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DIVERSITY OF ARBOREAL SPIDERS IN PRIMARY AND DISTURBED TROPICAL FORESTS

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ABSTRACT. This study investigates how arboreal spider communities in SE-Asian primary lowland rain forests change after anthropogenic disturbance. Two types of secondary forests were distinguished: 1) forests adjacent to each other, which finally merged into primary forest and 2) forests that were isolated by at least 10 km from the primary forest. Three forests of different age were investigated from each type and compared with undisturbed primary forest. All disturbed forests had been used some years for agriculture and were then left between 5 and 50 years to regenerate naturally. Spiders from at least seven trees per forest type were collected using insecticidal knockdown fogging and sorted to species or morphospecies level. Spiders represented between 5–10% of all canopy arthropods. A similar number of spiders were collected per square meter from all trees. However, communities in the primary forest differed greatly in their alpha- and beta-diversity and in community structure from those in the disturbed forest types. Diversity was high in the regenerating forests connected to the primary forest and approximated the conditions of the primary forest during the course of forest succession. In contrast, the isolated forests were of low diversity and communities showed little change during forest regeneration. These results indicate the importance of a species-source from which disturbed forests can be recolonized. However, even under optimal conditions this process needed decades before spider communities became similar to those of the primary forest. With no species-source available, spider diversity changed little during 50 years of forest regeneration. In the isolated forest we observed a drastic turnover from forest species towards species characteristic of open vegetation and shrubs. Our results give an indication of how large a loss in diversity can be expected in isolated forest fragments.

Keywords: Fogging, fragmentation, forest isolation, recolonization, species-source

The canopy of tropical lowland rain forests forms a highly complex habitat. Here lives the most diverse arthropod fauna of the world, which influences many ecosystem processes and ecosystem services (examples in Linsenmair et al. 2001; Basset et al. 2003). This assessment has been based on the faunistic-ecological analysis of taxa such as Coleoptera, Lepidoptera or Formicidae (e.g., Erwin 1983; Morse et al. 1988; Floren et al. 2001, 2002; Brehm et al. 2003; Davidson et al. 2003) while comparatively little work has been done on other groups. However, these latter groups can be rich in species and of great ecological importance, such as Araneae (Hoefer et al. 1994; Deeleman-Reinhold 2001; Santos et al. 2003) which, next to Formicidae, are the most abundant predators in the trees (Stork 1991; Floren & Linsenmair 1997; Wagner 1997). Despite political declarations, tropical forests are recklessly destroyed and reduced to forest fragments which are much simpler in species diversity and habitat complexity. Although this destruction will certainly change many ecosystem properties, the consequences of this transformation have never been adequately investigated. This study aims at providing such knowledge. We investigated the diversity and structure of arboreal spider communities in SE-Asian primary forests. Furthermore, we analyzed how communities differ in disturbed forest types and how they reorganized following anthropogenic disturbance. We collected arboreal spiders by insecticidal knockdown fogging. Besides primary forest, we studied 1) three secondary forests of different ages that merged into each other and finally into primary forest and 2) three isolated secondary forests of different ages which were separated by at least 10 km from the primary forest. This study design allowed us to assess the importance of species recolonization for the re-

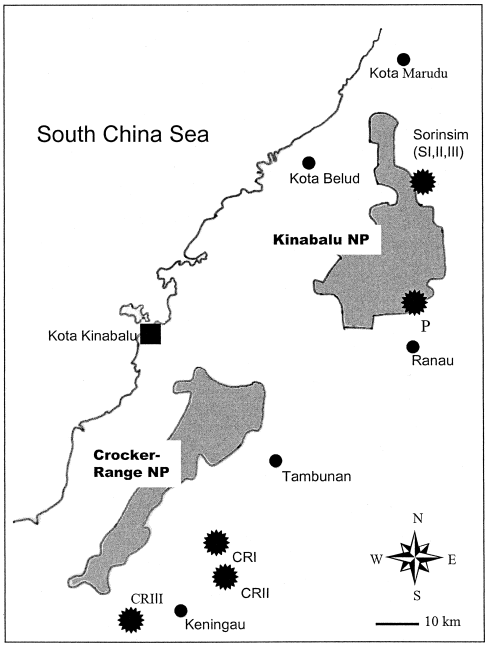

Figure 1.—Map of study sites. SI, SII, SIII were adjacent forests of 5, 15, and 40 years age that merged into primary forest at Kinabalu National Park substation Sorinsim. CRI, CRII, CRIII, were isolated forest plots of 10, 20, and 50 years age that were at least ten kilometers away from the primary forest. P = primary forest plots.

organization of spider communities during forest regeneration. After eight years of taxonomic analysis by the senior author we are now able to present the results of our investigation.

