Spider communities in Indonesian cacao agroforestry: diversity, web density and spatio-temporal turnover

Dissertation

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Chapter 1

General Introduction

Tropical rainforests under global change

Tropical rainforests are threatened by global change processes of which deforestation and habitat degradation into agricultural land are probably among the most important ones (Perfecto & Vandermeer, 2008) while constituting one of the major driving factors for the global biodiversity loss (Sala et al., 2000). In particular tropical forests in South East Asia suffer from accelerating deforestation rates with about five million hectares annually getting lost to agricultural expansion (Achard et al., 2002). Small-scale agroforestry systems that replace pristine tropical forests are of large interests because of their potential benefits to biodiversity conservation and ecosystem services (Rice & Greenberg, 2000; McNeely, 2004; Schroth et al., 2004), since complex agroforestry sites still provide a multistrata forest structure (De Clerck & Negeros-Castilli, 2000).

Indonesia is one of the world's most important hot spots in terms of biodiversity (Myers et el., 2000) but is also one of many areas where land use has prevailed (Scales & Marsden, 2008). Small-scale agroforestry systems in Indonesia, relative to other causes of deforestation, has been estimated in 1990 to be of major importance suggesting that shifting cultivators might be responsible for about 20 percent of forest loss (FWI/GFW, 2002).
In Central Sulawesi, pristine tropical forests are replaced by a mosaic of traditional agricultural systems, which are used for cultivating economically important cash crops such as rubber (*Ficus elastica*), coffee (*Coffea* spp.) and cacao (*Theobroma cacao*) (Siebert, 2002). Indonesia is the world´s third largest producer of cacao and the output of more than 485,000 t annually (ICCO, 2009) is produced mainly by smallholders on the island of Sulawesi (Misnawi & Teguh, 2008). Because of its location between the biogeographic Wallace's and Weber line and the long-term isolation from the Eurasian mainland (Audley-Charles, 1983), Sulawesi is known for a high proportion of endemic organisms making it a focus region for biodiversity conservation (Whitmore, 1998; Myers et al., 2000; Kessler et al., 2005).

Cacao agroforestry intensification

During the economic crisis in 1998, the weak rupiah and high world commodity prices produced a cacao boom (Potter, 2001) wherefore shaded cacao plantations became the major agroforestry system in Sulawesi (Belsky & Siebert, 2003). Traditionally, smallholder cacao farmers establish their cacao plantations by removing the forest understorey and use the shade provided by the remaining trees (Asare, 2006). Such multistrata agroforestry systems with a diverse shade tree cover, herb layer and well-developed leaf litter layer can offer a high variety of niches that are even suitable for forest species with specific habitat requirements (Philpott & Armbrecht, 2006; Bos et al., 2007; Delabie et al., 2007; Clough et al., 2009). In particular cacao agroforestry has been praised as one of the most complex, biodiverse agroecosystem types (Bhagwat et al., 2008).

Current management practises within Indonesian cacao agroforests follow a habitat simplification due to extensive weeding, removal of leaf litter, removal of natural forest trees and planting of a homogeneous shade tree cover from a single genus or a conversion into intensive full-sun monocultures. Biodiversity conservation across agroforestry systems has been related to low intensity management and remnant forest within the landscape, whereas species richness generally decrease with intensity of management and decreasing strata richness (Scales & Marsden, 2008). For instance ant communities are greatly affected by shade tree removal and habitat simplification leading to losses of nesting sites (Armbrecht et al., 2004; Philpott, 2005; Bisseleua et al., 2008).

General predators and ecosystem functioning

Deforestation and management intensification of agroforestry systems lead to a decline in biodiversity with consequences for a continued supply for ecosystem services (Perfecto et al., 2007; Scales & Marsden, 2008). The interest in the relationship between biodiversity and ecosystem functioning (e.g. pollination, predation, seed dispersal) has increased considerably (Duffy, 2003) and is accompanied by recent efforts in agriculture towards reduced pesticide use and sustainable land cultivation (Maloney et al., 2003). Many studies in temperate and tropical regions has demonstrated that spiders can control herbivore populations, an important ecosystem service within agricultural systems (Kajak et al., 1968; Nakasuji et al., 1973; Mansour et al., 1980; Fagan et al., 1998). While the diversity and functional role of ants has been intensively studied in coffee and cacao farms (e.g. Way & Khoo, 1992; Majer et al., 1994; Perfecto & Snelling, 1995; Vandermeer et al., 2002; Philpott & Armbrecht, 2006), studies on the ecology of spider communities in agroforests systems are still rare (Korinus, 2007; Perez-de La Cruz et al., 2007).

Spiders of cacao agroforestry systems in Indonesia

Spiders are abundant predators in natural as well as agricultural systems in temperate and tropical regions. But to date, compared with most plants and animal groups, spider species in tropical Asia are poorly known (Deeleman-Reinhold, 2001). Hence taxonomic identification to species level was challenging and in some cases species could only be identified to morphospecies level. Specimens were identified to the family, genus and species level when possible based on literature of e.g. Barrion and Litsinger (1995), Murphy and Murphy (2000), Deeleman-Reinhold (2001) and Proszynski (2007). Nearly all genera occourring on continental SE Asia have spread into the islands wherefore present sea-barriers seems to have only a marginal impact on spider species distribution (Deeleman-Reinhold, 2001).

Spiders were identified to 211 species that represented 27 families (see Appendix). Up to now some genus such as *Serendib* and *Utivarachna* (Clubionidae), both cacao tree inhabiting spiders, were found exclusively within undisturbed primary rainforests. The nomenclature follows Platnick et al. (2010). The family of Sparassidae has been revised by Dr. P. Jäger (Research Institute and Natural History Museum Senckenberg, Germany). Within the framework of a diploma thesis, W. Schulz (2006) studied litter-dwelling spiders in cacao agroforestry systems along a land-use gradient in Central Sulawesi. She found high densities of Oonopidae and Lycosidae, which are known to be common ground dwellers even within Dominican cacao agroforestry systems (Ovtcharenko, 2009). Simanjuntak (2001) referred to hunting spiders as Thomisidae, Salticidae and Oxyopidae as well as orb-web weaving spiders as Araneidae and Tetragnathidae which are effective predators for several pest insects in Indonesian cacao agroecosystems.

Study region and study system

The here presented study was conducted within cacao agroforestry systems in Central Sulawesi (Indonesia), within the Kulawi and Palolo valley, which verged on the margins of the Lore Lindu National Park (LLNP) (Fig. 1). The LLNP covers an area of about 2.300 km² and consists of lowland and submontane rainforest vegetation with an elevation ranging from 200 to 2,610 m above sea level. In 1982 the LLNP was declared as a UNESCO Biosphere Reserve. The climate of the research area is characterized by high temperatures that average 23°C. According to Metzner (1981), the mean annual precipitation is 2,237 mm in Kulawi and 1,797 mm in Kapirore (Palolo valley) but with no clear seasonal fluctuations. The LLNP is surrounded by a highly patchy agricultural landscape with heterogeneous land-use systems as irrigated rice fields, slash-and-burn cultivation with annual crops and agroforestry systems such as cacao (*Theobroma cacao*) and coffee (*Coffea* spp.).

Twenty-two cacao agroforestry sites were selected in the Kulawi valley on the west side of the NP and 21 in the Palolo valley, at the northern border of the NP. In each agroforestry site we established a 40 x 40 m plot. The 43 study sites formed a gradient in land-use intensity, differing in shade tree cover and shade tree diversity, weed and leaf litter management as well as distance to forest and elevation. The elevation of the research plots ranged from 400 to 950 m and the distances to the adjacent natural forest site from contiguous to dislodged plots with a maximum distance of 2400 m. The common shade trees were *Glyricidia sepium* (Fabaceae), *Aleurites moluccana* (Euphorbiaceae), *Erythrina* sp. (Fabaceae) and *Nephelium* sp. (Sapindaceae) and the weed layer was dominated by *Cytococcum accrescens* (Poaceae) and *Paspalum conjugatum* (Poaceae). Half of the plots were weeded every second month, the other half every six months. Agroforestry sites were selected to avoid collinearity of explanatory variables such as shade tree density and distance to forest. Table 1 gives an overview of the site characteristics with their range within the studied cacao sites.

Table 1 Landscape and plot characteristics of cacao agroforests at the study sites in Central Sulawesi, Indonesia.

Variable	Description	Min	Mean	Max
Elevation	in metres above sea level, untransformed	400	662	950
Forest distance	in metres, Distance to nearest forest patch over 2 ha in area	0	392	2400
Weed cover	in percent, untransformed	5.0	56.2	100.0
Weed height	in centimetres, averaged high of five samples per plot	9	32	107
Weed diversity	Species richness	2	14	24
Litter density	no. of leaves per $0.1 m^2$, average value of 5 samples per plot	25	88	172
No. of shade trees	untransformed	4	34	146
Shade diversity	Simpson's diversity Index ($1-D$; $D = \sum(n_i/N)^2$)	0.08	0.69	0.95

Min = Minimum, Max = Maximum

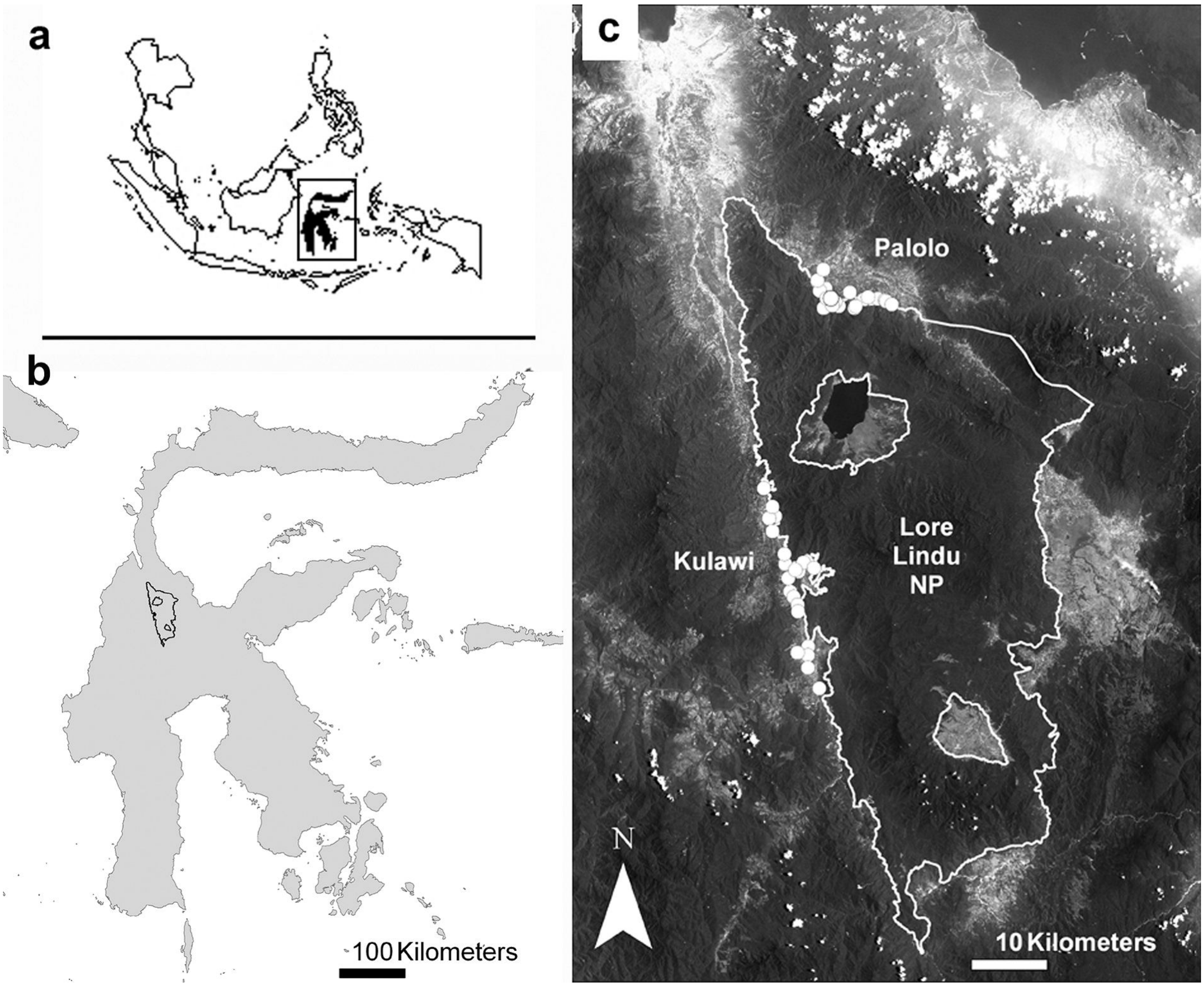


Figure 1 Map of the study area: (a) Sulawesi within the Indo-malay region (b) Location of the Lore Lindu National Park within Sulawesi (c) Lore Lindu National Park with its two populated enclaves (white lines) and the location of the 42 research plot (white dots) in Palolo and Kulawi valleys (source: Clough et al. 2009).

