

EFFECTS OF FOREST FRAGMENTATION ON CANOPY SPIDER COMMUNITIES IN SE-ASIAN RAIN FORESTS

Andreas Floren^{1*}, Tobias Müller², Christa Deeleman-Reinhold³, and Karl Eduard Linsenmair¹

¹Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg,
Am Hubland, D-97074 Würzburg, Germany

²Department of Bioinformatics, Biocenter, University of Würzburg,
Am Hubland, D-97074 Würzburg, Germany

³Sparrenlaan 8, 4641 GA Ossendrecht, Netherland

Abstract. Species diversity is by far highest in arthropods, and is in the tropics exceptionally high in the tree canopy. Until today canopy diversity has been neglected in research, however, so that the real impact of anthropogenic forest destruction on species diversity, as well as its functional importance can hardly be assessed. We collected canopy arthropods by insecticidal knockdown fogging in SE-Asian lowland rain forests between 1992 and 2001, and here we use spiders to investigate the consequences of slash-and-burn cultivation. We measured species diversity in a primary forest and in six forest fragments of different age and degree of isolation. Our statistical analysis suggests that neither year of sampling nor tree species significantly affected spider communities. By contrast, spider communities were clearly determined by forest isolation followed by forest age, both resulting in spider communities specific to different forest types. In respect of guild composition, spider communities in the isolated forests were most clearly affected with the result that orb-web weavers had increased at the expense of sheet-web weavers, agile hunters, and cursorial hunters. Species richness was positively correlated with forest fragment age only under conditions where colonization was possible. In those gradient forests which adjoined primary forests, communities approximated those in the primary forest within 40 years. In contrast, a distance of 10 km effectively prevented re-immigration, resulting in low-diversity communities that showed hardly any development in 50 years. Our data suggest that most primary forest spiders are habitat specialists with restricted dispersal ability, indicating that the erosion of biodiversity can only be stopped by a high degree of habitat connectivity. *Accepted 7 December 2010.*

Keywords: Araneae, mass extinction, fogging, guild structure, habitat connectivity, isolation, re-colonization.

INTRODUCTION

The question of how anthropogenic disturbance changes ecosystems is especially topical for tropical rain forests, where high species diversity coincides with the highest rates of forest destruction and least knowledge of how species diversity is related to ecosystem functioning. Scientific research has focused up to now on species richness (Erwin 1982, Horstmann *et al.* 2005, Ødegaard 2006), the mechanisms maintaining high species diversity (Terborgh 1992, Novotny *et al.* 2002), and how ecosystems change following anthropogenic disturbance (Lawton *et al.* 1998, Floren *et al.* 2001, Dunn 2004, Laurance 2006).

Twenty-five years ago insecticidal knockdown fogging studies in tropical lowland forests indicated that a large, perhaps the largest, proportion of species diversity occurs in tree canopies (Erwin 1982), but see Stork & Grimbacher (2006) and Hamilton *et al.* (2010). Arboreal species are not only critical for estimating global diversity but they are most essential for many ecosystem processes such as pollination, predation, etc. Nevertheless, canopy arthropods are still largely neglected in ecosystem analysis (Meijaard *et al.* 2005, Cyranoski 2007) and we have only vague ideas how many of these species will die out as a consequence of forest destruction (Pimm & Raven 2000, Seabloom *et al.* 2002) and whether arthropods can recolonize disturbed forests within a human lifespan (Lawton *et al.* 1998, Floren *et al.* 2001, Dunn 2004, Laurance 2006).

* e-mail: floren@biozentrum.uni-wuerzburg.de

In our study we investigated how canopy arthropod diversity changes following small-scale slash-and-burn agriculture, which is considered to be a main cause of deforestation in the tropics (Myers 2002, Cornell & Miller 2007). We distinguish different types of secondary forests according to their degree of isolation and according to forest age (time of natural regrowth after clearing). We contrast “gradient secondary forests”, which are defined as forests that merge into each other and finally into primary forests, with “isolated secondary forests” that have no direct contact with a primary forest. The latter forests were found at least 10 km distant from the primary forest.

Canopy arthropod communities are a good model system because they can be collected semi-quantitatively and in a tree-specific way by insecticidal knockdown (Floren & Linsenmair 1997, Floren 2010). In order to assess the consequences of forest destruction on the fauna we compare the diversity and structure of arthropod communities of specific tree species in secondary forests with those of a primary forest. Here we focus on spiders which, along with ants, are important predators in trees, accounting for between 3% and 10% of all arthropods (Stork 1987, Floren & Deeleman-Reinhold 2005). One advantage of using spiders is that they are of moderate diversity and could all be identified to species or morphotypes by one of us (C. D.-R.). Furthermore, spiders show little host-plant specificity as they prefer structurally similar rather than taxonomically similar or identical tree species. They are also considered good indicators of habitat disturbance because of their sensitivity to environmental changes (e.g. Scott *et al.* 2006, Sidclay *et al.* 2006, Buddle & Shorthouse 2008). In this analysis we assess the importance of small secondary forests for spider species conservation.