METHODS

Study sites.—Arboreal arthropods were collected by insecticidal knockdown fogging in a Dipterocarp lowland rain forests of Kinabalu National Park (500—650 meters a.s.l.) in Sabah, Malaysia on Borneo (6° 2.75′N, 116° 42.2′E) during various field periods from 1992—2001 (Table1). The area has a relatively constant climate with a main rainy season from November to February and a shorter one from June to July. The level of precipitation varies between 2000 and 4000 mm. In total, 15 trees of the genus *Aporusa* (Euphorbiaceae) were fogged, 6 trees of *Xanthophyllum affine* (Polygalaceae) and 9 trees of various other genera (for details see Horstmann et al. in press). The disturbed forests were situated at substation Sorinsim in Kinabalu National Park and in the vicinity of the Crocker Range National Park. A map of all forest types is shown in Fig. 1. Details on the study sites are published elsewhere (Floren et al. 2001; Horstmann et al. in press). All secondary forests were clear-cut for crop planting, abandoned and left for natural regeneration. Three forests of 5, 15 and 40 years, each of 5—6 ha (abbreviated SI, SII, SIII), which merged into one another and finally into primary forest, were investigated at National Park substation Sorinsim. Foggings were carried out from February—March 1997. Three isolated forest plots of 10, 20 and 50 years were found within at least 10 km distance from the primary forest of the Crocker Range National Park (abbreviated CRI, CRII, CRIII). They were about 4—6 hectares in size and surrounded by cultivated land (fruit, oil palm, rubber plantations, pastures, etc.). Fieldwork was carried out between January and February 2001. All disturbed forests had only a single canopy layer which was in no case closed and differed both in tree height and girth at breast height of the study trees.

Collecting methods.—A full description of the fogging method is given in Adis et al. (1998). Natural pyrethrum was used as an insecticide and all arthropods that dropped into the collecting funnels two hours following fogging were used in the analysis. In order to collect arboreal arthropods as completely as possible, 80—90% of a crown projection area was covered with collecting funnels installed beneath a tree. In total, 102 foggings were carried out, consisting of the first and subsequent foggings (mostly on consecutive days). Faunistic analysis is based on all these foggings while only the first foggings were used for community level analysis (Table 1). Seven primary forest trees were re-fogged after three years and two trees after an eight month period. Spider communities from these samples could not be distinguished from those of the first foggings and were, therefore, considered independent samples. As no tree species grew in all forests, a common tree was fogged in each forest type. However, as tree specific associations of broad-leaved trees are thought to be of minor importance for spiders and were also not indicated by our results, we refer to Floren & Linsenmair (2001) for the general discussion of this aspect. Analysis is based on

Table 1.—Forests investigated and focal trees. Individual trees were refogged several times on consecutive days. SI, SII, SIII = secondary forests connected with primary forests; CRI, CRII, CRIII = isolated secondary forests.

	Focal tree species	Number of foggings		Tree height (m)	Girth in breast height (cm)
		Fog 1	Re-fog		
Primary forest	*Aporusa lagenocarpa* *A. subcaudata* (Euphorbiaceae)	27	3	24–30	70.24 ± 18.12
SI (5 yrs.)	*Melochia umbellata* (Sterculiaceae)	8	10	6–8	57.91 ± 9.46
SII (15 yrs.)	*Vitex pinnata* (Verbenaceae)	11	4	18–20	106.44 ± 14.54
SIII (40 yrs.)	*V. pinnata*	10	5	20–25	148.44 ± 48.14
CRI (10 yrs.)	*Melanolepis glandulosa* (Euphorbiaceae)	8	—	6–8	83.16 ± 9.89
CRII (20 yrs.)	*M. glandulosa*	7	—	18–20	107.43 ± 14.54
CRIII (50 yrs.)	*M. glandulosa*	9	—	18–25	122.89 ± 23.20

adult spiders, which are stored in the collection of C. Deeleman.