Chapter outline

In chapter 2 the distribution of several spider web types within 420 cacao trees has been analysed to determine how web-building spider guilds relate to habitat variables and a numerically dominant ant species at three different spatial scales, comparing tree, plot and landscape features. We classified webs into five guilds: orb-weaver, sheet-weaver, tangle-weaver, lattice-weaver and line-weaver. While landscape context had little effect, spider web density can be enhanced through appropriate management at the tree and plot scale. A positive relation between density of several web types and local cacao canopy openness suggests that foliage density control through pruning and thinning could enhance spider web density on cacao trees. The presence of the aggressive *Philidris* ant was positively associated with density of orb-webs, while no pattern was found for other web types.

Chapter 3 focuses on data from twelve cacao agroforestry sites, in which the abundance, diversity and composition of spider communities of litter, herb and canopy layer were studied with reference to local management and landscape context. There were distinct stratum-associated composition patterns of spiders, where species diversity and abundance was influenced by management variables such as shade tree density and weed diversity but also by forest proximity, a landscape scale parameter.

The study presented within Chapter 4 addresses spatial and temporal species turnover of litter and canopy dwelling spiders in agroforests to gain insight into dynamic processes determining spatio-temporal patterns in community compositions. Both temporal and spatial turnover was affected mainly by habitat-scale variables. The largest effect was the positive relation of temporal species turnover to shade tree diversity. The lack of an impact of forest distance to turnover patterns is discussed.

Chapter 5 includes a summary and general conclusions that emerged from all presented studies.

Chapter 2

Spider web guilds in cacao agroforestry systems– comparing tree, plot and landscape scale management

Introduction

Spiders reach high densities in most terrestrial ecosystems of both temperate and tropical regions, but knowledge about distribution drivers and their functional role as generalist predators stems mostly from temperate arable systems (Riechert & Lockley, 1984; Sunderland & Samu, 2000; Maloney et al., 2003). Studies on the functional role of spider communities (Arachnida: Araneae) in tropical land-use systems are underrepresented and existing studies focus on changes in spider communities within habitats along different degrees of human disturbances but with no references to their functional importance (Chen & Tso, 2004; Floren & Deeleman-Reinhold, 2005; Tsai et al., 2006; Hore & Uniyal, 2008). Web-building spiders are almost strictly insectivorous and can be important biological control agents (Marc et al., 1999). Pérez-de La Cruz et al. (2007) found a highly diversified prey spectrum of orb-weavers in cacao plantations in Mexico. But how spiders react to management and how they interact with other components of the agroecosystem such as ants is largely unknown. In this study we quantified the web density on 10 trees in each of 42 plots in contrasting cacao agroforestry sites in Central Sulawesi to disentangle the contribution of variables at the tree, plantation and landscape scale to the densities of different spider web types, or "web guilds". Tropical agroforests such as coffee and cacao agroforestry have been praised as some of the most complex, biodiverse agroecosystems (Bhagwat et al., 2008). There is a wide range of different types of plantations, ranging from forest-like agroforests to unshaded monocultures, with a large variability in tree species composition, shade tree cover and cacao tree architecture. The current trend is to remove shade trees, creating a shift away from agroforests to monoculture plantations.

We analysed the effects of variables related to tree configuration (size, height), occupancy by the numerically dominant ant *Philidris* sp. (Clough et al. 2010), variables related to plot management such as shade tree and litter management, as well as variables related to the position of the plot in the landscape, namely elevation and distance to natural forest, on the density of different spider web types.

We hypothesized that all three spatial scales significantly contribute to spider web density with each web type being differently affected. From an applied point of view, this would mean a need to take all scales into account when developing management schemes.

Materials and methods

Study sites

The study was conducted within 42 cacao agroforestry sites along the margin of Lore Lindu National Park (1°30′ S, 120°10′ E) in Central Sulawesi, Indonesia (Fig. 1.). Twenty-one cacao agroforestry sites were selected in the Kulawi valley on the west side of the NP and 21 in the Palolo valley, at the northern border of the NP. In each agroforestry site we established a 40 x 40 m plot. An overview of parameter variability among the research plots is given in Table 2.1.

Survey

All spider webs were recorded by web visualisation from ground-level to 4 m height once on each of 420 cacao trees (10 trees per plot) from January until March 2008. A commercial hand water sprayer (for ornamental plants) was used to increase the visibility of spider webs. We recorded web type, web size, height and position within the cacao tree. We defined seven locations within a tree: stem, fruit, branch, leaf, twig, crotch and the space between adjacent tree canopies. We classified webs into five guilds: orb-weaver, sheet-weaver, tangle-weaver, lattice-weaver and line-weaver (see below).

Spider guilds

The two-dimensional webs of orb-weavers are round and the central component constructed in a single surface (Fig. 2.1, Appendix 2.1). The principal part of sheet-webs is a horizontal sheet which can be domed. In contrast, lattice-webs were defined as two-dimensional web constructions that had a planar sheet with quadrangular meshes. Tangle-webs consist of an irregular, three dimensional retreat connected to the surroundings with strong anchor lines (Benjamin & Zschokke, 2003). Line-webs consist of only few filaments and constitute a reduced or a modified web, which is usually star-shaped and restricted to hub and radii (Jocqué & Dippenaar-Schoeman, 2007).

Although there is a high plasticity in the intrafamiliar, but also in intraspecific web construction (Vollrath et al., 1997; Benjamin & Zschokke, 2003; Blackledge & Zevenbergen, 2007; Bonte et al., 2008), a rough assignment of spider families to web guilds is possible. The guild classification follows Uetz et al. (1999), Höfer & Bresovit (2001), Hore & Uniyal (2008) as well as personal observations. Previous species determinations and literature revision of web-builders showed that orb-web builders associated with cacao trees belonged to the families Araneidae, Uloboridae, Tetragnathidae and Nephilidae, while several species of Araneidae and Uloboridae reduced their web construction to a few filaments and constitute, along with a few Theridiidae species, the guild of line-weavers. Some species of the closely related spider families Theridiidae built lattice-webs, while the Theridiidae *Achaearanea* sp. is also known to weave tangle-webs. Sheet-webs are built by representatives of Theridiidae, furthermore by Linyphiidae, Psechridae and Hahniidae. Hence, different spider web types may come from the same spider family. The Theridiidae were the most diverse family with respect to number of different web types produced.

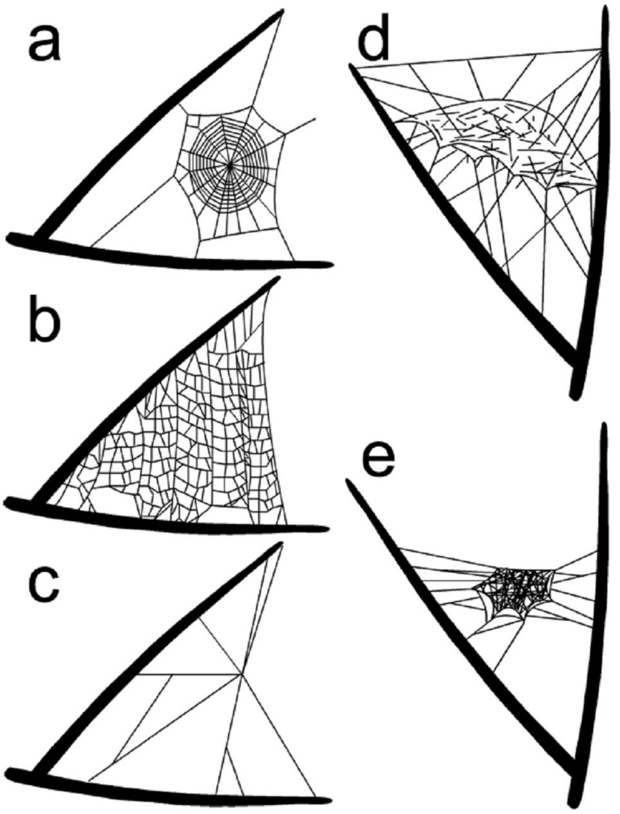


Figure 2.1 Exemplary web constructions of the adopted five spider web guilds: (a) orb web, (b) lattice web, (c) line web, (d) sheet web and (e) tangle web.

Tree architecture and environmental variables

The following parameters were measured on all trees: total height (TH), stem height (SH), averaged length of foliage-free main branches (FFB), averaged distance to neighbouring cacao trees (DNC) and number of neighbouring shade trees (NNST). In addition, the canopy openness in a height of 1.30 m above ground (CanOp1.3) of each tree was recorded using hemispherical photographs. At plot level, we recorded elevation (ELE), forest distance (FD), weed cover (WC), weed height (WH), litter density (LD), number of shade trees (NST) and shade tree diversity (TD). Distance to the nearest forest is based on satellite images of the study area displayed and managed with ArcGIS 9.2 (ESRI). Weed cover and height as well as litter density were measured once at five random points in the plot, and averages were calculated. The percentage weed cover was estimated at each point with a radius of 2 m and litter density is defined as the average number of *Theobroma cacao* and shade tree leaves per 0.1 m^2. Shade trees either inside the plot, or with the crown overlapping the 40 x 40 m plot, were identified to species level and shade tree diversity calculated using Simpson's diversity index.

Table 2.1 Explanatory variables used in general linear models to explain spider web abundance on tree, plot and landscape scale.

Variable name	Description	Min	Mean	Max
Tree height	in centimetres, from ground to foliage end, untransformed	288	497	780
Stem height	in centimetres, untransformed	12	129	420
Foliag-free branches	in centimetres, averaged lenght	75	241	594
Dist. next cacao tree	in centimetres, averaged lenght	166	320	518
Shade trees	number of neighboured shade trees, untransformed	0	1	5
Canopy openness	in percent, 1.30 m above ground,	3.8	12.1	32.3
Philidris sp.	Factor with two level, presence and absence	–	–	–
Elevation	in metres above sea level, untransformed	400	662	950
Forest distance	in metres, Distance to nearest forest patch over 2 ha in area	0	392	2400
Weed cover	in percent, untransformed	5.0	56.2	100.0
Weed height	in centimetres, averaged high of five samples per plot	9	32	107
Litter density	number of leaves per 0.1m^2, average value of five samples per plot	25	88	172
No. of shade trees	untransformed	4	34	146
Shade tree diversity	Simpson's diversity Index (1-D; $D = \sum(n_i/N)^2$)	0.08	0.69	0.95

Ant data

The presence-absence data of the numerically dominant *Philidris* spp. (Formicidae: Dolichoderinae) were surveyed on the same 420 cacao trees from July until November 2007. Standardized plates of 25 cm diameter, which were equipped with two baits of 2 cm^3 of tuna in oil and two sponges saturated with 70% sugar solution, were placed in the main ramification of each experimental cacao tree. The plates were observed for one hour while every 15 minutes the abundance of all ant species occurring at the baits feeding on fish or sugar was counted (Clough et al. 2010). Species of *Philidris* sp. form large nests containing many thousands of workers in cavities of living plants or in rotten wood above the ground. *Philidris* workers are very aggressive when disturbed and will swarm in large numbers to attack intruders (Shattuck, 1999).

Data analysis

The determinants of web density were analysed using linear mixed models for Poisson-distributed data with plot as a random grouping factor. We tested for overdispersion by fitting the models with an overdispersion scale correction factor. If the latter was close to 1 then the model was recalculated with a normal Poisson distribution, otherwise we kept the scale correction factor ("quasipoisson model"). To avoid overfitting, model selection was done as follows: we first fit all tree-scale parameters and discarded variables one by one that had no effect on web density. In a second step, we integrated variables measured at a larger scale (plot, landscape). For each spider guild and the total web abundance the full model, the null model and models with all valid combinations of the explanatory variables including first-order interactions were generated. To identify the relative support for each model, we used Akaike´s Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). While the best-fitting model in the set has the minimum AICc score, differences in the AICc scores between each model and the best model (Δ_i = AICc_i – $\mathrm{AICc}_{\mathrm{min}}$) and also the Akaike weights (w_i) for each model were calculated. All models with ΔAICc less than 2 entered the best-model subset for model-averaged estimates that were obtained by computing means and standard errors of the estimates weighted by the model weights. In the same manner we calculated quasi-Poisson models while using quasi AICc (QAICc).

The analyses were conducted in *R* version 2.8.1 (R Development Core Team, 2008) with additional functions provided by the *R* packages *lme4* (Linear mixed-effects models using S4 classes, Bates et al., 2008) and *MuMIn* (R functions for model selection and model averaging, Bartoń, 2009).

Results

We recorded a total of 5143 spider webs. Line-weavers, building webs of only few or single filaments, constituted the most abundant web guild on cacao trees with a percentage of 41.9. The orb-weavers, with 1528 webs, were the second most abundant guild on cacao trees (29.7 %). The percentage of lattice-webs, sheet-webs and tangle-webs ranged from 12 % to 7 % of the total. Most webs were built between branches, leaves and twigs, while crotches also provided the required structural complexity for web-building. Crotches were equally used by all spider web guilds, however tangle-weaver showed a clear preference for this part of the cacao tree (Fig. 2.2). The differences in distribution among the different tree structures suggest guild-specific web-building requirements. Guilds that build mostly large-sized webs such as sheet- and orb-weavers were found preferentially in the often more structurally complex tree crown, while tangle- and lattice-weavers were found consistently on almost all tree positions, but only rarely between two neighbouring cacao tree canopies.

