepilok Forest. This is due to the high proportion of unique species (M1-98: 22 of 49 species [44.9%]; M1-99: 28 of 61 species [45.9%]), in contrast to the species-rich large plots (e.g. L1-98: 27 of 105 species [25.7%]), since the Chao2 estimator reacts particularly sensitively to uniques. The low estimates of Chao2 also influenced the means of all six estimators of the two plots, yielding the lowest values with 64.1 and 66.8%. The general high sampling efficiency together with a similar performance and high saturation of the species accumulation curves demonstrates that the applied sampling method yielded a high number of the present species in the various forests.

Rank abundance distribution

The distributions of the large forest were across most ranks higher in abundance and also displayed a longer tail. Differences existed in the number of uniques and rare species: the plots of the medium and small forests always demonstrated similarly low numbers compared to the large primary forest of Danum Valley. However, even though there were substantially lower total species numbers, the plots in the smaller forests included proportionally more unique and rare species in the community (rare species: large plots, mean: 57.1%; medium plots, mean: 72.3%, small plot: 64.4%). Unlike the unique and rare species, the most common species in the small and medium forests were present in a similar number of samples as those in the large forest. Consequently, the curves of the smaller primary forests are compressed in shape, directly affecting the evenness of the distribution.

Renyi index, species number at sites and species density

Diversity ordering (the Renyi index) demonstrated the differences between the large plots and the plots in the forest fragments: higher values over all scale parameters, and similar diversities in S1-00 and M2-99. At the smaller spatial scale of sampling sites, the pattern was confirmed: there were significantly lower species numbers in Sepilok Forest and Kebun Cina (16 or 21 species compared to an average of 46 species in Danum Valley). The species numbers at sampling sites within the fragments were also lower than those recorded on average in different logged-over forests (22–31 species; Brühl 2001). The smallest scale in the analysis, the density of ant species per square meter, clearly showed the difference between the forest fragments and the contiguous forest and suggested a tremendous thinning of the leaf litter ant community in those forests. This thinning, where ants were absent in up to 15% of the samples (Sepilok Forest), might be one reason for the loss of species in the forest fragments at higher spatial scales.

Community composition

The communities of the Danum Valley plots were more similar to each other and distinctly different from the communities of the Sepilok Forest and Kebun Cina plots. The species-rich communities in Danum Valley showed less spatial variation and were more stable through time than in the Sepilok Forest plots, with their fewer species. There was a higher turnover in space and time in Sepilok Forest, possibly due to fluctuations in just a few species, which has a pronounced effect on the species-poorer community. The Sepilok Forest and Kebun Cina forest litter ant communities cannot be separated due to a similar species composition with shared species. In contrast, most of the rare species in Danum Valley are only found in the contiguous forest, separating its community effectively from those in the fragments. The leaf litter ant communities of the fragments resembled thinned subsets of the larger primary forest, with species present at lower densities.

At the plot level, the number of species in the fragments had been reduced to 47.5% of the Danum Valley value. The leaf litter ant communities can be assumed to be drawn from an identical local species pool because (1) the soils and forest type of Sepilok Forest and Kebun Cina are similar to those of Danum Valley, the large primary forest; and (2) the distances between the forests did not translate into proportional distances in MDS. Consequently, the reduction in species number and the changes in community composition in the smaller forest fragments most likely represent the effect of fragmentation, although one cannot completely exclude the possible influence of geographic variation due to (for example) differences in rainfall on species diversity and community composition. The difficulty with rainforest fragmentation studies is always (in Sabah, and probably not only there) that the available forest remnants are not situated in a way that would allow perfect replication of plots with exactly the same environmental conditions, as often required by ecologists, who are more concerned with theory than with the practical considerations necessary to study pressing questions.

Forest fragmentation influences on the ant community were also obvious in other studies. Army ants were among the first to disappear from the small forests in Panama (Franks and Fletcher 1983). A study conducted in the Amazon of 100 ha forest remnants (Carvalho and Vasconcelos 1999) concentrated on twig-nesting ants (52 species), a small proportion of the leaf litter ant community. Findings with respect to species richness and density were very similar to those of the Sabah study: in contiguous forests, species richness and abundances were significantly higher and a greater nest density was found for most species (65.8%). It was suggested that populations of ants are maintained by immigrants from external source populations and isolated populations are therefore extinction-prone. This would be particularly true if the surrounding matrix consisted of pasture or open habitat instead of secondary regrowth forest.

In the oil palm plantations surrounding the remaining forest islands in Sabah, we could only record 13 ant species characteristic of forest leaf litter (Brühl 2001). Most ant species of the forest leaf litter ant community are therefore effectively isolated in the forest fragments, which was also demonstrated by the reduction in genetic variation in two ant species in the same study plots (Bickel 2001).