Data analysis.—Spider communities in forest types were compared using alpha- and beta diversity indices (Magurran 1988). William's alpha (after Fisher et al. 1943) is a widely used parametric index of diversity, which is largely independent of sample size. Simpson's index describes the probability that a second individual drawn from a population should be of the same species as the first. It is mainly influenced by common species and therefore a measure of equitability (the larger the value the greater the equitability). Sample sizes were standardized by using rarefaction statistics (Hurlbert 1971; Hayek & Buzas 1997). For this purpose, spiders of all fogged trees per forest type were pooled and diversity was expressed as the number of expected species within an equal sub-sample size (this corresponded with the 65 species identified from all 306 specimens in the isolated forest CRI). If rarefaction values are computed for increasing sub-samples and plotted graphically, the resulting curve can be interpreted as a species accumulation curve, which gives information on the structure of spider communities in each forest type (Achtziger et al. 1992). Shinozaki curves were calculated to compare communities on the beta-diversity level (Shinozaki 1963; Achtziger et al. 1992). They are expected species accumulation curves based on qualitative (presence / absence) data of species. Their steepness provides information about the overall completeness of the sampling effort. Furthermore, Soerensen's quantitative index of similarity was calculated. Differences in means of beta-diversity between forest types were tested with a Mantel test using a randomization test (Monte Carlo). The number of randomized runs was 1000. For a between forest comparison, the fogging data were standardized for a crown projection of $1m^2$ and a leaf cover of 100%.

RESULTS

From all 102 foggings, 6999 spiders were collected and sorted to 578 species in 29 families (Appendix 1). Scientific names were found for 107 species of which 75 species (12.9%) were new for Borneo. The five most abundant families, declining in rank-order, were Theridiidae, Salticidae, Araneidae, Thomisidae, and Clubionidae, together representing between 73% and 94% of all spiders in each forest. These families contributed also between 75% and 84% of all species. Theridiidae represented 153 species, Salticidae 111 species, Araneidae 80 species, Thomisidae 74 species, and Clubionidae 31 species. Spiders provided on average between 4.6% and 9.8% of all arthropods in a community (Table 2). Differences in the relative proportion of spiders per tree were detected only between the youngest isolated forest CRI and the primary forest, CRI and SII, and CRI and SIII (ANOVA, $F = 4.235$, df = 6, $P < 0.01$, Tamhane post-hoc tests for unequal variances were carried out, $P < 0.05$). The number of collected spider individuals, standardized on $1m^2$ collecting sheets and 100% leaf cover, differed not significantly between tree species or forest types, only between the primary forest and SII where spider numbers were lowest (ANOVA,