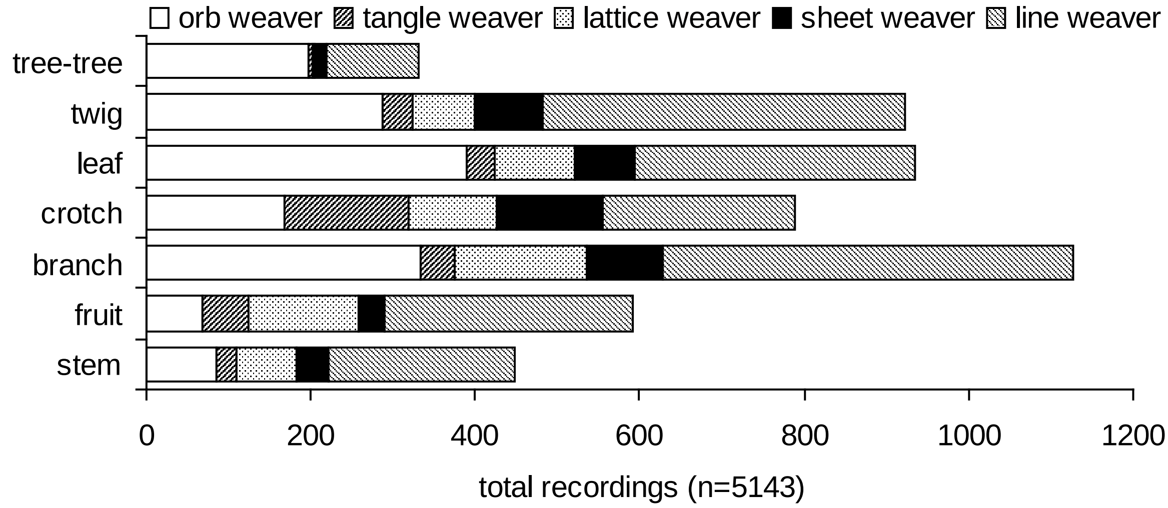


Figure 2.2 Variations in spider guild abundance among tree habitat positions in cacao agroecosystems.

The model-averaged parameters (Table 2.2) show the importance of tree architecture in determining the composition of web-building spider guilds on cacao trees. Of the parameters characterizing tree architecture, canopy openness was the most important factor affecting the abundance of all types of spider webs on cacao trees. With the exception of tangle-webs, all web types occurred in higher densities on cacao trees with a more open cacao canopy. Thereby the model-averaged coefficient and its standard error deviated within the determined spider guilds. Accordingly the canopy openness of cacao trees exerted the strongest impact on the orb- and lattice-weaving spider guild. Increased stem heights and elongated bare branches had a negative effect on the abundance of spider webs. Total tree height and the distance to neighbouring cacao and shade trees seem to be less important parameters for the distribution of web-building spider guilds.

On the plot scale, web abundance increased with higher density of shade trees. In particular the spider guilds lattice- and tangle-weaver showed an enhanced web density in more shaded cacao plots (Fig. 2.3). In addition, elevation affected the composition of the spider web assemblages, with an increase in density with altitude for all web types except lattice-webs, which decreased, and line-webs for which only the effect of shade tree density could be detected. The impact of the parameters forest distance, weed cover and litter density was restricted to individual guilds (Table 2.2). The diversity of the shade trees did not appear to have any impact on changes in web abundance.

The impact of the ant species *Philidris* sp. was restricted to orb-weavers, shown by the high positive coefficient of the averaged model.

Table 2.2 Multi-Model averaged estimates for coefficients of tree architectural and environmental parameters determining spider web abundance on cacao trees (SH: stem height, FFB: foliage-free main branches, CanOp1.3: Canopy openness in 1.30 m, ELE: elevation, FD: forest distance, WC: weed cover, LD: litter density, NST: number of shade trees).

	TOTAL	ORB	TANGLE	LATTICE	SHEET	LINE
Intercept	2.280 ± 0.722	-1.500 ± 1.110	-3.200 ± 0.798	2.060 ± 0.882	-2.630 ± 0.776	1.850 ± 0.451
tree scale						
SH	-0.001 ± 0.001	-0.002 ± 0.001	–	–	0.001 ± 0.001	-0.002 ± 0.001
FFB	-0.001 ± 0.001	-0.001 ± 0.001	–	–	–	-0.002 ± 0.001
CanOp1.3	0.022 ± 0.019	0.024 ± 0.014	-0.004 ± 0.018	0.028 ± 0.011	0.005 ± 0.016	0.018 ± 0.013
Philidris sp.	–	0.345 ± 0.181	–	–	–	–
plot scale						
ELE	–	0.004 ± 0.001	0.003 ± 0.001	-0.004 ± 0.001	0.004 ± 0.001	–
FD	–	–	–	-0.001 ± 0.001	–	–
WC	–	–	–	–	-0.008 ± 0.004	–
LD	–	–	–	-0.004 ± 0.004	–	–
NST	0.004 ± 0.006	–	0.012 ± 0.004	0.013 ± 0.004	–	0.003 ± 0.004

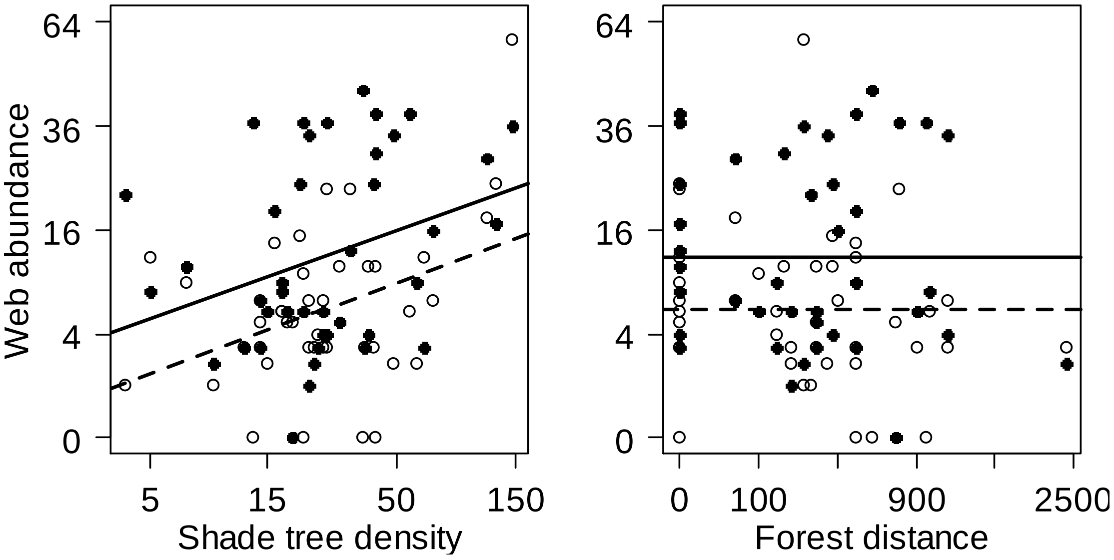


Figure 2.3 Impact of the plot scale parameters shade tree density and forest distance (m) on two spider web guilds: tangle webs (○, dashed line) and lattice webs (●, solid line).

Discussion

The determinants of web-building spider communities in tropical agroforestry systems are largely unknown. In this study we investigated how smallholder management (tree architecture, shade and litter management) and landscape context affect spider web density and composition in cacao agroforests.

Tree architecture

Cacao trees in smallholder plantations differ widely in terms of tree architecture as a result of different pruning strategies. Spiders are known to react strongly to changes in small-scale vegetation structure. De Souza & Martins (2005) compared the abundance of foliage-dwelling spiders among seven plant species comprising a gradient of levels of structural complexity. There more spiders colonized the high foliage density branches relative to the low density branches. Similarly, we found an inverse relation between spider web abundance in cacao trees and the length of foliage-free branches. The foliage structure and density of a tree regulates the living conditions of spiders regarding web construction, prey availability, hiding places, microclimate conditions such as temperature and humidity, mating behaviour as well as inter- and intraspecific competition. Besides vegetation structure, microclimate conditions play an important role in the microhabitat selection of spiders (Biere & Uetz, 1981) and the characteristics of their community that occur in the cacao tree. The parameter canopy openness determines the foliage and branch density and therewith shade conditions. Because of the different microhabitat structure requirements for web constructions (e.g. available space, anchor points on substrate, microclimate conditions) of each spider family, the architectural complexity of a cacao tree should affect the abundance and diversity of weaving spiders. The orb- and line-weavers that dominated the web guild structure on cacao trees showed a high dependence on tree structural complexity, while the abundances of tangle-, lattice- and sheet-weavers were additionally influenced by environmental conditions like forest distance, weed cover and litter density. The positive effect of canopy openness on abundance of several web guilds shows the importance to control foliage density through appropriate pruning practices. Thinning the cacao canopy enhances spider web abundance on cacao trees.

Shade tree and litter management

While at the tree scale, trees with high canopy openness had higher densities of spider webs, at the plot scale we found a positive correlation to the number of shade trees and total number of spider webs, which suggests that despite increasing canopy cover measured below the cacao canopy, shade trees are very important for web-building spiders. Shade trees contribute considerably to habitat heterogeneity and complexity, a determining factor for spider community composition and diversity (Korinus et al., 2007). Direct solar radiation due to a low density of shade trees may cause fluctuations in microclimate conditions, which implies a decrease in suitable habitats for spider species which require stable temperatures and humidity (Riechert & Tracy, 1975; Suter, 1981; Prinzing, 2001). In addition, the canopy cover of shade trees can shield spider webs from damage or destruction by rainfall and wind. Shade tree diversity had no effect on web density, suggesting that the close correspondence between the vegetation and their spider web composition is related to vegetation architecture and cover rather than its diversity (Marc et al., 1999).

Previous studies into the relationship of shade tree canopy cover and arthropod diversity of cacao agroforestry sites in this region showed that removing shade trees causes great losses of invertebrate species richness (Steffan-Dewenter et al., 2007). Klein et al. (2002) found a reduced predator–prey ratio in intensified cacao agroecosystems due to low shade tree diversity and associated changes in microclimate.

Elevation and landscape context

The sensitivity of spiders to changes in habitat structure and to the composition of agricultural landscapes has been shown (Uetz et al., 1999; Clough et al., 2005; Schmidt et al., 2008; Baldissera et al., 2008). In addition to vegetation structure, elevation has been highlighted as relevant for spiders (Urones & Puerto, 1988), but reasons for an increase of spider density with increasing altitude are still not clear (Russel-Smith & Stork, 1994). In our study the density of orb-, tangle- and sheet-weavers was positively related to elevation. Araneidae, a typical and widespread family of weaving orb-webs, have a great dispersal potential and belong to the ballooning spiders (Bishop, 1990). They have broad environmental tolerance but depend on the physical structure of the environment (Jiménez-Valverde & Lobo, 2007). This is why the density of orb-webs appeared to be more influenced by tree architecture than the surrounding landscape.

We found that the overall spider web density on cacao trees was not influenced by distance to forest (Fig. 2.3). Hence the presence of near-natural habitat may be more important in annual systems than in several-year-old perennial systems such as agroforests, where local management is more important.