METHODS

Study areas and disturbance history. Investigations were carried out in the rain forest (500–700 m a.s.l.) of Sabah, Borneo, Malaysia, at different sites of the Crocker Mountain Range, within two National Parks: the Crocker Range National Park (1399 km², established in 1964) and the Kinabalu National Park (754 km², established in 1984). These mountains were covered by continuous forest until the early 1980’s when logging activities lead to the isolation of both areas from each other. According to local botanists D. Sumbin (Kinabalu Park Herbarium) and L.

Madani (Herbarium Forest Research Centre Sandakan) the forest can be described as mixed dipterocarp hill forest. The plots investigated were of similar altitude and similar botanical diversity (see also Ipor *et al.* 2002). Similarity of forest types is also suggested by similar species of spiders that were collected by hand from the lower vegetation in earlier years by C.D.-R. (Deeleman-Reinhold 2001).

Fieldwork was carried out in three gradient- and three isolated secondary forests of different ages, which were connected to or isolated from the primary forest (see also Floren & Deeleman-Reinhold 2005). The three gradient forest types were located close to the Kinabalu National Park (Fig. 1). We had no access to isolated forests in the same area but found suitable forest plots close to the Crocker Range National Park. Due to low abundance of tree species in the primary forest, and because no tree species was found growing in all forest types, common tree species – representative of the canopy – were chosen for each forest type separately. The focal trees in the primary forest were Phyllantaceae of the genus *Aporusa* (Phyllantaceae were recently separated from the Euphorbiaceae; the old name was used in our earlier publications), but arthropods were collected from other tree species as well (number of foggings in brackets): *Aporusa lagenocarpa*, Phyllantaceae (6); *A. subcaudata*, Phyllantaceae (7); *A. maingayi*, Phyllantaceae (1); *A. sp.*, Phyllantaceae (1); *Xanthophyllum affine*, Polygalaceae (6); *Garcinia nervosa*, Guttiferae (1); *Ochanostachys amentacea*, Olacaceae (1); *Palaquium rostratum*, Sapotaceae (1); *Barringtonia scortechinii*, Lecythidaceae (2); *Dacryodes laxa*, Burseraceae (1); *Ficus leptogramma*, Moraceae (1).

All trees belonged to the lower canopy (average height 24 m) because fogging of high canopy trees is difficult and requires extensive clearing of the ground vegetation in order to install the collecting funnels, which was not possible in the protected zone of the National Park (see also Floren & Linsenmair 1997). Phyllantaceae trees were found in three clusters in the primary forest, separated by a maximum distance of 3 km from each other. Arthropod communities at the order level differed neither in diversity nor in species composition between clusters and between tree species (Floren & Linsenmair 1997, 2003). The secondary forests had been clear cut and abandoned between 5 and 50 years ago after at least two years of agricultural usage. All were similar in size, ranging between 4 and 6 ha. In particular, these were three gradient forests of 5, 15, and 40 years (G1, G2, G3),

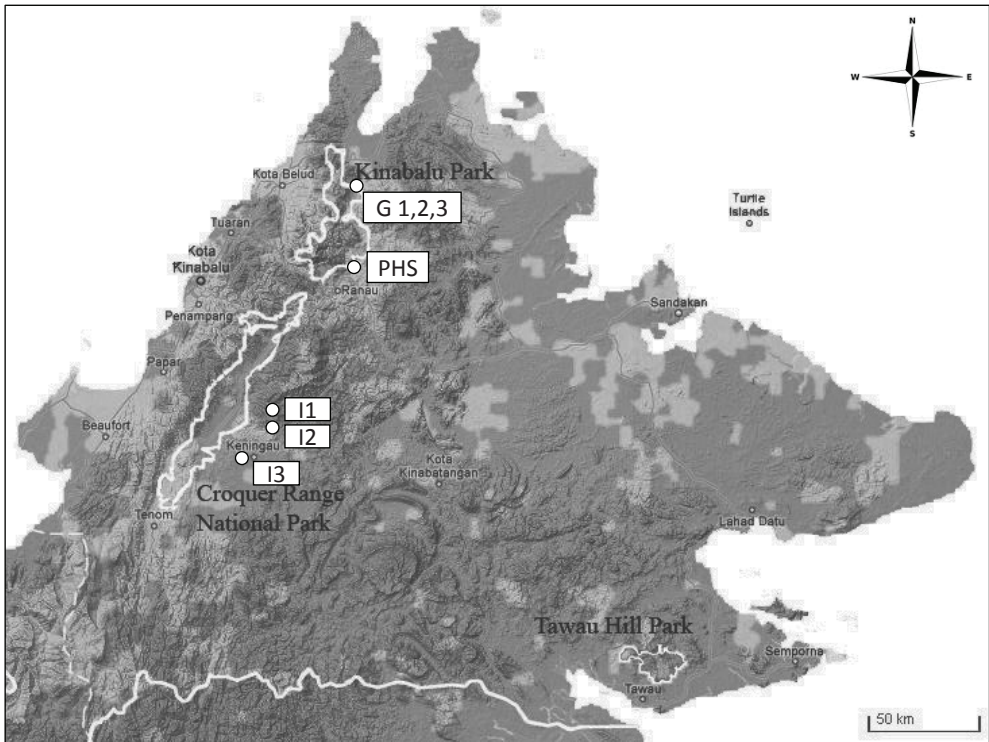


FIG. 1. The Crocker Range Mountains enclosing the Crocker Range NP and the Mount Kinabalu NP. The areas investigated are marked: PHS = Poring Hot Spring, lowland rain forest in Kinabalu NP, G = gradient forests, I = isolated forests.