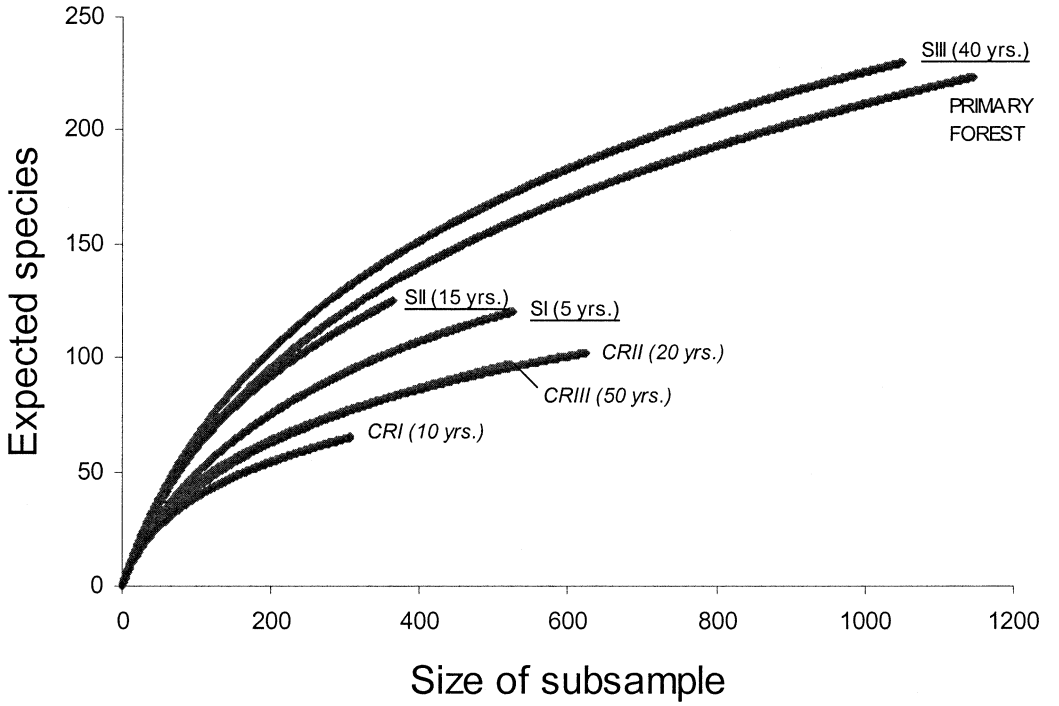

Figure 2.—Rarefaction curves of spider communities based on all foggings.

$F = 2.358$, $P < 0.05$, Tamhane post-hoc test, df = 6, $P < 0.05$). Most abundant in the forests close to the primary forest was *Talaus nanus* (Thorell 1892) (Thomisidae) with 297 individuals, followed by *Ogulnius* sp. (Theridiosomatidae) with 103 individuals, and *Molione kinabalu* (Yoshida 2003) (Theridiidae) with 74 individuals. The isolated forests were numerically dominated by *Ocyllus* sp. (Thomisidae) with 75 individuals followed by *Tetragnatha hasselti* (Thorell 1890) (Tetragnathidae) with 51 specimens. Family diversity depended on sample size and was highest in the primary forest. Rarefaction statistics allow comparison of forest types that have been sampled with different efficiency. On a rarefied sub-sample of 306 individuals (corresponding to the number of spiders of the smallest sample CRI) a similar number of families, namely 22, were observed in SII and the primary forest. The number of spider families was least in the isolated forest plots. Rarified species numbers and, correspondingly, William's alpha were highest in the primary forest and in SIII. Again these indices were clearly lower in the isolated forests where alpha-diversity had changed little even after 50 years compared to the 'Sorinsim-forests'. Rarified species numbers were higher both in SI and SII than in CRI and CRII (related to the gradient forests these were 30.9% and 33.0%, respectively), and 41.7% more species were collected in SIII compared to CRIII. An approximate value for the loss of species following anthropogenic disturbance is the relation of species numbers to primary forest species numbers (Floren & Linsenmair 2005). Only 22.0% of the primary forest species number was collected in the isolated forest CI, the most severely disturbed forest with the lowest number of species. Relative proportion of singletons in each forest type was lowest in the primary forest (32.4%) and increased in the disturbed forests. Despite the large sampling effort in the primary forest, there were still 96 species represented by only one individual. In contrast to the proportion of singletons per forest type, the mean proportion of singletons of all tree specific communities per forest type was a better discriminator between primary and disturbed forests despite high variance between tree specific communities. The average proportion of singletons was highest and not significantly different in the primary and the

old secondary forest SIII (Table 2). The primary forest (mean 25.8 ± 11.8) differed from the isolated forests CRI (mean 10.3 ± SD 4.2) and CRIII (mean 16.2 ± SD 3.6) (ANOVA, $F = 7.647$, df = 6, $P < 0.001$, Tamhane post-hoc test, $P < 0.001$ and $P < 0.01$, respectively). In all other forests, spider communities differed not significantly in respect to the proportion of singletons per community. Equitability, as measured by Simpson's index, was least in the disturbed forests and most in SII and SIII. Due to the numerical dominance of an individual species, unknown genus cf. *Pycnaxis* sp. (Thomisidae), which occurred on 13 out of 27 trees with maximum 71 and 86 individuals per tree, the primary forest evenness was lower. However, excluding this species from the analysis resulted in an index of 84.0, confirming high evenness for all other species.