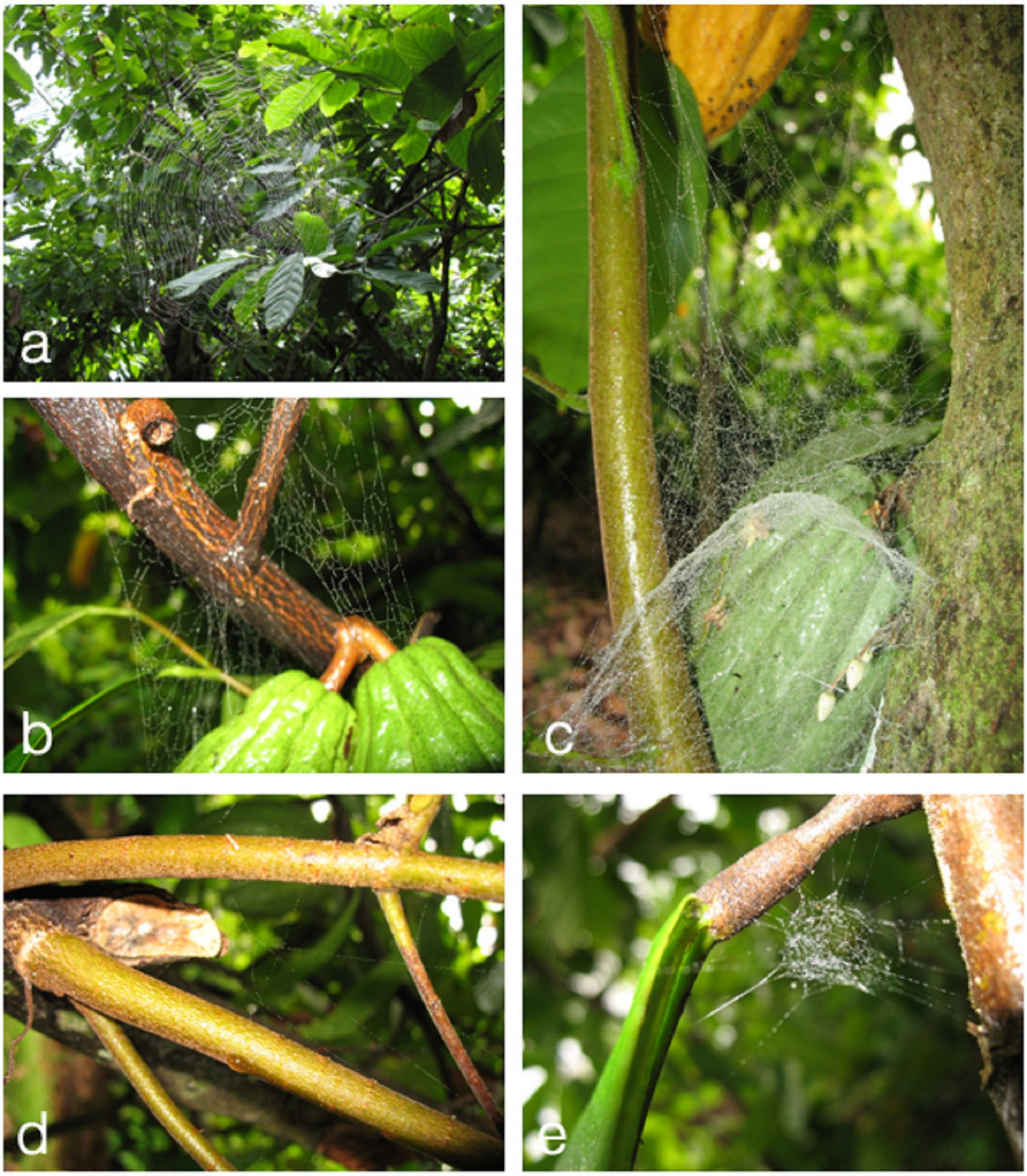
Ant-spider patterns

In our study the impact of the ant species *Philidris* sp. was restricted to orb-weavers, which increased in web density. Documented interactions between ants and spiders suggests a complicated relationship (Vandermeer et al., 2002) and existing results are idiosyncratic. Halaj et al. (1997) found that excluding *Camponotus*-ants from Douglas firs affected neither species composition nor changes in the abundance of web-building spiders. In contrast Floren & Otto (2002) found that spider communities of oak trees with *Formica polyctena* ants harboured significantly more spider individuals and differed in family and species composition from control trees. They also found a positive impact of ants on orb-weaving spiders, while sheet-weaving spiders either avoided ant-harboring trees (Theridiidae) or were positively related to ants (Linyphiidae) as has been also found in Vandermeer et al. (2002). A positive relation of ants and spiders may results from an increased prey density in and around ant nests where trophobionts produce honeydew. Honeydew constitute a main food resource of *Philidris* ants (Maeyama & Matsumoto, 2000) but also for prey insects which are attracted in higher proportion (I. Perfecto, pers. comm.). However, impacts of ants on spider communities need to be investigated in more detail and on a family or a rather species level. Hence this study could not clarify how *Philidris* ants changed composition of web-building spider guilds on cacao trees. *Philidris* ants were active only during the morning hours (personal observation), so possible competition between web-building spiders and *Philidris* may be avoided. It may be argued that the delay between ant and spider web survey decreases the possibility to detect interactions, but shifts in presence-absence data of *Philidris* are unlikely to have taken place over just one and a half month (A. Wielgoss, pers. comm.).

Summary

In complex tropical agroecosystems such as agroforests, management determines plant architecture and vegetation composition, but little is known on how these attributes, together with the presence of ants as well as landscape context, determine spider web density. In Sulawesi, Indonesia, we surveyed the distribution of several spider web types within 420 cacao trees to determine how web-building spider guilds relate to habitat variables and a numerically dominant ant species at three different spatial scales, comparing tree, plot and landscape features.The most frequently recorded webs belonged to the line- and orb-web type. At tree scale, web density was positively related to canopy openness while at plot scale, a higher number of shade trees was related to a higher web density. At landscape scale, the elevation determined the distribution patterns of web-building spiders. Presence of *Philidris* ants was positively associated with density of orb-webs, while no pattern was found for other web types. Results suggest spider web density could be increased by pruning of cacao trees while keeping shade trees density in cacao plots. The results emphasize the need to consider scale dependency of crop management and the different, web-guild specific responses that may be related to different functional roles of spiders as a high-density predator group in agroforestry.

Appendix



Appendix 2.1 Five abundant web types that are found on cacao trees: (a) orb web, (b) lattice web, (c) sheet web, (d) line web and (e) tangle web.

Chapter 3

Spider diversity in cacao agroforestry systems, comparing vertical strata, local management and distance to forest

Introduction

In recent years, the interest in tropical agroforestry systems as a means of combining sustainable land cultivation with biodiversity conservation increased considerably (Bhagwat et al., 2008). Cacao agroforestry systems are considered to play an important role in biodiversity conservation because of the habitat structural complexity that can be maintained, providing habitat for numerous forest species (Beer et al., 1998; Rice & Greenberg, 2000; Schroth & Harvey, 2007). Traditionally, smallholder cacao farmers establish their cacao plantations by removing the forest understorey and use the shade provided by the remaining trees (Asare, 2006). The vertical and horizontal strata configuration are modified, but valuable resources of the forest vegetation and natural ecosystem processes are protected (De Clerck & Negeros-Castilli, 2000). However, current management trends within agroforests entail severe habitat simplification due to extensive weeding, removal natural forest trees, planting one or few shade-tree species or even a conversion into intensive full-sun monocultures, as has been described from Indonesian cacao (Siebert, 2002).

The important ecological role of multi-stratum shaded agroforests for biodiversity conservation could be shown for birds, bats, ants and other wildlife (Estrada et al., 1997; Wunderle & Latta, 1998; Klein et al., 2002; Faria et al., 2006; Philpott & Armbrecht, 2006; Bos et al., 2007; Delabie et al., 2007; Clough et al., 2009). However Schroth and Harvey (2007) and McNeely and Schroth (2006) emphasize that there is still a lack of knowledge about the relative role of landscape structure and local management for the composition of communities.

Spiders are important predators of insect pests in temperate and tropical regions (Marc & Canard, 1997; Maloney et al., 2003; Nyffeler & Sunderland, 2003). They show distinct responses to environmental changes and management practises of agroecosystems (Balfour & Rypstra, 1998; Halaj et al., 2008). However, whereas the diversity and functional role of ants, another ubiquitous and mainly predatory arthropod group, has been intensively studied in coffee and cacao agroforestry (Way & Khoo, 1992; Majer et al., 1994; Perfecto & Snelling, 1995; Vandermeer et al., 2002; Philpott & Armbrecht, 2006), studies on the ecology of spider communities in agroforests are rare (Korinus, 2007; Perez-de La Cruz et al., 2007). Here, we use data from twelve differently managed cacao agroforestry systems in Indonesia to investigate the abundance, diversity and composition of spider communities at three spatial scales: (i) stratum, i.e. litter, herb and cacao canopy layer, (ii) plot-level shade, litter and weed management and (iii) landscape context, i.e. distance to natural forest. We tested the following hypotheses:

Spider communities of cacao agroforestry systems show a vertical stratification from the litter to the herb and canopy layer with a stratum-specific community structure.

Local shade-tree density of cacao agroforest systems and proximity of the forest edge as a species pool positively affect spider abundance and diversity.

Communities of different strata show contrasting responses to management and landscape.

Materials and Methods

Study region

The study was conducted within 12 cacao agroforestry systems in the Kulawi valley along the eastern margin of Lore Lindu National Park (LLNP) in Central Sulawesi, Indonesia (Fig. 1). The systems were characterized by different level of habitat complexity due to various management practices of smallholders. Table 3.1 gives an overview of the measured habitat parameters with their range within the studied cacao plantations. In each agroforestry site we established a 40 x 40 m plot.

Table 3.1 plot characteristics of cacao agroforests at the 12 study sites in Kulawi valley.

Variable	Description	Min	Mean	Max
Litter density	number of leaves per 0.1m², average value of five samples per plot	40	72	110
Weed cover	in percent, untransformed	16	58	96
Shade tree density	number of shade trees per plot, untransformed	13	48	125
Forest distance	in metres, Distance to nearest forest patch over 2 ha in area	0	267	1150

Sampling design

Litter-dwelling spider communities of 12 cacao agroforestry sites were sampled using four roofed pitfall traps (diameter = 20 cm) per plot. Canopy-dwelling spiders were caught on five trees per plot, each tree being fitted with one branch eclector (after Simon, 1995) (Fig. 3.1). Traps were emptied every month between May 2007 and March (litter samples) or April 2008 (canopy samples), resulting in 10 and 11 distinct samples per plot for the litter spiders and canopy spiders, respectively. We used a 1:1 mixture of ethylene glycol and water as preservation liquid in both trap types. From February 14th until 22nd 2008 dip netting samples from all 12 research plots were taken. The samples were standardized and taken along an approximately 55 m long diagonal transect within the plot. All adult spiders were identified to species or morphospecies, while juveniles were excluded from the statistical analyses.

Figure 3.1 Trap system that was used for spider sampling within cacao agroforestry sites: brancheclector in a cacao tree canopy (left) and roofed pitfall trap (right).

Parameters

Shade tree density was recorded by counting trees either inside the plot, or with the crown overlapping the 40 x 40 m plot. The common shade trees in these plots were *Gliricidia sepium* (Fabaceae), *Aleurites moluccana* (Euphorbiaceae), *Erythrina* sp. (Fabaceae) and *Nephelium* sp. (Sapindaceae). Distance to the nearest forest is based on satellite images of the study area displayed and managed with ArcGIS 9.2 (ESRI). Weed cover and leaf litter density were measured once at five random points in the plot, and averages were calculated. The percentage weed cover was estimated at each point within a radius of 2 m and leaf litter density is defined as the average number of *Theobroma cacao* and shade tree leaves per 0.1 m^2.

Data analyses

Data were pooled per plot and stratum. The impact of management practises and distance to forest on spider abundance and species richness of the three habitat strata were analysed using linear mixed effect models (LMEs). The LME models included interactions of the parameters with stratum. Plot was included as a random factor, thus accounting for the nesting of strata within plot. A stepwise backward selection strategy provided by the stepAIC-function in the package *MASS* in the program R (R Development Core Team, 2003) was used to find the most parsimonious regression explaining variation of spider abundance and species richness. To visualise the variability of spider species composition within litter layer, herbaceous layer and cacao tree canopy we used Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980; Oksanen & Minchin, 1997). For the DCA pooled plot data were used, a piecewise linear transformation conducted and rare species were down-weighted.

Results

A total of 1417 adult spiders were collected belonging to 26 families and 213 species. Guild composition of hunting and web-building spiders were similar within canopy and litter communities. Within both strata, 85% of the individuals belonged to hunting spiders, whereas herbaceous layer communities were characterised by high abundances (77%) of web-building spiders. Within the litter layer, the two Lycosidae *Trochosa ruricoloides* as well as *Venonia* sp.1 and *Oedignatha spadix* (Corinnidae) were the most abundant species and made up 56% of all adult individuals (n = 709). Within the herbaceous layer (n = 174), *Leucauge celebesiana* and *L. decorata* (Tetragnathidae) were dominant, while the canopy spider community (n = 534) was numerically dominated by *Thorelliola ensifera* (Salticidae) (n = 52) and *Clubiona* sp.1 (Clubionidae) (n = 83). We found a strong vertical stratification of spider species, where litter and herbaceous layer communities shared only two species. Five species, mainly web-building spiders, occurred within both weed and canopy layers. Results from the DCA ordination show a stratum-specific community composition (Fig. 3.2). Spider communities of herbaceous layer exhibited highest variability in community composition, whereas leaf litter and canopy communities were much more homogeneous.

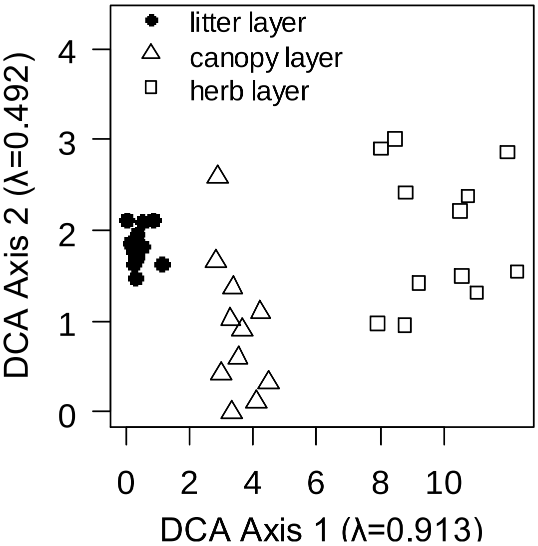


Figure 3.2 Plot of detrended correspondence analyses (DCA) for litter (○), canopy (△) and herb (□) layer spider species assemblages observed within cacao agroforestry systems in Central Sulawesi, Indonesia (12 sites each).