which were all close together and merged into primary forest. We also investigated three isolated secondary forests aged 10, 20, and 50 years (I1, I2, I3), which were at least 10 km distant from any primary forest. In the gradient forest G1 the frequent pioneer tree *Melochia umbellata* (Sterculiaceae) was selected, while *Vitex pinnata* (Verbenaceae) was the focal tree in G2 and G3. The three isolated forests, I1, I2, and I3 were found near the Crocker Range National Park enclosed by an area of cultivated land mostly used for farming and gardening. The most common tree in all sites was a species of *Melanolepis* sp. (Euphorbiaceae). One tree of *Clerodendron* sp. (Verbenaceae) was fogged in I1 and one *Saraca dentata* (Fabaceae) in I3.

Only a single canopy layer had formed in all secondary forests and was in no case closed. Floral diversity and structural complexity increased very evidently with time of forest regeneration, both in the gradient and in the isolated forests, but clearly

differed even in the oldest secondary forests from the primary forest (Floren & Deeleman-Reinhold 2005, Horstmann *et al.* 2005); see also Turner (1997) and Sodhi *et al.* (2004).

All forest types were more or less equally sampled: 27 trees were fogged in the primary forest, 29 in the gradient forests, and 24 in the isolated forests. Primary and gradient forests formed a continuum while all isolated forests were surrounded by smallholder fields. Periods of fieldwork were in the primary forest from February to April, mostly 1996 (13 trees) and 1998 (9 trees), in the secondary forests 1997, and in the isolated forests 2001. Only adult spiders were used in the analysis because juveniles could not be identified to species. Voucher species are kept in the collection of C. Deeleman-Reinhold. Due to changes in the identification of species, data differ a little from those published in Floren & Deeleman-Reinhold (2005).

Guild classification. In order to identify structural changes in communities we categorized spiders to

four guilds according to their hunting strategies, following the recommendations of Hatley and MacMahon (1980), Halaj *et al.* (1998), and Uetz *et al.* (1999): 1. OW = orb-weavers (Anapidae, Araneidae, Deinopidae, Mysmenidae, Psechridae, Tetragnathidae, Theridiosomatidae, Uloboridae); 2. SW = space-web builders (Cyatholipidae, Dictynidae, Hahniidae, Linyphiidae, Pholcidae, Scytodidae, Theridiidae); 3. CH = cursorial hunters (Clubionidae, Corinnidae, Gnaphosidae, Oonopidae, Salticidae), and 4. AP = ambush predators (Ctenidae, Hersiliidae, Heteropodinae, Mimetidae, Oxyopidae, Palystinae, Philodromidae, Pisauridae, Selenopidae, Sparassidae, Sparianthinae, Thomisidae, Zodariidae).

Collecting method. The method of insecticidal knock-down fogging is well established today. Natural pyrethrum, dissolved in highly refined white oil, was used as insecticide. It is highly specific to arthropods and biodegrades in sunlight in a few hours. The vegetation beneath the study tree was cut and 80–90% of the crown projection was covered with collecting sheets, allowing us to collect almost complete arthropod communities from each tree. Fogging was conducted from the ground or from within the tree crown, depending on the size of the tree and the weather conditions (Floren 2010).

Statistical analyses. All statistical analyses were carried out under the statistical programming environment R (Ihaka & Gentleman 1996). Species-accumulation curves were computed in order to assess sampling efficiency (Gotelli & Colwell 2001). We plotted an average species-accumulation curve for randomly shuffled data (runs = 1000) in order to remove the effect of sample order and to obtain a smoothed curve. We fitted and shortly extrapolated a nonlinear arcsinh-model ($y(x) = b \operatorname{arcsinh}(a \cdot x)$) to the data to better characterize the accumulation curves. This model showed the best overall fit and is characterized by only two parameters. The parameter a is inversely proportional to the point of highest curvature $\text{PHC} = 1/(2^{1/2} a)$, while b describes the degree of dilation of the curve. We used the hierarchical Ward clustering algorithm in order to find compact clusters on correlation distances of presence/absence data (Ward 1963, Everitt 1980, Suzuki & Shimodaira 2004). The robustness and the strength of the clustering is proven by bootstrap analysis (number of runs was 1000) (Felsenstein 1985, Shimodaira 2002, 2004). Differences in guild composition were tested with a Kruskal-Wallis test. Post-hoc comparisons were performed using the method of Conover as implemented in the R-Package *agricolae* (Conover 1999).