Rarefaction curves did not level off with increasing size of sub-samples (Fig. 2). However, in contrast to the isolated forests, the curves were much steeper in the primary and the connected Sorinsim-forests indicating that spider communities were not collected representatively. Also Fig. 2 shows the clear separation between forest types, indicating that spider communities recovered much faster in the Sorinsim forests, which were adjacent to the primary forest, than in the isolated forests (see also Table 2). The increase of the rarefaction curve of SII indicates that the rate of species collection was similar to that of the primary forest. Prominent was the high species diversity of the 40 year-old forest SIII. Figure 3 shows the species frequency distribution of all spiders from all pooled foggings. Increasing the sample size always resulted in many new species indicating that the regional species pool was not sampled representatively by the 80 first foggings. Computing Shinozaki-curves for the four largest families, however, showed that they were collected reliably by fogging.

Comparing mean similarities of tree-specific spider communities (expressed by the Soerensen index, Fig. 4) showed clear differences between forest types (Mantel-test, Monte Carlo randomization, $z = -0.583362$, $P < 0.001$). In the primary forest and also in SI, SII, and SIII, 70% to 80% of all species were found only on one tree. In contrast, tree specific spider communities in the isolated forests shared many more species and consequently communities showed a significantly higher overlap in species.

Most spiders were found only in one forest type: 155 species (52%) of primary forest species were restricted to the primary forest, 149 species (48%) and 62 species (38%) respectively were only found in the adjacent and the isolated forests. Changes in spider communities came along with drastic faunistic changes. For example, 96 widespread ubiquitous species (species distributed in the Malay Archipelago) were identified. Their proportion was highest in the isolated forests representing 56 of all 160 species (35%), 69 ubiquitous species (21.9%) were collected in the primary forest and 63 species (18.9%) in the connected 'Sorinsim' forests (Appendix 1). Most of the ubiquitous species were Araneidae, Theridiidae and Tetragnathidae and could be identified to the species level, like *Neoscona vigilans* (Blackwall 1865), *N. punctigera* (Doleschall 1857), common *Cyclosa* and *Gasteracantha* species, *Chrysso spiniventris* (O.P-Cambridge 1869), *Takayus lyricus* (Walckenaer 1842), *Tetragnatha hasselti* (Thorell 1890) and *Mesida gemmea* (van Hasselt 1882) (Platnick 2005; Yin et al. 1997; Zhu 1998; Zhu et al. 2003; Yoshida 2003).

DISCUSSION

Anthropogenic destruction of tropical rain forests makes it necessary to assess the immediate and the long-term consequences for man and nature. Only on the basis of such knowledge is a sound nature protection plan possible. This, however, requires a high effort of basic research because even the extent of species richness is not known for most taxa (Basset et al. 2003). In this paper we present such a basic study for arboreal spiders, which we collected by pyrethrum knockdown fogging in primary and secondary lowland rain forests of Sabah, Malaysia on Borneo. Next to Formicidae, spiders are the most abundant group of predators in tropical lowland forest canopies (Adis et al. 1984; Stork 1991; Floren & Linsenmair 1997, 2001). Our study confirmed high species diversity of arboreal spiders. Despite a total of 102 foggings, the regional species pool was not sampled representatively and new species are still being found in new samples (Deeleman pers. obs.). There is a need to extend investigations, including further yet unsampled habitats, and

Table 2.—Comparison of spider communities between forest types. Analysis is based on first foggings only. Means are given with standard deviations. * = Data are standardized for a crown projection of $1m^2$ and a leaf cover of 100%. SI, SII, SIII = secondary forests connected with primary forests; CRI, CRII, CRIII = isolated secondary forests.

	Prim. forest	SI 5 yrs.	SII 15 yrs.	SIII 40 yrs.	CRI 10 yrs.	CRII 20 yrs.	CRIII 50 yrs.
Mean rel. prop. of spiders per forest	5.6	7.2	4.6	5.9	9.8	6.3	6.4
No. of families	28	15	24	24	11	15	19
Rarefied no. of families (m = 306)	21.6	14.5	22.2	20.5	11	14.1	16.2
No. of species	296	120	127	230	65	97	102
Rarefied no. of species (m = 306)	122	94	115	132	65	77	77
William's alpha	87.5	48.6	67.1	91.0	25.3	35.4	34.6
Total number of spiders collected	2488	525	365	1048	306	523	625
Standardized mean abundance*	19.6 ± 15.63	13.0 ± 7.8	6.4 ± 2.9	14.8 ± 5.3	15.8 ± 6.2	11.7 ± 8.1	11.6 ± 6.6
Singletons	96 (32.4%)	46 (38.3%)	61 (48.0%)	86 (37.4%)	27 (41.5%)	40 (41.2%)	35 (34.3%)
Mean proportion of singletons of all trees	25.8 ± 11.8	17.4 ± 7.9	17.5 ± 6.3	33.8 ± 10.3	10.3 ± 4.2	17.6 ± 6.9	16.2 ± 3.6
Simpson-index	30.6	20.3	41.3	44.1	16.3	18.0	22.6