Table 3.2 Effect of managment practises (weed cover, leaf litter density) and landscape context on spider abundance (left) and species richness (right) within canopy, herb and litter layer. Table shows changes in fit of the linear mixed effect model after backward selection (stepAIC).

	d.f.	*AIC*	*LRT*	*P*
< none >		288.081		
Weed cover	1	292.796	6.715	0.010
Forest distance	1	288.438	2.357	0.125
Layer x Leaf litter density	2	290.892	6.810	0.033

	d.f.	*AIC*	*LRT*	*P*
< none >		208.569		
Layer	2	255.900	51.331	<.0001
Leaf litter density	1	209.684	3.115	0.078
Weed cover	1	209.674	3.105	0.078

We found a positive impact of weed cover on spider abundance and species richness, affecting all habitat strata (Fig. 3.3b, 3.3d). Further, spider abundance of litter and canopy layers decreased with an enhanced leaf litter density (Table 3.2). This effect was also found for species richness, but was higher for the litter-inhabiting than for the canopy and herb dwelling communities (Fig. 3.3c). On community level we found no effect of forest distance and shade tree density on spider abundance or species richness. However, individual abundant species showed species-specific responses to management and landscape changes. For instance, the positive response of *Oedignatha spadix* (Corinnidae) to an increased leaf litter density was opposite to that of the overall community (Fig. 3.4). Species-specific responses were also found on landscape level, at which densities of a canopy dwelling jumping spider (*Thorelliola ensifera*) and a litter dwelling wolf spider (*Venonia* sp.1) increased with distance to forest (Fig. 3.5).

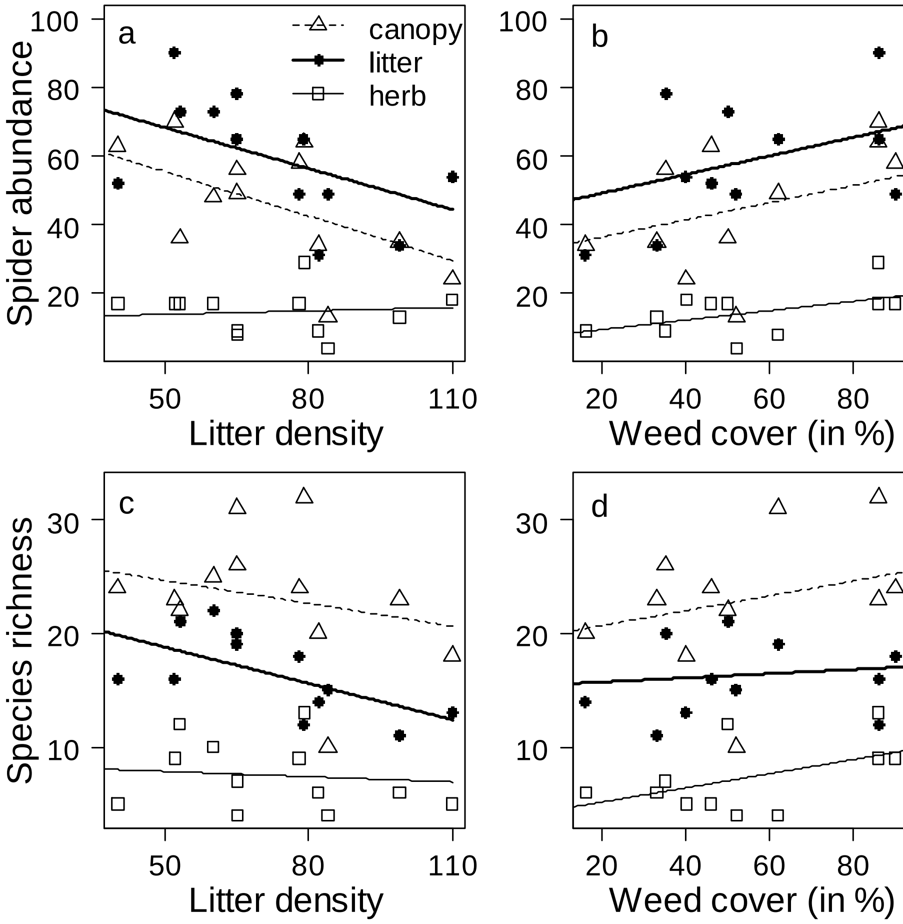


Figure 3.3 Impact of leaf litter density and weed cover on spider abundance (a,b) and species richness (c,d) within canopy (△,---), herb (□,——) and litter layer (●,——) communities.

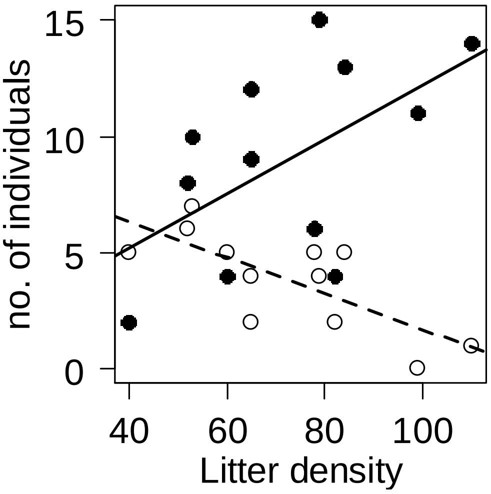


Figure 3.4 Positive response of *Oedignatha spadix* (Corinnidae) (●, solid line) on enhanced leaf litter density ($N = 12$, $F = 4.496$, $P = 0.059$, adjusted $R^2 = 0.241$) while in general litter spider community, represented by *Artoria* sp.1 (Lycosidae) ($N = 12$, $F = 12.040$, $P = 0.006$, adjusted $R^2 = 0.501$) (○, dashed line), was negatively affected.

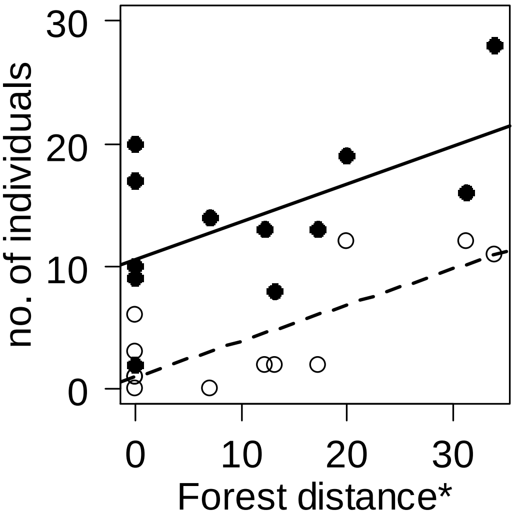


Figure 3.5 Impact of forest distance on spider abundance of *Trochosa ruricoloides* (Lycosidae) (●, solid line) and *Thorelliola ensifera* (Salticidae) (○, dashed line) (Lycosidae: $N = 12$, $F = 4.762$, $P = 0.054$, adjusted $R^2 = 0.255$; Salticidae: $N = 12$, $F = 14.070$, $P = 0.004$, adjusted $R^2 = 0.543$) (* = square root transformed).

Discussion

We report the first comprehensive study of the effects of local management and landscape context on abundance, richness and composition of spider communities in cacao agroforests.

Vertical stratification

We sampled three habitat strata: litter layer, herbaceous layer and cacao tree canopies. As expected, we found the strata to be distinct in the composition of their spider communities. Vertical distribution patterns of spiders have been reported from forests, monoculture crop plants and even within litter layer (Enders, 1974; Simon, 1993; Sørensen, 2003; Wagner et al., 2003; Pekár, 2005; Larrivée & Buddle, 2009). The cacao tree canopy layer was characterized by high abundances of Salticidae and Clubionidae, which are common families of higher tropical forest strata (Russel-Smith & Stork, 1995; Sørensen, 2004) and belong to the spider guild of aerial running hunters (Höfer & Brescovit, 2001). Salticidae forage during the day and Clubionidae during the night, so competition between the members of the two families is presumably low. The spiders of the herbaceous layer were dominated by Tetragnathidae, which use a web for prey capture and constructed webs mainly on herbaceous plants and grasses, although this family also occurred within the higher canopy strata. Ground-dwelling hunters such as the lycosids *Trochosa ruricoloides* and *Venonia* sp.1, and *Oedignatha spadix* (Corinnidae) compose the specific spider assemblage of cacao agroforest leaf litter. Spider assemblages of leaf litter and canopy layer were less variable than those of the herbaceous layer (Fig. 3.2), presumably due to the disturbance of the latter by the farmers' weed management.

Plot-level management: weeds, litter and shade trees

Spider communities responded to local management and landscape-level change in a stratum- and species-specific way. In general not all species in an assemblage are equally influenced by changes in vegetation structure (Steffan-Dewenter & Tscharntke, 2000) and responses of spider species to habitat heterogeneity depend on their ecological requirements.

Leaf litter density was negatively associated with spider abundance, and the reduced spider density was associated with a decline in species richness. Ecosystem services such as decomposition can be expected to change with land use (Didham et al., 1996) and high leaf litter densities within cacao agroforests appeared at our sites to be an indication for disturbed decomposition processes due to intensified use of herbicides, fungicides and insecticides. These pesticides can cause a great reduction and even extinction of important litter decomposers such as spring tails (Collembola) (Frampton, 1999), which are an important prey resource for spiders (Lawrence & Wise, 2000). Although during this study no herbicides and pesticides were applied, in the run-up to this investigation cacao plantations were treated regularly by smallholders. This interpretation is supported by the stronger presence of *Oedignatha spadix* (Corinnidae) within cacao study sites with high leaf litter density (Fig. 3.4). The close related *Oedignatha scrobiculata* is described as species which is only found in severely disturbed habitats (Deeleman-Reinhold, 2001). Both species could be detected in a mixed population on the Lesser Sunda Island, a reference for similar habitat requirements and by which *Oedignatha spadix* could act as indicator species for highly disturbed habitats.

Altieri and Nicholls (2007) emphasize the importance of a rich floral undergrowth within agroforestry systems, because it increases abundance and efficiency of predators and parasitoids and thereby, reduces insect pest populations. In our study, weed cover had an impact on spider abundance within litter, weed and canopy layer. Structural complexity within agricultural habitats is known to be an important influencing factor on spider population dynamics (Rypstra et al., 1999, Langellotto & Denno, 2004). This effect may be due to enhanced prey density (Halaj & Wise, 2002), more structure for web attachment (McNett & Rypstra, 2000), more favourable microclimatic conditions and an additional refuge from intraguild predation (Gunnarsson, 1990). The weed layer impacts spider abundance in cacao agroforestry systems beyond the herb strata and the enhancement of spider abundance through higher weed cover demonstrate the utility of multi-strata management for maintaining spider diversity and associated predation (Del Amo & Ramos, 1993; De Clerck & Negeros-Castilli, 2000).

Korinus et al. (2007) identified shade trees as substantial contributors to habitat heterogeneity and complexity within cacao agroecosystems, which enhance considerably spider diversity. However our results revealed no relation between a more closed shade canopy and spider abundance or species richness. Belshaw and Bolton (1993) and Estrada and Fernandez (1999) compared leaf litter ant species richness along transects from primary forest, over cacao agroforestry systems to pastures in Ghana and Colombia, respectively. They found no differences in ant species richness along this land use gradient and reasoned that the forest conversion into cacao agroforests in Ghana had only a marginal effect on species richness of the leaf litter ant fauna (Belshaw & Bolton, 1993).

Distance to forest

A higher species richness of traditional shaded agroforests close to natural forest has been described for forest birds (Estrada et al., 1997; Anand et al., 2008; Clough et al., 2009), bats (Estrada et al., 1993), pollinators (Klein et al., 2002), parasitic Hymenoptera (Sahari, 2004) and other invertebrates (Bos et al., 2007). For spiders, we found no effect of forest edge proximity on species richness, however species level densities of *Trochosa ruricoloides* (Lycosidae), a litter dwelling spider, and *Thorelliola ensifera* (Salticidae), which inhabits cacao tree canopies, were enhanced with distance to the forest. Both species are known to have a widespread distribution within the tropical landscape of South East Asia and seems to prefer habitats with a more open canopy (Koh, 1989). Hence with distance to forest there may be a shift of species dominance in favour of generalists with higher sun tolerance.

Summary

Naturally shaded cacao agroforestry systems provide a complex, multi-stratum habitat. Spiders are abundant and diverse in these systems and can be economically important predators, but surprisingly little is known on the determinants of spider communities in agroforests. Here, we use data from twelve differently managed cacao agroforestry systems in Indonesia to investigate the abundance, diversity and composition of spider communities at three spatial scales: (i) stratum, i.e. litter, herb and cacao canopy layer, (ii) plot-level shade, litter and weed management and (iii) landscape context, i.e. distance to naturalt forest. Canopy and litter communities were dominated by hunting spiders and the herb communities by web-building spiders. In general, species overlap between strata was low and herb layer communities exhibited highest variability in community composition. Spider communities of all strata were positively affected by weed cover, a stratum-overlapping management influence. High leaf litter density within cacao agroforestry systems was accompanied by a decrease in spider abundance, which appeared to be due to pesticide treatments reducing litter decomposition and populations of potential prey. On a community level, we found no effect of forest edge proximity on spider abundance or species richness, but species-specific responses showed that with distance to forest there appeared to be a shift of species dominance in favour of generalists. Our results showed an impact of all three spatial scales, from the microhabitat and local plot management to the landscape context, and suggest a focus beyond shade management is required to understand determinants of spider community in cacao agroforestry systems.

Appendix

Appendix 3.1 Minimal model for the impact of managment practises and landscape context on spider abundance within canopy, herb and litter layer. Table shows results after stepwise backward selection.