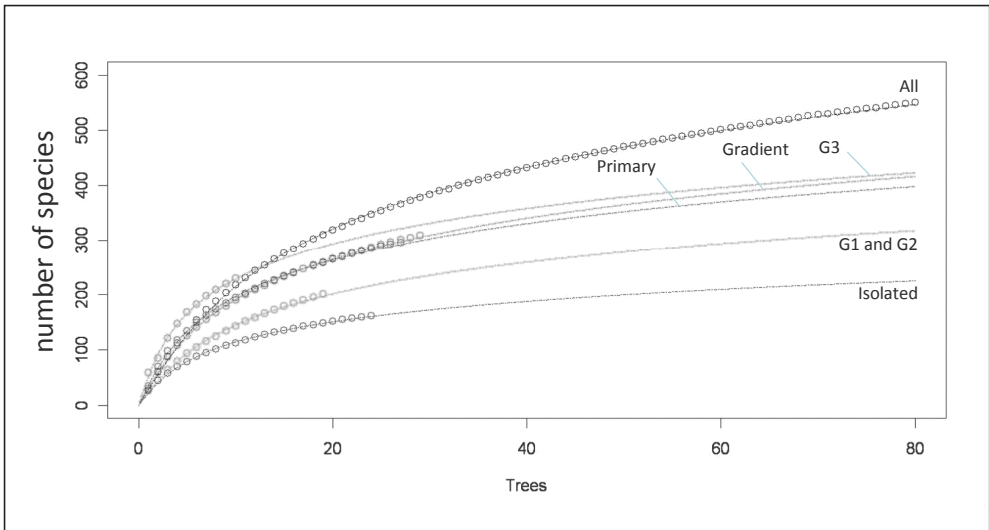


FIG. 2. Species-accumulation curves for different groups of forest types. The overall diversity is high, and in the old gradient (G3) similar to the primary forest. Species richness was almost representatively collected in the isolated and the young gradient forests (G1 and G2). To characterize the curves and to extrapolate species richness within the scope of the total sample size an arcsinh-regression-model showed the best fit.

RESULTS

Species-accumulation curve. In order to undertake a statistically meaningful analysis we collected the largest sample size of canopy arthropods currently available, consisting of collections from 80 fogged trees in or close to a primary forest National Park. From these, a total of 5952 adult spiders was sorted to 550 species in 33 families. We investigated seven forest types, which were distinguished by forest age (time of natural regeneration after agricultural usage had been abandoned) and degree of isolation. The primary forest was included as a baseline in our analysis to assess the consequences of anthropogenic disturbance.

In our investigation the combined species-accumulation curve was still steep (Fig. 2), indicating that many more species must be expected in further samples. Clear differences appeared, however, when curves were plotted for specific forest types (primary, gradient, and isolated forests). These were caused by larger species similarities within than between forest types. The isolated forests are clearly separated as they were poorest in species numbers (162 species) and in species accumulated with increasing sampling effort. In contrast, the gradient forest curve (309 species) could not be distinguished from the primary forest (296 species). Analysis showed, however, that species were not distributed homogeneously between the gradient forests of different ages. Due to higher overall system complexity, we expect species richness to be highest in the primary forest. High species richness was also detected in the 40-year-old gradient forest (G3, 230 species). Species numbers in the young gradient forest exceeded those from the isolated forests, demonstrating the importance of primary forests for forest regeneration. We tested a large variety of models (Thompson *et al.* 2003) of which our arcsinh-model showed the best overall performance while having simultaneously only two parameters.

Characterization of spider communities by cluster analysis. We used hierarchical clustering to derive an overall cluster tree (Fig. 3). Although whole communities were used in the analysis, we found distinct, perfectly separated habitat-specific communities of spiders in all forest types. Only five of all 80 sampled trees were assigned to a forest other than where they grew, and no sample was assigned to another forest type. The cluster tree based on all species abundances (not shown) looked very similar to the tree in

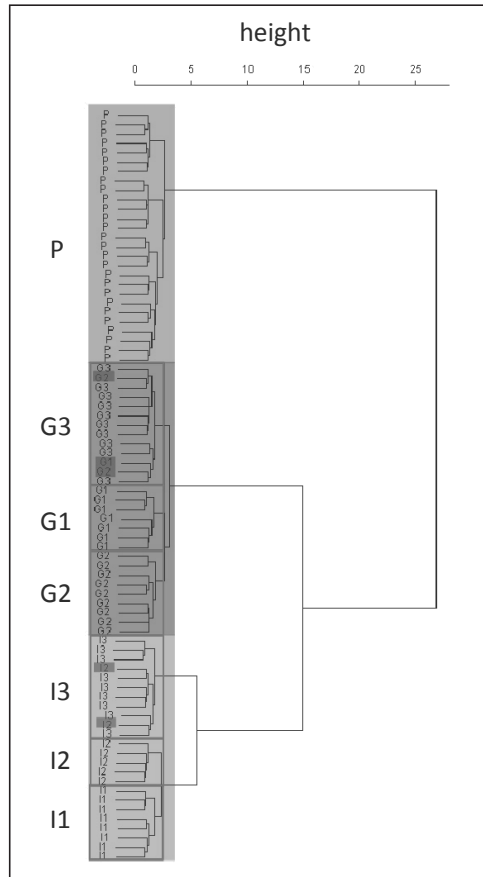


FIG. 3. Overall cluster tree. Communities are clustered by the Ward algorithm (Ward 1963) based on the correlation distances. Forest types (shaded boxes) are clearly separated from each other (P = primary, G = gradient, I = isolated forest), showing that each forest type harbors characteristic spider communities. In each forest type cluster, trees are clustered according to their age. With respect to this interpretation only five trees are wrongly assigned, as indicated by dark rectangles.