compare spider diversity with that reported in the few studies that have been carried out so far in the region (Russell-Smith and Stork 1994, 1995; Deeleman-Reinhold 2001) in order to assess the extent of diversity and to investigate the role spiders play in ecosystem functioning (New 1999).

Primary forests differ conspicuously from disturbed forests in habitat complexity. As a consequence, the diversity, structure, and dynamics of arthropod communities also change in disturbed forests (Floren et al. 2001). This was also confirmed, convincingly, for arboreal spiders. Using the primary forest as a basis, we investigated how spider communities changed in various secondary forests of different ages; that is to say in forests of different disturbance levels. Our data do not allow us to perform a full community level analysis because local species pools have not been sampled representatively and differences between communities might simply be due to collecting new species. However, we can compare data after standardization, e.g. by using rarefaction statistics, comparing relative proportions of a parameter or by looking for changes in community structure and faunistic composition. On the basis of such comparisons, primary forests are clearly distinguishable from the adjacent secondary forests (SI, SII, SIII) merging into the primary forest, which are, themselves, clearly separated from the isolated forests (CRI, CRII, CRIII). As demonstrated by our data, the comparatively small distance of 10 km to the primary forest forms an effective barrier preventing species recolonization when the surroundings are cultivated land.

Spider density was similar in all forests indicating that the number of spiders collected by fogging did not depend on the tree species or the level of disturbance of the secondary

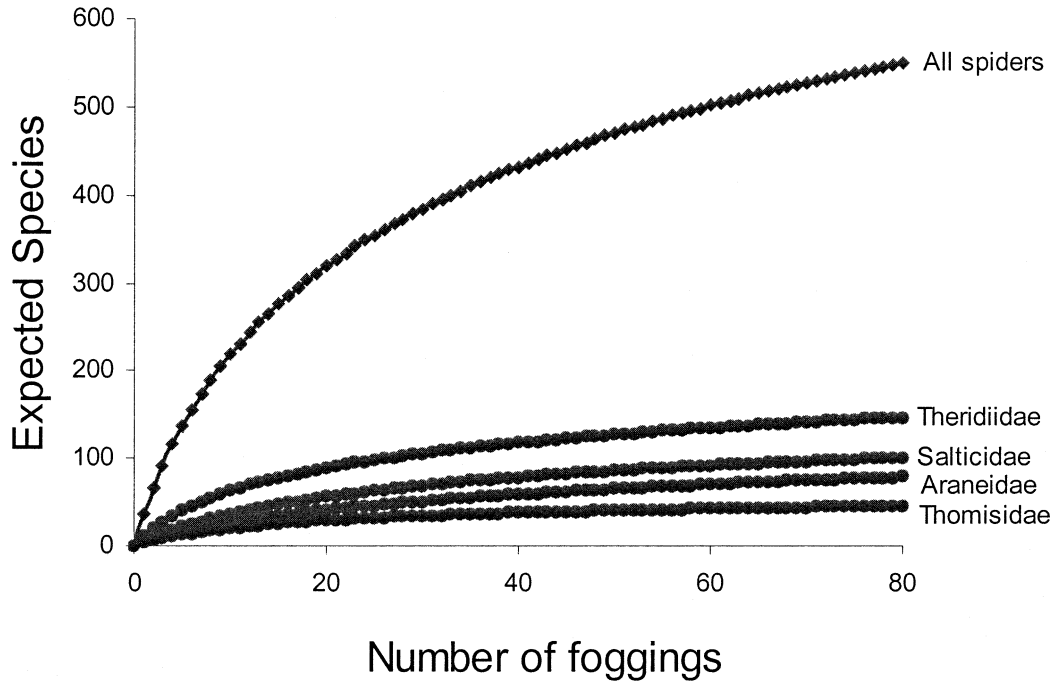

Figure 3.—Shinozaki curves of spider communities based on all foggings.