Variable	Coefficient	Std. Error	d.f.	t-value	p-value
Intercept	71.158	15.097	20	4.713	< 0.001
Weed layer	-79.831	17.483	20	-4.566	< 0.001
Canopy layer	-11.824	17.483	20	-0.676	0.5066
Litter density	-0.376	0.175	8	-2.153	0.0634
Weed cover	0.219	0.083	8	2.646	0.0295
Forest distance	0.247	0.174	8	1.423	0.1925
Weed layer x Litter density	0.484	0.234	20	2.073	0.0513
Canopy layer x Litter density	-0.024	0.234	20	-0.104	0.9181

Appendix 3.2 Minimal model for the impact of managment practises and landscape context on spider species richness within canopy, herb and litter layer. Table shows results after stepwise backward selection.

Variable	Coefficient	Std. Error	d.f.	t-value	p-value
Intercept	18.154	3.628	22	5.004	< 0.001
Weed layer	-8.917	1.569	22	-5.683	< 0.001
Canopy layer	6.750	1.569	22	4.302	< 0.001
Litter density	-0.063	0.036	9	-1.750	0.114
Weed cover	0.049	0.028	9	1.747	0.115

Chapter 4

Species turnover gradients within spider communities of cacao agroforestry systems in time and space

Introduction

The understanding of processes which drive faunal composition variability in space and time has important implications for the elaboration of conservation priorities and management strategies in biodiversity conservation (Rodrigues et al., 2000; Condit et al., 2002; White et al., 2006). The change of species compositions between communities on spatial scale can be accounted for biological mechanism as environmental heterogeneity (Gilbert & Lechowics, 2004; Entling et al., 2007), niche-based community processes (Nekola & White, 1999), species-sorting (Cottenie, 2005), dispersal limitations (Seidler & Plotkin, 2006; Jiménez-Valverde et al., 2010) and neutral theory (Hubbell, 2001). Shurin (2007) outlines two potential factors for changes in community compositions over time: environmental heterogeneity (abiotic model) and the linkage between diversity and species' colonisation and extinction rates (biotic model). Within biodiversity studies, the classic approach to determine habitat quality is a comparison of species richness along environmental gradients but without considering the temporal change in community compositions. However, Basset (1997) emphasised that due to a steady inflow of transient species, new species accumulate also temporally to insect communities, wherefore temporal turnover dynamics of community compositions are as ecologically significant as spatial turnover dynamics (Preston, 1960; Adler & Lauenroth, 2003; Adler et al., 2005; Novotny & Weiblen, 2005; White et al., 2006). The contribution and drivers of spatial and temporal species turnover are largely unknown and despite a growing interest in the drivers and ecological functions of biodiversity, studies addressing these issues are few. Here, we analyse spatial and temporal species turnover patterns in tropical spider communities of tropical agroforests. These belong to the most complex and biodiverse agroecosystems (Bhagwat et al., 2008) and are well suited as model systems, because management differences between individual agroforests result in easily quantified, systematic differences in habitat complexity (Greenberg et al., 2008). We established study plots in 12 cacao agroforestry systems with contrasting shade tree and weed layer management. Structural components such as shade tree and weed layer contribute considerably to habitat heterogeneity and complexity, a determining factor for spider diversity in cacao agroecosystems (Korinus et al., 2007). Additionally, the plots were chosen along a gradient of distance to natural forest (the Lore Lindu National Park and Man-and-Biosphere reserve). Distance of study sites to natural forest was included in our study because species turnover rates (temporal and spatial) may depend on the influx of species from nearby sources (Floren & Deelemann-Reinhold, 2005; Tylianakis et al., 2005). We compared two components of the cacao spider community: litter and cacao tree canopy dwelling spiders. Responses of arthropod communities to habitat heterogeneity suggest that compositional changes of canopy and litter dwelling spider communities may be differently affected by habitat and landscape variables due to their differences in environmental requirements and dispersal capability via ballooning (Bishop & Riechert, 1990; Greenstone, 1990). Lastly, we were interested in which the degree of species accumulation differed over time and sampling sites and assumed, as has been suggested in Preston (1960) and verified in Adler & Lauenroth (2003), a faster species accumulation in time than space due to this study design implemented within one habitat type on a regional scale.

Material and Method

Study area

The study was conducted within differently managed cacao agroforestry sites along the margin of Lore Lindu National Park (1°30′ S, 120°10′ E) in Central Sulawesi, Indonesia (Fig. 1). In each agroforestry site we established a 40 x 40 m plot and sites were characterized by different levels of vegetation structure (e.g. shade tree density) and weeding frequency, a management practice. Half of the plots were weeded every second month (high weeding frequency), the other half every six months (low weeding frequency).

Sampling design

Litter dwelling spider communities of 22 cacao agroforestry sites were sampled using four roofed pitfall traps (diameter = 20 cm) per plot. Canopy-dwelling spiders were studied within a subset of 12 plots and caught on five trees per plot, each tree being fitted with one branch eclector (after Simon, 1995) (Fig. 3.1). Traps were emptied every month between May 2007 and March (litter samples) or April 2008 (canopy samples), resulting in 10 and 11 distinct samples per plot for the litter spiders and canopy spiders, respectively. We used a 1:1 mixture of ethylene glycol and water as preservation liquid in both trap types. All adult spiders were identified to species or morphospecies, while juveniles were excluded from the statistical analyses. To determine differences in spatial and temporal species turnover of canopy and litter communities, we analysed the subset of 12 cacao agroforestry sites, in which both trap types were installed.

Environmental parameters

The data of geographical distance and distance to forest are based on satellite images of the study area displayed and managed with ArcGIS 9.2 (ESRI). Geographic distances between sampling sites ranged from 474 m to 24.6 km. The distances between sampling sites and natural forest ranged from 0 to 1150 km. Shade trees inside the plot or with the crown overlapping the 40 x 40 m plot were counted (shade tree density) and identified to species level. Shade tree diversity and weed diversity are a measure of species richness. Weed cover was visually assessed at five random points in each plot and average values calculated. Euclidean distance matrices of environmental parameters and geographical distances were correlated among each other. However linear regressions revealed a significant positive relation between distance to forest and shade tree diversity ($R^2 = 0.36$, $P = 0.04$).

Data analysis

Temporal (temporal-β_{SIM}) and spatial (spatial-β_{SIM}) species turnover for canopy and litter spider community were estimated using Simpson-based multiple-site dissimilarity measure (β_{SIM}) (Baselga, 2010):

$$\beta_{SIM} = \frac{\left[\sum_{i<j} \min\left(b_{ij}, b_{ji}\right)\right]}{\left[\sum_{i} S_i - S_T\right] + \left[\sum_{i<j} \min\left(b_{ij}, b_{ji}\right)\right]}$$

where S_i is the total number of species in site *i*, S_T is the total number of species in all sites considered together and b_{ij}, b_{ji} are the number of species exclusive to site *i* and *j*, respectively compared by pairs (spatial-β_{SIM}). The temporal-β_{SIM} was calculated with S_i as the total number of species at time *i*, S_T is the total number of species over the total sampling period and b_{ij}, b_{ji} are the number of species exclusive to at time *i* and *j*, respectively compared by pairs. This multiple-site (rsp. multiple-time) measure calculates the pure spatial turnover while excluding patterns of species loss (nestedness) in the beta-diversity measure (Baselga 2010). Low values of β_{SIM} indicate low species turnover (low dissimilarity), high values indicate high species turnover (high dissimilarity). Analyses were conducted in R version 2.8.1 (R Development Core Team, 2008) using the R code for β_{SIM} provided in Baselga (2010). We tested for correlations between spatial species turnover and environmental parameters and geographic distance using Mantel tests with two dependent matrices (spatial-β_{SIM} between canopy samples, spatial-β_{SIM} between litter samples). The impact of environmental conditions on temporal- β_{SIM} and species richness was analysed using generalised linear models (GLM). For each spider composition the full model, the intercept-only model and models with all valid combinations of the explanatory variables including first-order interactions were generated. We identified the relative support for each model using Akaike´s Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). While the best-fitting model in the set has the minimum AICc score, and differences in the AICc scores between each model and the best model ($\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{\mathrm{min}}$) as well as the Akaike weights (w_i) for each model were calculated. All models with ΔAICc less than ten entered the best-model subset for model-averaged estimates that were obtained by computing means (= AMC: averaged-model coefficient) and standard errors of the estimates weighted by the model weights. The relative importance of each parameter (RPI) was computed and is the sum of the model weights of the models in which the parameter was included. Mantel tests were computed with the *vegan* package (Oksanen et al., 2005) and model-avering with *MuMIn* package (Bartoń, 2009) for R. Non-parametric estimators of species richness (Jackknife1, Jackknife 2, Chao and Bootstrap) were used for calculating the inventory completeness of canopy and litter samples over the total sampling time. The completeness is defined as the percentage fraction of observed species richness to estimated species richness.

Results

Spatial species turnover

The spatial species turnover along the study area was higher within canopy spider communities ($\beta_{spatial} = 0.850$) than litter spider communities ($\beta_{spatial} = 0.776$).

Partial Mantel tests of spatial species turnover and environmental parameters (Table 4.1) indicated a correlation ($r = 0.30$, $P = 0.05$) between higher weed diversity and an increase in dissimilarity of canopy spider communities (Fig. 4.1). The correlation coefficient was also positive but not significant for litter spider communities ($r = 0.29$, $P = 0.64$). We found no significant correlations between higher species turnover rate and geographical distance, shade tree characteristics or distance to forest.

Table 4.1 Partial mantel test between each spider community and geographical distance and environmental matrices. *P*-values were calculated permuting 999 times the response variable, * < 0.05.

	Pearson *r*					
		Environmental parameters				
	Geographical distance	forest distance	shade tree density	shade tree diversity	herb density	herb diversity
canopy	-0.17	-0.04	0.16	-0.01	0.08	0.30*
litter	0.14	-0.16	-0.15	-0.15	-0.08	0.29

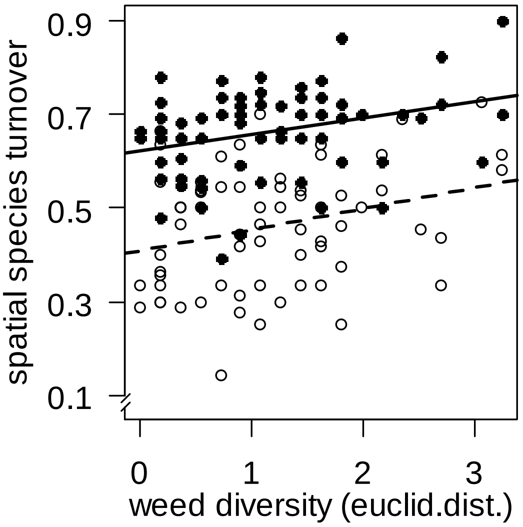


Figure 4.1 Euclidean distance of weed diversity between study sites in relation to spatial species turnover within litter communities (○, dashed line) and canopy communities (●, solid line).

Temporal species turnover

The temporal turnover rates within canopy dwelling spider communities was significant higher (t = 7.5972, *d.f.* = 11, P < 0.001) than in litter spider communities (Fig. 4.2). The multi-model comparison revealed that temporal turnover rates of both communities were differently affected. Within cacao tree canopies, shade tree diversity was the most important influencing parameter (Table 4.2) and had a significant positive impact on temporal heterogeneity of communities (Fig. 4.3). A more diverse weed layer leads to more similar species patterns over time within litter spider compositions.

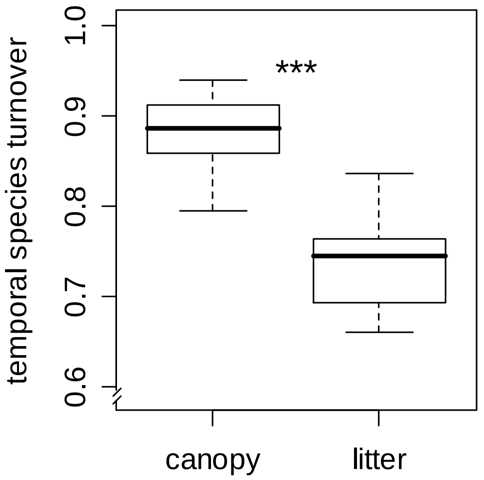


Figure 4.2 Mean temporal species turnover within canopy and litter spider communities (N = 12, *t* = 7.5, *d.f.* = 11, $P < 0.001$).

Table 4.2 Impact of environmental parameters on temporal species turnover within canopy and litter communities: model-averaged coefficients (AMC) and relative importance of the variable (RPI, ranges from 1: variable present in any likely models to 0: not present in any likely model).