Fig. 2, showing the same mismatches thus emphasizing the high habitat specificity of spider communities. The same result was observed when using the Jaccard-index as a distance measure. Furthermore, repeating the whole analysis but excluding singletons showed only a few differences to the original clustering (data not shown).

Figure 3 shows seven clearly separated spider communities, which differ in respect of forest age and

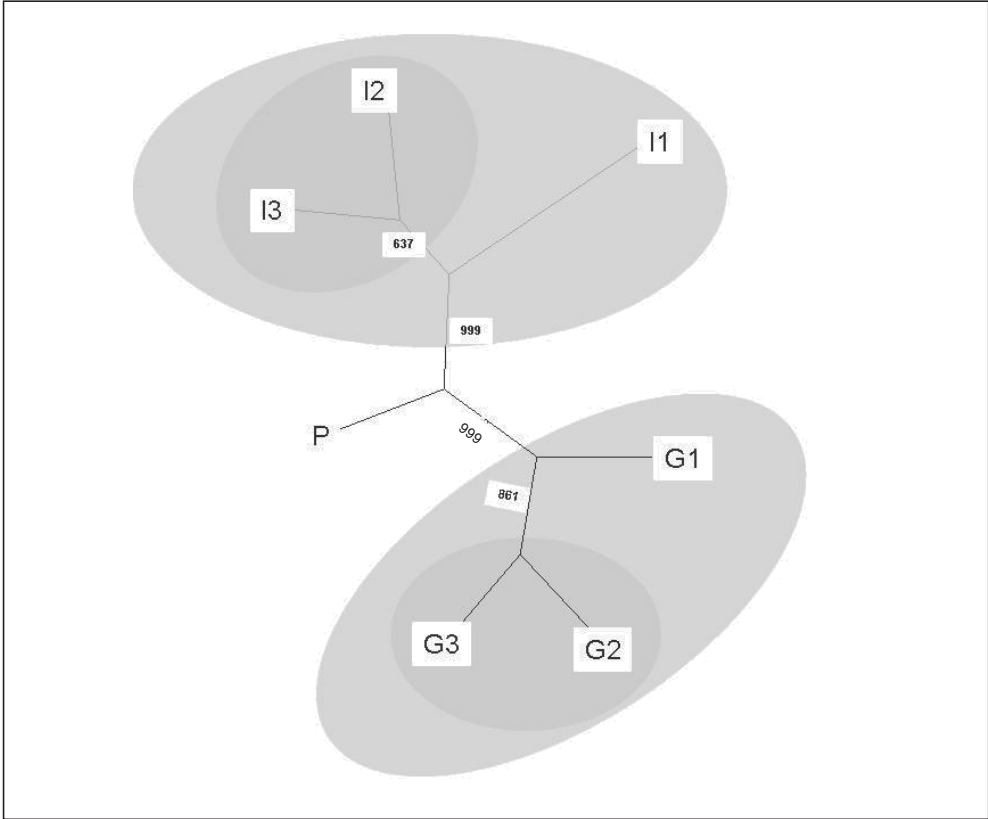


FIG. 4. Cluster tree of all seven forest types characterized by degree of isolation and forest ages. The large ovals comprise forest types of the same degree of isolation. Surprisingly, the older forests group together (dark ovals) and not those forests more closely related by age (G1, G2 and I1, I2). Numbers refer to bootstrap values representing strength of classification.

isolation. This allows us to perform a meta-community analysis to study the relationship between the degree of forest disturbance and community composition. Again we apply the Ward clustering, this time based on correlation distances of presence/absence data for the combined forest types (primary, gradient, isolated forest; Fig. 4) where the spider species per forest type are represented in one vector. The robustness and the strength of the classification signal are demonstrated by high bootstrap values. In accordance with the results presented above, isolation is identified as the most important factor, separating the primary forest from both the gradient and the isolated forests with 99.9% bootstrap support. Among the isolated and the gradient forests the separation between the two older forests becomes

weaker, as reflected by bootstrap values of 63.7% and 86.1%. This is caused by greater community similarity indicating weaker re-immigration dynamics from the primary forest, an effect observed not only for the gradient forests, which differed in tree species (*V. pinnata* in G1, *M. umbellata* in G2 and G3) but also for the isolated forests (which were all dominated by *Melanolepis* sp.).

With regard to guild composition, all trees in all forest types showed a distribution of specimens similar to the four distinguished guilds. Overall, orb-web-building spiders were always dominant, providing 65.46% of all 5952 spider specimens. Following in rank were cursorial hunters with 21.72%, space-web weavers with 7.14%, and ambush predators with 5.68%. Significant differences were detected mainly

for the isolated forests (Fig. 5), which differed in the proportion of orb-web-weaving spiders, and were found to harbor significantly more OW-spiders than the primary and the gradient forests (KW-test, $\chi^2 = 14.9$, $p < 0.001$). In contrast, the other guilds were collected in lower proportions (AP guild: KW-test, $\chi^2 = 6.23$, $p < 0.04$; SW guild: KW-test, $\chi^2 = 8.72$, gradient versus isolated forests, $p < 0.012$; CH guild: KW-test, $\chi^2 = 8.66$, primary versus isolated forests $p < 0.003$, gradient versus isolated forests $p < 0.02$).