forest. Changes in spider communities occurred already at the family level (number of families collected per forest type) and were recognizable especially by the dominance of species from the families Theridiidae, Thomisidae, Salticidae, Araneidae, and Clubionidae. Dominance of individual species was highest in the most disturbed forests. Above all, high species diversity in SII and SIII indicate that the spider fauna recovered much faster in the forests close to the primary forest than in the isolated forests. An approximation to the conditions of the primary forest during the course of forest succession is obvious in most parameters analyzed and is in correspondence with similar findings for Formicidae and Coleoptera (Floren et al. 2001; Floren & Linsenmair 2001). In contrast, diversity in the isolated forests was significantly lower and changed only a little during forest regeneration. Species numbers give an impressive example: even in the 5 year-old pioneer forest SI, we found more species than in the 50 year-old isolated forest CRIII. Interestingly, the 40 year-old forest SIII was richer in species than the primary forest. A probable reason for this is that many primary forest species had already become established in SIII and were able to coexist with species that were more successful under the disturbance regime.

Although spider communities of the connected forests SII and SIII resembled those of the primary forest in many respects, there were still clear differences. While the proportion of singletons was larger than 30% in each forest type and did not correlate with the degree of disturbance, the mean number of singletons per tree community distinguished the primary and the old secondary forest SIII from all other disturbed forests. The number of singletons per tree-specific community was lowest in CRI, the youngest isolated and most disturbed forest fragment investigated. The low proportion of singletons per community corresponded with low overall diversity in the disturbed forest fragments and seems to be a good discriminator between primary, old-secondary and more severely disturbed forests. Community equitability also changed with forest disturbance from even communities in the primary forest to uneven communities in the disturbed forests. Similar changes are usually observed as a consequence of anthropogenically disturbance of forests (e.g., Leigh et al. 1993; Laurance 1994; Daily & Ehrlich 1995). The reason for the high abundance of

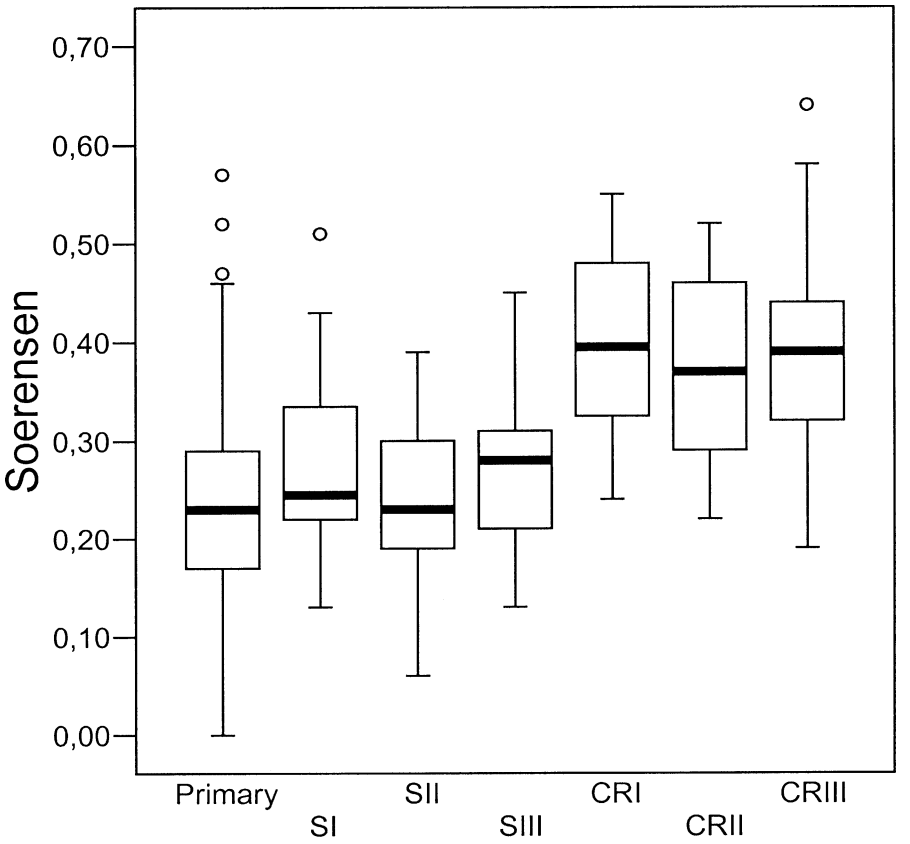

Figure 4.—Mean beta-diversities (measured by the Soerensen-index) between all spider communities of each forest type, expressed as Box Plots. The boxes cover 50 percent of all values (wiskers 75%) and show the median. A circle indicates outlier values between one and three times the box length.