Forest fragmentation studies have concentrated on a range of other taxa, although studies in the tropics in general are rare. In the BDFFP experiment a very different leaf litter insect fauna composition was observed in isolated forest patches (Didham 1996). The beetle community revealed a lower species richness and a different composition in 100 ha fragments (Laurance and Bierregaard 1996; Didham 1997). The butterfly community within the fragments lost many species, but in the end showed higher species richness than in the contiguous forest due to open habitat species invading the fragments (Brown and Hutchings 1997). Of the vertebrates, birds were often analysed in fragmentation studies. Insectivorous understory birds declined in abundance and species richness in small forest fragments (1–10 ha) in Brazil, the first to disappear being army ant followers (Stouffer and Bierregaard 1995). One possible factor in the decrease in abundance and density of many species may be higher nest predation in fragments, as found in Colombia and Malaysia (Arango-Velez and Kattan 1997; Cooper and Francis 1998). In the BDFFP project, fragmentation did not result in species loss in the frog community, but composition was substantially altered in forest remnants due to invasions of matrix species (Gascon 1998). In a study of various VJR in Malaysia, medium-sized mammal species were absent from forest fragments below 160 ha, depending on the surrounding vegetation (Laidlaw 1996, 2000). Possible changes in ecosystem function due to altered animal communities in forest fragments are summarised by Didham (1996), although hard data is still scarce.

Most of the above-mentioned studies were conducted as part of the BDFFP project in Brazil. The largest forest fragment size there is 10 km^2 (Debinski and Holt 2000). One interesting result of our study in Sabah is that even a comparatively large-sized forest fragment exceeding 40 km^2 could not support the high proportion of leaf litter ant species of a contiguous primary forest.

Other evidence of the immense effects of forest fragmentation on forest ants comes from an even smaller forest isolate in Sabah. In the Labuk Road Forest Reserve (0.46 km^2 with a forest core of ca. 0.10 km^2), in the proximity of Sepilok Forest, a change in general ant activity was observed. In the large forest of Danum Valley, tuna baits were detected and occupied by ants within 10 min; in Labuk, ants were absent at most baits even after an hour, and instead birds started feeding at the baits (T. Bickel, personal communication). This indicates that there was a severe and extreme reduction in the density and activity of litter-dwelling ants in this forest fragment.

Interestingly, we did not find huge differences between the number of ant species in the medium and small forest plots, although there is an immense difference in fragment size. A few forest species common in logged-over forests (Brühl 2001) increased in abundance in the forest fragments, notably *Lophomyrmex bedoti*, but most forest species became rare in the isolates. Additionally, there was a set of species that is possibly also present in the matrix of regrowth, logged-over forest and fruit plantations around the fragments, including invasive tramp ants (Schultz and McGlynn 2000). In Labuk Road Forest Reserve, at least three tramp ants were recorded: *Monomorium pharaonis, M. floricola* and *Anoplolepis gracilipes*, the last neither present in Sepilok Forest nor in Kebun Cina. The increasing invasion of tramp species and ants from the surrounding agricultural matrix with a smaller fragment size keeps the recorded species number of all studied forest fragments at a similar level, although their size varies considerably. An analysis of community composition consequently provides more information than mere comparison of species numbers.

With the rapid and destructive conversion of one of the world's oldest rainforest ecosystems and an acknowledged and manifest biodiversity crisis, more studies on other animal groups in the remaining forest fragments in Sabah are urgently needed. If similar patterns to those as observed in leaf litter ants emerge, large areas of Sabah will have lost a major portion of their biodiversity, since most of the remaining primary forest is conserved in small to medium-sized VJR, especially in the lowlands in the east, with Sepilok Forest as one of the largest forest remnants. The rate of biodiversity loss in comparatively large fragments contradicts estimates that even isolates <100 ha can retain a relatively large proportion of their biodiversity even decades after isolation (Turner and Corlett 1996). With confirmation of the pattern in other taxa, the implications for efficient management design aiming to preserve the majority of the biodiversity of the country would be tremendous and current strategies would need rethinking. In view of the results of this study, it would seem reasonable for conservation efforts to focus on primary forest fragments within logged-over forests and aim at connectivity between forest isolates. It would be also most beneficial to include the size of a forest in management strategies and not only the condition of the forest.

Acknowledgements

We thank Chey Vun Khen and Arthur Chung of the Forest Research Center in Sandakan for all their help during our stay in Sabah. Robert Ong, Ruben Nilus and Hubert Petol of the same institution provided us with valuable information on forest fragments. Permission to conduct research in Sabah was granted by the Economic Planning Unit, the Forestry Department of Sabah and the Danum Valley Committee, and is gratefully acknowledged. Thanks are due to Barry Bolton, Okido Hirofumi, Eguchi Katsujuki, Rudy Kohout, John Lattke, Fabrizio Rigato and Seiki Yamane for their help with the identification of ants. We are also thankful to Lutz Kulenkampff of the MGSFMP for logistical support. This study is project number DV 163 of the Danum Valley Rainforest Research and Training Programme and was supported by a DAAD Ph.D. scholarship to C.A.B. (D-98-19438).

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