Recolonization dynamics. The importance of species recolonization for forest regeneration is shown in Fig. 6, where secondary forest age is plotted against species richness. Our experimental design allowed us

to eliminate the effects of size and distance of forest fragments from the primary forest, and to focus on forest isolation and forest age. The respective curves for the gradient and isolated forests were almost parallel, demonstrating that recolonization dynamics were constant and differed little between species from primary forest and all species. Again it is obvious that recolonization was more rapid in the young forests than in the older forests, resulting in a consistent path of both curves. Surprisingly, species richness of the 50-year-old isolated forest was not higher compared with the 20-year-old isolated forest, although one should have expected higher richness in the structurally more complex old isolated forest. This indicates that most spiders were not able to bridge a distance

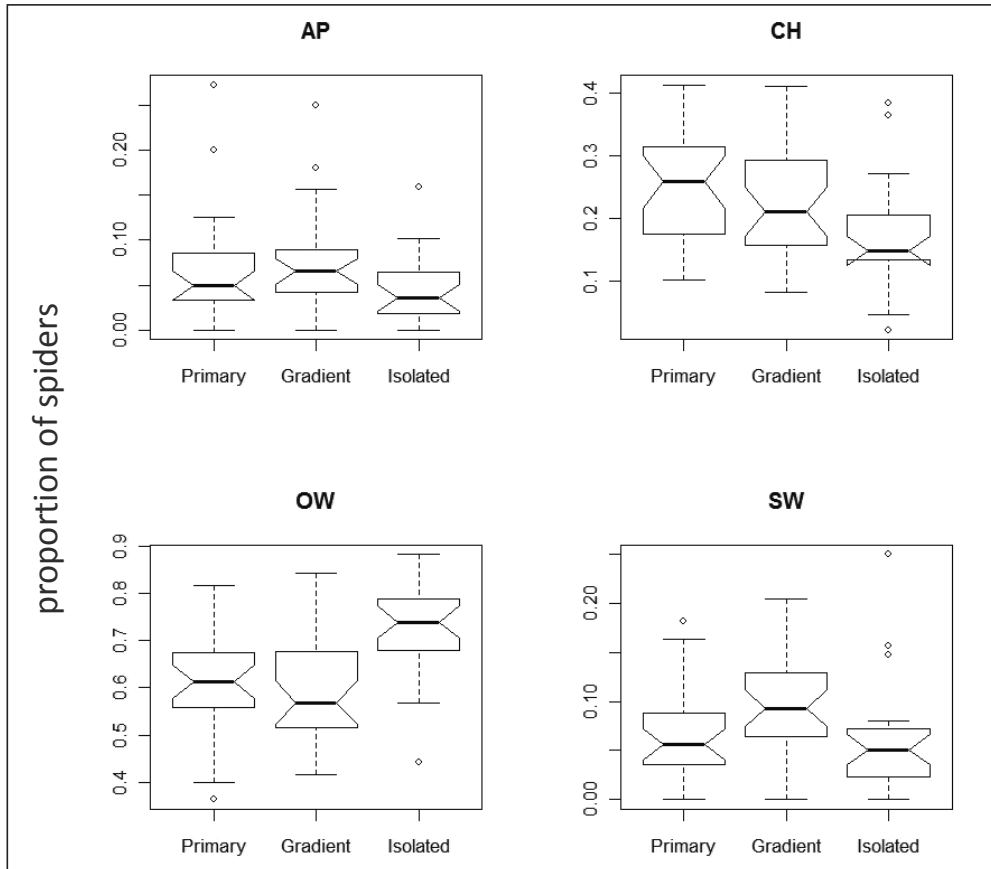


FIG. 5. Changes in guild composition of spider communities in different forest types. Compared with the primary and the gradient forests, the isolated forest had significantly more orb-web weaving spiders per tree while proportions of the other guilds had decreased. AP = ambush predators, CH = cursorial hunters, OW = orb-web weavers, SW = sheet-web weavers.