	Environmental parameters				
	forest distance	shade tree density	shade tree diversity	herb density	herb diversity
canopy					
RPI	0.12	0.10	0.94	0.54	0.12
AMC (± SE)	-0.0001±0.0003	–	0.0056±0.0019	-0.0007±0.0004	–
litter					
RPI	0.06	0.56	0.07	0.13	0.84
AMC (± SE)	–	-0.0004±0.0004	–	–	-0.0049±0.0026

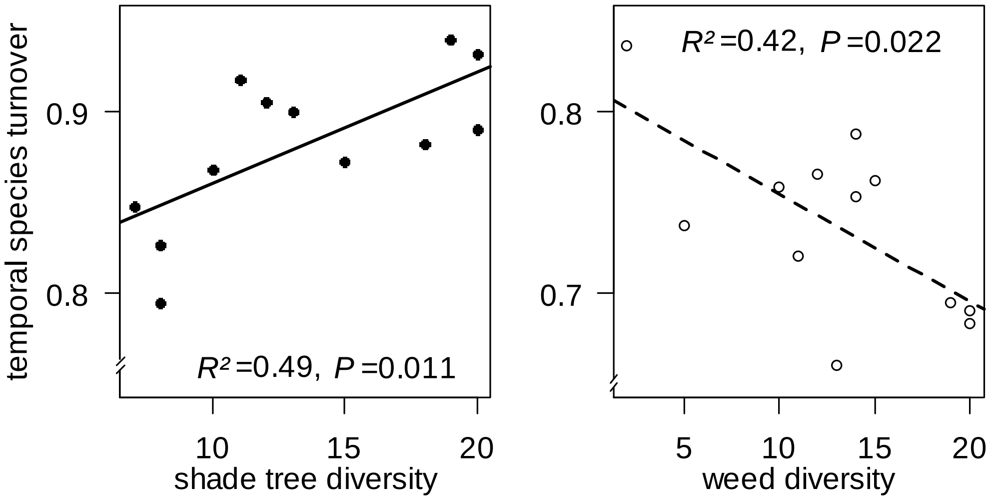


Figure 4.3 Impact of shade tree diversity and weed diversity on temporal species turnover within canopy communities (left) and litter communities (right).

Species richness

The multi-model averaging results revealed high standard errors of the averaged-model coefficients (AMC) for most environmental variables, which is also reflected in negligible RPI (< 0.5). Thus no consistent impact of environmental parameters on species richness neither within canopy communities nor litter communities could be detected.

Spatio-temporal species turnover

We used species accumulation curves based on the samples aggregated per plot or per month to compare the species accumulation over time and between plots (Fig. 4.4). The slope of the species accumulation curve over time was slightly steeper than over space within litter layer spider communities.

The first-order Jackknife (Jack1) estimator of each plot over total sampling time indicated an average species completeness of 60% per plot for canopy layer (Jack2 = 47%, Chao = 36%, Bootstrap = 79%) and 65% for litter layer (Jack2 = 52%, Chao = 45%, Bootstrap = 81%).

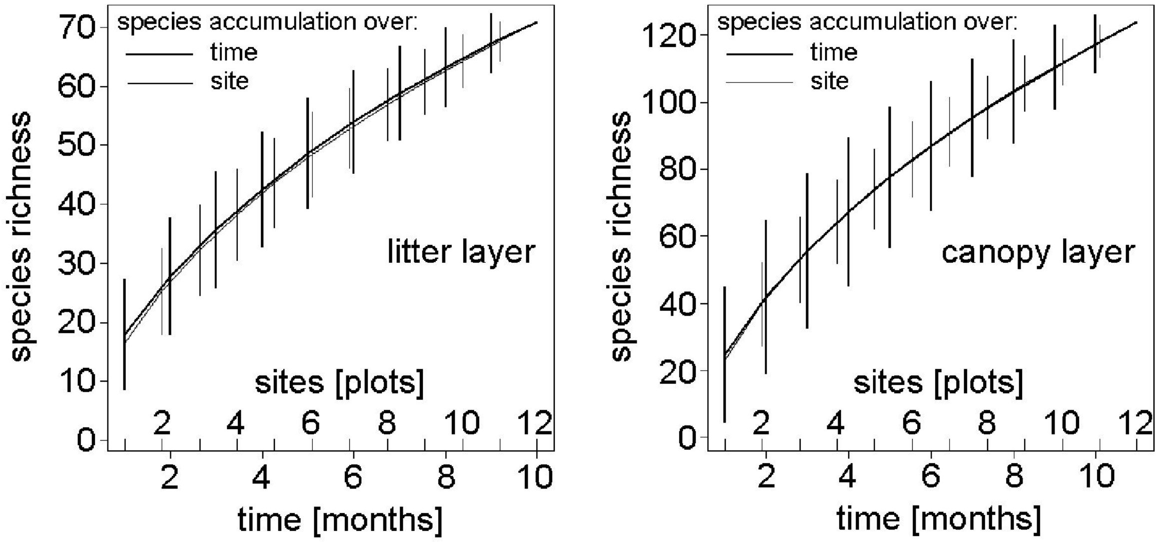


Figure 4.4 Species accumulation curves of litter (left) and canopy layer (right) communities over time (bold line) and sites. Errors bars are 1 SD.

Discussion

This study demonstrates how management practices such as shade tree cultivation and weed management within cacao agroforestry systems can influence compositional change of spider communities through time and space.

Spatial turnover

Our results support findings that spider species turnover is related to spatial environmental change (Beals, 2006; Entling, 2007). Dissimilarities in spider communities between cacao agroforestry sites were related to weed diversity but not to forest distance, which we had expected *a priori*. Dissimilar weed species composition between sites led to dissimilar spider communities in the cacao tree canopy. Weed diversity may have an indirect impact on spider community composition via prey abundance and diversity or a direct impact by supporting species which use weed and canopy layer for prey capture. Although composition changes in spider communities are thought to be primarily governed by habitat architecture rather than by plant diversity (Marc et al., 1999), Beals (2006) found a high impact of plant species diversity on variation in spider communities.

Forest distance has been predicted to impact species turnover between sampling sites, because forests are a major source of species diversity (Floren & Deelemann-Reinhold, 2005; Tylianakis et al., 2005). The absence of an impact of distance to forest on spatial species turnover could be explained by the relatively short distance of the study sites to natural forest. In addition, it is also possible that source effects are masked by the landscape wide dominance of perennial habitat in the form of cacao plantations. In such a setting landscape effects may be restricted to spider species preferring natural forest habitat. Hence for the spider community as a whole, local variables seems to be more important predictors for spatial turnover than distance to natural forest.

According to the microspatial heterogeneity hypothesis (MacArthur & MacArthur, 1961), the higher species turnover within cacao tree canopy communities could be a result of a structurally more complex microhabitat, that is provided to a greater extent by cacao tree canopies than by leaf litter. This leads to higher species diversity in the canopy, and possibly also to the increased species turnover rates on regional scale.

Temporal turnover

Shade tree diversity considerably increased temporal turnover within canopy inhabiting spider communities. Shade tree diversity may influence temporal turnover of spider communities in several ways, e.g. by providing protection from extreme solar radiation and stabilising moisture conditions (sheltering), increasing prey density and diversity, increasing habitat complexity and architectural diversity, providing a greater diversity of microhabitats. Within Jamaican shaded coffee plantations, Johnson (2000) found that shade tree canopies harbour many more individuals than coffee trees. Hence exchange of spider communities between shade and cacao tree canopies may mean that, temporary guests from shade trees increase temporal species turnover within cacao tree spider communities.

While the number of species shared by sites decreased with larger differences in weed diversity, plots sampled through time had lower species turnover when weed diversity was enhanced. This contrasting relationship between regional long-term interactions and local short-term processes are known from other studies (Leibold et al., 1997; Adler & Levine, 2007). In our study the variability in temporal species turnover within litter communities can be explained by two interacting parameters: weed diversity as structural habitat component and weeding that constitute a disturbance of habitat structure which can change temporal dynamics of spider communities through recurrent species reshuffling. Within the 12 cacao agroforestry sites we found a tendency of a lower weed diversity and higher temporal species turnover within plots that were weeded every two months (high weeding frequency) than every six months (low weeding frequency). However as the 12 studied cacao agroforestry sites constitute only a subset of a larger set of 22 plots in which biodiversity and agroecological research was conducted, the number of plots with low (n = 4) and high (n = 8) weeding frequency was unbalanced and hence we did not include weeding frequency in previous calculations. However, when taking all 22 cacao study sites into account, the ratio of low and high weeding frequency was balanced and calculations revealed a significant impact of weeding frequency on weed diversity and on temporal species turnover (Appendix 4.1a, 4.1b). Within the larger set of 22 cacao study sites, we found a significant increase in temporal species turnover with a high weeding frequency, which in turn induced a significant decrease in weed diversity. Hence, temporal species turnover of litter spider communities is influenced by weed management practices including weed diversity and weeding frequency.

The apparently minor contribution of forest proximity to temporal species turnover may be due to a correlation between shade tree diversity and distance to forest. Upon removing shade tree diversity from the models, the relative parameter importance (RPI) of distance to forest increased considerably (Appendix 4.2), implying a decrease in temporal species turnover with distance to forest, but only within canopy spider communities.

White et al. (2006) refer to two processes for species accumulation in time: increased sampling from a static species pool and non-random changes in species composition at a site through time. Hence differences in temporal species turnover between litter and canopy communities could be explained by differences in community composition and richness as the canopy layer included more species than litter layer. Further biological processes such as species-specific phenology, intra- and interspecific competition, extinction and colonisation rates cause non-random changes in temporal species turnover.

While temporal species turnover was either affected by weed diversity (litter spiders) or shade tree diversity (canopy spiders), these variables did not affect total species richness. The commonly used approach to use exclusively local species richness (or species diversity) as indicator for habitat quality might result in an underestimate environmental effects. In White et al. (2006) analyses of datasets of species-time relationships often revealed a decrease in temporal turnover with increasing local richness and *vice versa*, which was explained by environmental factors which could influence species richness and turnover in opposite direction. Hence species richness cannot be reliably compared across sites without information about both the temporal and spatial scale of sampling (Rosenzweig, 1995; Adler & Lauenroth, 2003; White et al., 2006).

Spatial versus temporal turnover

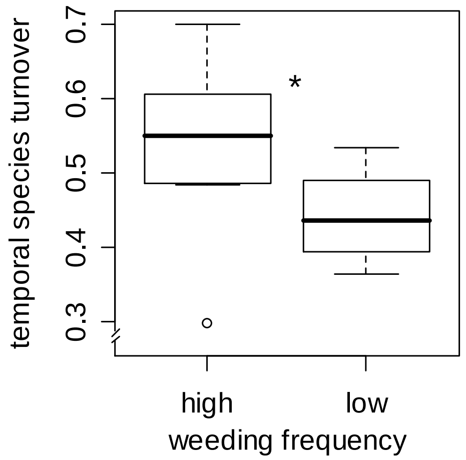
We expected a higher species accumulation within spider communities through time compared to space because of the sampling that was implemented within one habitat type and on regional scale. We found the slopes of species accumulation curves computed over space and time to differ only marginally, which means that the spatial species turnover between sites separated on average by 10 km was similar to the temporal species turnover within a site between month in less than a year. In other words, local spider richness is temporally surprisingly dynamic. While it may be expected that species accumulation in time will slows when the sample size increases (Adler & Lauenroth, 2003), the scale considered within this study is ecologically relevant, given that numerous ecological interactions take place at the tree and plot scales.

Summary

To gain insight into dynamic processes determining spatio-temporal patterns in community composition, we studied spatial and temporal species turnover of litter and canopy dwelling spiders in agroforests. We sampled spiders for almost a year in 12 cacao agroforestry systems where contrasting shade and weed management resulted in contrasting habitat complexity. In addition plots were situated at different distances from natural forest. We investigated the relative contribution of species turnover between sites (spatial beta diversity) and between months (temporal beta diversity) and the effect of habitat and landscape variables on these turnover values. We found the number of species occurring locally to depend to a similar degree on spatial and temporal patterns, although turnover differs between canopy and litter dwelling spiders. Both temporal and spatial turnover was affected mainly by habitat-scale variables, with no significant effect of forest distance. The largest effect was the positive relation of temporal species turnover to shade tree diversity. Our results suggest not only that snap-shot or aggregated species richness measures may not adequately represent diversity patterns through time, but that ignoring turnover may result in bias when evaluating the effect. Hence more attention should be given to the effect of temporal turnover when studying community patterns of functionally important groups such as spiders, which are major predators in agroecosystems.

Appendix

Appendix 4.1a Impact of weeding frequency on weed diversity within the 22 study sites (*t* = -3.115, *df* = 18.273, *P* = 0.006).



Appendix 4.1b Impact of weeding frequency on temporal species turnover of litter spider communities within the 22 study sites (*t* = -2.576, *df* = 14.952, *P* = 0.021).

Appendix 4.2 Impact of environmental parameters on temporal species turnover within canopy and litter communities without shade tree diversity: model-averaged coefficients (AMC) and relative importance of the variable (RPI, ranges from 1: variable present in any likely models to 0: not present in any likely model).

	Environmental parameters			
	forest distance	shade tree density	herb density	herb diversity
canopy				
RPI	0.65	0.10	0.54	0.12
AMC (± SE)	-0.0013±0.0011	–	–	–
litter				
RPI	0.07	0.56	0.13	0.85
AMC (± SE)	–	–	–	-0.0049±0.0026

Chapter 5

Summary & General Conclusions

Summary

Primary rainforests and the associated biodiversity are disappearing from tropical landscapes at accelerating rates due to agricultural expansion. Cacao agroforestry systems are commonly established at the margin of natural forests in Indonesia and constitute a habitat with a considerable tree cover, which may benefit biodiversity conservation and ecosystem services in addition to providing income for the local population. However, current management is dominated by severe habitat simplification due to extensive weeding, removal natural forest trees, planting one or few shade-tree species or even a conversion into intensive full-sun monocultures.