the thomisid new genus & species cf. *Pycnaxis*, a species which seems unrelated to any other species and which has been found exclusively in the primary forests in Sabah, is not currently understood. It might be connected to the El Niño droughts of the year of collection in 1998. Spider communities became structurally simpler in the disturbed forests, because fewer species were found with median abundance classes. In the isolated forests we found a dominance of a number of common widespread web-building spider species: for instance several *Gasteracantha* and *Tetragnatha* species, *Mesida gemmea* (Hasselt 1882), and a number of smaller theridiid species. Several tiny (2—3 mm) widespread oonopid and theridiid species were found exclusively in the primary forests; these species probably live among the roots of epiphytic plants.

Our results led us to conclude that recolonization from primary forests is absolutely necessary for the restoration of species diversity. If such species-sources are lacking, the restoration of spider diversity and spider communities proceeds only slowly if at all. These data indicate that the time necessary for recovery of arthropod diversity is usually greatly underestimated. The process of recolonization needs decades even under optimal conditions. In contrast, we sampled only rudimentary spider communities in the isolated secondary forest stands where no recolonization occurred. Even after 50 years of forest regeneration, spider communities were of low diversity and dominated by common species characteristic of open vegetation and shrub. Today small forest fragments dominate the landscape and already 40 year old forests are under high pressure by local people and the wood industry. Our study led us to suspect that the loss of spider species diversity will be

immense with primary forests lacking as species-sources from which recolonization can start.

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Appendix 1.—Number of species per family and number of widespread species in all fogging samples.

Sampling area	Primary forest		Secondary forests close to prim. forest		Secondary isolated forests		Total
No. of foggings	30		48		24		102
No. of families	26		23		20		29
	Ind.	Sp.	Ind.	Sp.	Ind.	Sp.	Total sp.
Oonopidae	150	6	47	5	75	5	7
Pholcidae	147	10	3	2	7	2	11
Scytodidae	6	1	0	0	1	1	1
Clubionidae							
Clubioninae	230	17	54	15	21	4	24
Systariinae	18	3	0	0	0	0	3
Eutichurinae	14	2	12	2	5	1	4
Corinnidae							
Castianeirinae	40	9	64	7	10	3	10
Trachelinae	34	3	31	2	0	0	4
Phrurolithinae	2	1	17	1	2	1	3
Gnaphosidae	8	3	11	4	0	0	5
Sparassidae	71	6	59	7	42	3	10
Ctenidae	2	1	1	1	0	0	1
Selenopidae	3	1	0	0	0	0	1
Salticidae	334	59	426	65	72	19	111
Zodariidae	9	2	11	3	0	0	3
Oxyopidae	41	6	45	8	0	0	8
Pisauridae	0	0	21	1	1	1	1
Thomisidae	570	31	767	54	223	19	74
Philodromidae	15	2	5	2	12	1	2
Hahniidae	21	1	0	0	0	0	1
Hersiliidae	65	6	28	3	14	1	6
Linyphiidae	47	6	33	4	4	2	8
Theridiidae	562	80	600	83	631	53	153
Mimetidae	24	2	2	1	0	0	2
Theridiosomatidae	1	1	109	5	7	2	6
Tetragnathidae	98	10	117	10	171	9	19
Araneidae	151	36	307	44	97	29	80
Mysmenidae	0	0	10	6	2	1	7
Anapidae	0	0	5	2	1	1	3
Uloboridae	32	4	41	3	32	1	5
Dictynidae	43	1	0	0	0	0	1
Psechridae	2	2	0	0	1	1	2
Deinopidae	2	2	0	0	0	0	2
Total species		314		332		160	578
Identified widespread species		69		63		56	
Percentage widespread species		21.9%		18.9%		35.0%	