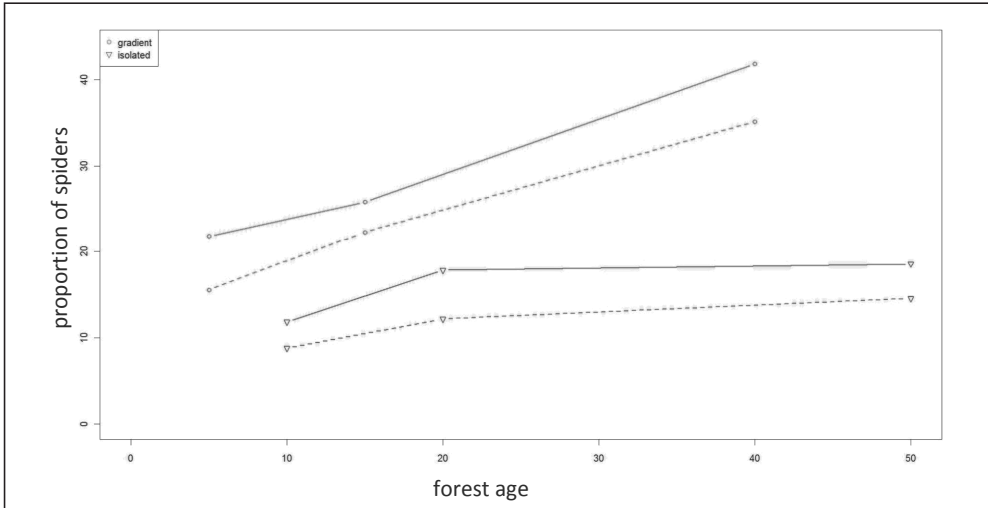


FIG. 6. Recolonization dynamics in the gradient and isolated forests. Each dot denotes the species proportion found in a particular forest type (G1, G2, G3, and I1, I2, I3, respectively) relative to all collected species (solid line) and to the primary forest species (dashed line). The flat curves refer to the isolated, the steep curves to the gradient forests. In contrast to the high recolonization rate in the gradient forests, the rate in the isolated forest is near constant.

of 10 km between the primary and the secondary forests. The dramatic impact of a restricted recolonization is underlined by the fact that the 50-year-old isolated forest had not even reached the diversity of the 5-year-old gradient forest.

DISCUSSION

Due to anthropogenic forest destruction, primary forests are today more and more fragmented, creating small isolated forest plots with different disturbance histories (Curran *et al.* 2004, Sodhi *et al.* 2004, Wright 2005). The impact on species diversity is difficult to assess, particularly with respect to species extinction and the corresponding loss of ecosystem functioning and ecosystem services (Cardinale *et al.* 2006, Laurance 2006, Hector & Bagchi 2007). This is due to the fact that there is neither reliable information about the current extent of arthropod biodiversity nor do we know how many species have already died out or are on the brink of extinction. As a consequence, assessments could hardly be more controversial: the assumption of a sixth major species mass extinction (Pimm & Raven 2000, Thomas *et al.* 2004) contrasts with the opinion that species loss would be insignificant (Lomborg 2001) or could still

be prevented in degraded habitats (Wright & Muller-Landau 2006, Cyranoski 2007). However these assessments are based almost exclusively on plants and vertebrates. In the case of S.E. Asia, the number of species threatened with extinction is considered not particularly alarming (Sodhi *et al.* 2004) and includes only a few invertebrate species: 10 molluscs and 2 “other” invertebrates (IUCN 2007). Canopy arthropods have not been considered at all in such assessments, although a large proportion of species diversity is found in the canopy of tropical forests (Erwin 1982, Horstmann *et al.* 2005, Ødegaard 2006). Our analysis is one of the first that investigates how canopy spiders, one of the mega-diverse groups of arthropods (Colwell & Coddington 1994), from secondary forests of varying age and degree of isolation, differ from those of a primary forest.

Spider communities in forests with continuous colonization and communities in isolated forests. The forest fragments investigated by us measured 4 and 6 hectares in size and were created by shifting cultivation, which is considered as one of the most important causes of forest destruction (Myers 2002, Cornell and Miller 2007). We analyzed the differences between primary and secondary forests not only with respect to univariate response metrics, such as species rich-

ness and diversity, which are highly sensitive to sampling effort, but also with respect to community level changes in order to get a clearer view of the consequences of anthropogenic disturbance in these systems (Barlow *et al.* 2007).

High tropical species diversity makes an ecological analysis particularly difficult, since the regional species pool is rarely sampled representatively. Consequently, differences in species communities can usually not be related to differences between forest types (Floren & Linsenmair 2005). By showing species-accumulation curves we not only demonstrate that there are still many more species to be expected in the regional species pool but also that the forest types differ greatly between each other. The perfect fit of our arcsinh-model allows a limited extrapolation of the species-accumulation curves, leaving no doubt that further foggings would follow the curves in the range of the total sample size, even if our data do not allow an overall estimation of diversity. Low species richness in the isolated forests is particularly obvious. Furthermore, there is a qualitative difference between the young and the 40-year-old gradient forest, where primary forest species coexist with species usually found in disturbed forests. For a closer faunistic view see Floren & Deeleman-Reinhold (2005).

Although we analyzed one of the largest datasets of canopy spiders available today (representing a total of 80 individually fogged trees and 550 spider species), we are aware that our analysis is complicated by the lack of forest-type-specific replicates, indicating the necessity of further investigations. However, our results clearly show that gradient and isolated forest types build consistent classes that are independent of their age (Figs 3, 4). In addition, the primary forest cluster is supported by a very high bootstrap value, showing that all trees in primary forest are more similar to each other than to other trees in other forest types. Future investigations will show how other primary forests will fit into this pattern. By contrast, we observed no tree-specific clustering, indicating that the parameter "tree species" is not the main factor influencing the composition of spider communities (as also indicated by correspondence analysis; data not shown). Despite the high floristic and structural complexity of the primary forest, these communities formed a homogeneous cluster (without mismatches), demonstrating a qualitative difference compared to all secondary forests.

The implications of forest fragmentation. Arboreal spiders demonstrate the implications of forest frag-

mentation, suggesting that the consequences might be significant. While it was not unexpected that species diversity decreased most in the isolated forest fragments, we were surprised by the extent of species loss and the long periods of time needed before species richness in these forests would regenerate. Just by using a simple clustering algorithm (Fig. 3), we found that spider communities are firstly determined by the degree of isolation (clearest separation between shaded boxes), and secondly by the age of the forest (frames within shaded boxes in Fig. 3). We originally assumed that species richness is positively correlated with fragment age; however, our data indicate that there is a great difference between gradient and isolated forests. While species numbers increased with increasing forest age under conditions where colonization was possible, species richness in communities of the isolated forests hardly changed within 30 years. Independent of forest age, spiders were not able to colonize isolated forest fragments or to survive in structurally and microclimatically altered habitats. Colonization was only observed when secondary forests were connected to a primary forest, but even in these gradient forests recolonization needed decades for species richness to approximate to that in the primary forest. Furthermore, spider communities of the 40-year-old gradient forest still differed significantly from those in the primary forest in species composition, species evenness, and the mean proportion of singletons of all trees. For further information, including a species list, see Floren *et al.* (2001) and Floren & Deeleman-Reinhold (2005).

Although habitat structure was only coarsely characterized it was evident that the forests changed greatly in diversity and structure with increasing age of regeneration (see Turner 1997, Horstmann *et al.* 2005). The old secondary forests were dense and contained a lot of dead wood while the canopy was almost closed. However, the old secondary forests were also still clearly different from the multilayered primary forest. As the distribution of spiders depends largely on habitat structure (Wise 1993, Halaj *et al.* 1998), we expected and found changes in the community structure which were most evident in the isolated forests. The increased proportion of orb-weaving spiders seemed to have occurred at the expense of the other guilds. These results deviate from other investigations where the highest proportions of orb weavers were found in diverse, structurally complex tropical forests (Greenstone 1984) but lower proportions in secondary forests (e.g. Tsai *et al.*

2006). Such opposing results hint at the great variation in how communities can change following anthropogenic disturbance. Structural changes depend largely on the local habitat conditions, including the microclimatic conditions (Pinto-Leite *et al.* 2008) and further biotic factors like the availability of prey organisms (Greenstone 1984, Horváth *et al.* 2005). Investigating these factors by using a standardized protocol would facilitate analysis greatly, as the measurement of habitat heterogeneity is very inconsistent, making across-study comparisons difficult (Tews *et al.* 2004).

The effects of isolation on the ability of arthropods to colonize forest fragments have also been investigated by other researchers (Benedick *et al.* 2006, Chacoff & Aizen 2006, Vasconcelos *et al.* 2006) but are here quantified for the “mega-diverse” group of the Araneae (Colwell & Coddington 1994). Recolonization rates varied, being more rapid in the young forests than in the older forests, resulting in the grouping of the older forest types and indicating that generalist species colonize young forests. If the rate of recolonization had changed uniformly with forest age we would have expected lower differences in communities being chronologically more aligned, so that G1(I1) and G2(I2) could be separated from G3(I3). But in fact it is always the spider communities of the young forests that differ most from the older ones, independent of the tree species present. As demonstrated by the bootstrap values (Fig. 4), this phenomenon was more pronounced in the isolated than in the gradient forests.

The conservation value of small forest fragments. Our results differ from other investigations, which rather emphasize the conservation value of small forest fragments, even although they also show a negative correlation of species richness with size of the forest fragment or with increasing edge effects (e.g. Sodhi *et al.* 2004, Benedick *et al.* 2006, Vasconcelos *et al.* 2006, Barlow *et al.* 2007). Our data on canopy spiders suggest that most spiders in the primary forest are habitat specialists with low dispersal ability. We suggest that, given such conditions, isolated forest fragments would not change in diversity even after hundreds of years. Species diversity in forest fragments following natural regeneration even after more than 50 years improved only when a primary forest was nearby, serving as a source from which re-colonization could take place. This suggests that most spiders were not able to bridge distances larger than 10 km of agricultural fields or plantations. The observed dra-

matic loss of canopy species was associated with a complete faunistic turnover, characterized by the dominance of common and widespread generalist species (Floren & Deeleman-Reinhold 2005).

Given that most species are habitat specialists with low dispersal ability only a few species would be able to survive in small secondary forest fragments (Brook *et al.* 2003, Floren & Linsenmair 2003, 2005; Laurance & Goosem 2008). These are realistic conclusions but should be supported by further studies. However, if our conclusions are correct and if most canopy species are really not able to survive permanently in forest fragments, then the observed loss of 80% of species in the isolated forest fragments might be close to the effective rates of species extinction. This figure is close to the 82% of bird species lost in Singapore, which has been documented since the year 1819 (Brook *et al.* 2003). Given this scenario, anthropogenic disturbance may indeed cause mass extinction, although there is still a great debate how much forest destruction we can afford. Our data suggest that the erosion of biodiversity can only be stopped by a high degree of habitat connectivity. This is alarming and requires further investigations, as well as a stop to rampant forest destruction.

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