In two valleys at the margin of the Lore Lindu National Park in Central Sulawesi, Indonesia, we investigated the factors shaping spider communities in cacao agroforests. This represents the first comprehensive study of the effects of local management and landscape context on web density as well as abundance, richness and composition of spider communities in an agroforestry system. We collected spider data in a total of 42 differently managed cacao agroforestry sites. First, spider web densities of five web-building spider guilds on 10 cacao trees per plot were analysed with respect to tree and plot management (e.g. pruning, shade cover and weeding), landscape features (plot elevation, forest distance) and the presence of a numerically dominant *Philidris* ant species. Secondly, based on a continuous one year multi-strata sampling of spiders within a subset of 12 agroforestry sites, we investigated drivers of abundance and species richness of web-building and hunting spiders of litter, herb and canopy layer at the plot and landscape scale. Thirdly, we analysed how spatial and temporal changes in species richness are affected by different habitat structures, such as shade tree cover and weed diversity, or by landscape context such as distance to forest.

On 420 cacao trees we found 5147 spider webs. Densities of webs of different types were differentially affected by habitat variables, while most frequently recorded webs (≈ 42 %) were of the line web type, a simple construction of a few filaments. The orb web weaving spider guild, including Araneidae, Tetragnathidae and Uloboridae, was also abundant on cacao trees (≈ 30 %). At tree scale, web density was positively related to canopy openness and at plot scale, a higher number of shade trees was related to a higher web density. At the landscape scale, the elevation determined the distribution patterns of web-building spiders. The presence of *Philidris* ants was positively associated with density of orb webs, while no pattern was found for other web types. This positive relation of ants and spiders may have

resulted from an increased prey density in and around ant nests where trophobionts produce honeydew, which attracts prey insects. Our results suggest spider web density could be increased by pruning of cacao trees while keeping shade trees density in cacao plots.

Analysis of the one-year sampling within 12 agroforestry sites showed that canopy and litter communities were dominated by hunting spiders and the herb communities by web-building spiders. In general, species overlap between strata was low and herb layer communities exhibited highest variability in community composition. Spider communities of all habitat strata were positively affected by weed cover, while an increase in leaf litter density was accompanied by a decrease in spider abundance, which appeared to be due to previous pesticide treatments reducing litter decomposition and populations of potential prey. On a community level, we found no effect of forest edge proximity on spider abundance or species richness, but species-specific responses showed that with distance to forest there seems to be a shift of species dominance in favour of generalists.

The analysis of temporal and spatial turnover revealed that the number of species occurring locally depends to a similar degree on spatial and temporal patterns, although interannual turnover differs between canopy and litter dwelling spiders. Both temporal and spatial turnover were affected mainly by habitat-scale variables, with no significant effect of forest distance. The largest effect was the positive relation of temporal species turnover to shade tree diversity. These results showed not only that snap-shot or aggregated species richness measures may not adequately represent diversity patterns through time, but that ignoring turnover may result in bias when evaluating the effect of management or landscape context.

General conclusions

The area under cacao cultivation by smallholders on the island of Sulawesi is still growing, accompanied by forest encroachment (e.g. on Sulawesi, in the 1980s and 1990s about 50 % of the cacao area was planted in formerly forested areas, Rice & Greenberg, 2000) and conversion of shaded cacao agroforests into intensive full-sun monoculture. The development and implementation of agricultural management balancing human needs, sustainable land cultivation and biodiversity conservation is a major challenge (Landis et al., 2000; Watt et al., 2002; Steffan-Dewenter et al., 2007; Perfecto & Vandermeer, 2008) due to the ecological and socio-economic complexity of smallholder agroforestry systems.

The study presented in chapter 2 disentangled the relative contribution of habitat variables at tree-, plot- and landscape-scale in determining spider-web density and web-type composition in cacao agroforestry. While landscape context had little effect, spider web density can be enhanced through appropriate management at the tree and plot scale. The positive relation between density of several web types and local cacao canopy openness suggests foliage density control through pruning and thinning could enhance spider web density. In addition, the positive effect of plot-scale shade tree density on spider web density acts as a warning against the removal of shade trees, which is nowadays a widespread practice in the study region.

Our results on drivers of spider abundance and species richness of vertically stratified spider communities in cacao agroforests showed a high impact of habitat structural component not directly related to shade trees, namely weeds and litter. This suggests new avenues for managing agroforest and plantation landscapes for spider communities, at which the conservation of a diverse spider fauna can be accomplished by reducing chemical treatements. But more data on spider taxonomy and the specific functional role of spiders within agroforestry systems are needed, especially with respect to their ability to act as top-down predators for biological pest control, for this knowledge to be applied in sustainable agroforest management and biodiversity conservation.

Beta-diversity is as important as alpha-diversity for conservation, because species turnover influences diversity at large scales (Condit et al., 2002). We found temporal and spatial turnover of similar magnitude, but differing between litter and canopy spider communities. Both were affected by the same variable (weed diversity) across space, but by different variables across time. The positive impact of shade tree diversity on temporal turnover suggests ongoing management intensification of cacao agroforestry systems, which is often associated with removal of shade trees or mono-specific shade (Scales & Marsden, 2008) may affect arthropod species communities in more complex ways than currently recognised. Our results suggest not only that measures of diversity that do not recognise turnover, in particular temporal turnover, may not be adequate. We suggest more attention should be given to the effect of spatial and temporal turnover on ecological effects of spider communities, such as predation. The knowledge about spatial and in particular temporal heterogeneity of community compositions and how temporal composition change is affected by environment is fundamental, as this has wide implications, for example as to the number of different spider species interacting with prey species or other ecosystem components. More studies including temporal aspects of species communities are required in conjunctions to biodiversity conservation but also to biological control within agroforestry systems.

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References

Achard, F., Eva H.D., Stibig, H.-J., Mayaux, P., Callego, J., Richards, T. & Malingreau, J.-P. (2002) Determination of deforestation rates of the world's humid tropical forests. Science, 297, 999−1002.

Adler, P.B. & Lauenroth, W.K. (2003) The power of time: spatiotemporal scaling of species diversity. Ecology Letters, 6, 749−756.

Adler, P.B., White, E.P., Lauenroth, W.K., Kaufman, D.M., Rassweiler, A. & Rusak, J.A. (2005) Evidence for a general species-time-area relationship. Ecology, 86, 2032−2039.

Adler, P.B. & Levine, J.M. (2007) Contrasting relationships between precipitation and species richness in space and time. Oikos, 116, 221–232.

Altieri, M.A. & Nicholls, C.I. (2007) Ecologically Based Pest Management in Agroforestry Systems, in: Batish, D.R., Kohli, R.K., Jose, S., Singh, H.P. (Eds.), Ecological Basis of Agroforestry, CRC Press. Boca Raton, FL, pp. 95–108.

Anand, M.O., Krishnaswamy, J. & Das, A., (2008) Proximity to forests drives bird conservation value of coffee plantations: implications for certification. Ecological Applications, 18, 1754–1763.

Armbrecht, I., Perfecto, I. & Vandermeer, J. (2004) Enigmatic biodiversity correlations: Ant diversity responds to diverse resources. Science, 304, 284−286.

Asare, R. (2006) A review on cocoa agroforestry as a means for biodiversity conservation. World cocoa Foundation Partnership Conference, Brussels.

Audley-Charles, M.G. (1983) Reconstruction of eastern Gondwanaland. Nature, 306, 48−50.

Baldissera, R., Ganade, G., Brescovit, A. & Hartz, S. (2008) Landscape mosaic of Araucaria forest and forest monocultures influencing understorey spider assemblages in southern Brazil. Austral Ecology, 33, 45−54.

Balfour, R.A. & Rypstra, A.L. (1998) The influence of habitat structure on spider density in a no-till soybean agroecosystem. Journal of Arachnology, 26, 221–226.

Barrion, A.T. & Litsinger, J.A. (1995) Riceland spiders of South and South East Asia. CAB International, Wallingford, England.

Bartoń, K. (2009) MuMIn: R functions for model selection and model averaging. R package version 0.12.0, <http://r-forge.r-project.org/projects/mumin/>.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19, 134–143.

Basset, Y. (1997) Species-abundance and body size relationships in insect herbivores associated with Papua New Guinea forest trees, with particular reference to insect host-specificity, in: Stork, N.E., Adis, J. & Didham, R.K. (Eds.), Canopy arthropods, Chapman & Hall, London, pp. 237–264.

Bates, D., Maechler, M. & Dai, B. (2008) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-28, <http://lme4.r-forge.r-project.org/>.

Beals, M. L. (2006) Understanding community structure: a data-driven multivariate approach. Oecologia, 150, 484-495.

Beer, J., Muschler, R., Kass, D. & Somarriba, E., (1998) Shade management in coffee and cacao plantations. Agroforestry Systems, 38, 139–164.

Belshaw, R. & Bolton, B., (1993) The effect of forest disturbance on the leaf-litter ant fauna in Ghana. Biodiversity and Conservation, 2, 656–666.

Belsky, J.M. & Siebert, S.F. (2003) Cultivating cacao: Implications of sun-grown cacao on local food security and environmental stability. Agriculture and Human Values, 20, 270−285.

Benjamin, S. & Zschokke, S. (2003) Webs of theridiid spiders: construction, structure and evolution. Biological Journal of the Linnean Society, 78, 293−305.

Bhagwat, S., Willis, K., Birks, H. & Whittaker, R. (2008) Agroforestry: a refuge for tropical biodiversity? Trends in Ecology & Evolution, 23, 261−267.

Biere, J. & Uetz, G. (1981) Web orientation in the spider *Micrathena gracilis* (Araneae: Araneidae). Ecology, 62, 336−344.

Bishop, L. & Riechert, S.E. (1990) Spider colonization of agroecosystems: mode and source. Environmental Entomology, 19, 1738−1745.

Bisseleua, D.H.B., Missoup, A.D. & Vidal, S. (2008) Biodiversity conservation, ecosystem functioning, and economic incentives under cocoa agroforestry intensification. Conservation Biology, 23, 1176−1184.

Blackledge, T. & Zevenbergen, J. (2007) Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*. Animal Behaviour, 73, 855−864.

Bonte, D., Lanckacker, K., Wiersma, E. & Lens, L. (2008) Web building flexibility of an orb-web spider in a heterogeneous agricultural landscape. Ecography, 31, 646−653.

Bos, M.M., Steffan-Dewenter, I., & Tscharntke, T. (2007) Shade tree management affects fruit abortion, insect pests and pathogens of cacao. Agriculture Ecosystems & Environment, 120, 201−205.

Burnham, K. & Anderson, D. (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York.

Chen, K. & Tso, I. (2004) Spider diversity on Orchid Island, Taiwan: a comparison between habitats receiving different degrees of human disturbance. Zoological studies, 43, 598−611.

Clough, Y., Kruess, A., Kleijn, D. & Tscharntke, T. (2005) Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. Journal of Biogeography, 32, 2007−2014.

Clough, Y., Dwi Putra D., Pitopang R. & Tscharntke T. (2009) Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. Biological Conservation, 142, 1032–1041.

Clough et al. (2010) Biodiversity patterns and trophic interactions in human-dominated tropical landscapes in Sulwesi (Indonesia): plants, arthropods and vertebrates, in: Tscharntke, T., Leuschner, C., Veldkamp, E., Faust, H., Guhardja, E., Bidin, A. (Eds.), Tropical rainforests and agroforests under global change – Ecological and Socio-economic valuations. Springer Verlag, Berlin, pp. 15-71.

Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Nuñez V., P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H., Losos, E., & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. Science, 295, 666–669.

Cottenie, K. (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters, 8, 1175-1182.

De Clerck, F. & Negeros-Castilli, P. (2000) Plant species of traditional Mayan homegardens of Mexico as analogs for multistrata agroforests. Agroforestry Systems, 48, 303–317.

Deeleman-Reinhold, C.L. (2001) Forest spiders of South East Asia. Koninklijke Brill NV, Leiden, The Netherlands.

Delabie, J. H., Jahyny, B., Nascimento, I. C., Mariano, C. S., Lacau, S., Campiolo, S., et al., (2007) Contribution of cocoa plantations to the conservation of native ants (Insecta: Hymenoptera: Formicidae) with a special emphasis on the Atlantic Forest fauna of southern Bahia, Brazil. Biodiversity and Conservation, 16, 2359–2384.

Del Amo, R.S. & Ramos, P.J. (1993) Use and management of secondary vegetation in a humid- tropical area. Agroforestry Systems, 21, 27–42.

Didham, R.K., Ghazoul, J., Stork, N.E. & Davis, A.J., (1996) Insects in fragmented forests: a functional approach. Trends in Ecology & Evolution, 11, 255–260.

Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters, 6, 680–687.

Enders, F. (1974) Vertical Stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. Ecology, 55, 317–328.

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R. & Nentwig, W. (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche, Global Ecology and Biogeography, 16, 440–448.

Estrada, A., Coates-Estrada, R. & Meritt, D. Jr. (1993) Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography, 16, 309–318.

Estrada, A., Coates-Estrada, R. & Meritt, D.A. (1997) Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. Biodiversity and Conservation, 6, 19–43.

Estrada, C., Fernandez, F., 1999. Diversity of ants (Hymenoptera: Formicidae) in a successional gradient of a cloud forest (Narino, Colombia). Revista de Biologia Tropical, 47, 189–201.

Fagan, W., Hakim, A., Ariawan, H. & Yuliyantiningsih, S. (1998) Interactions between biological control efforts and insecticide applications in tropical rice agroecosystems: the potential role of intraguild predation. Biological Control, 13, 121−126.

Faria, D., Laps, R.R., Baumgarten, J. & Cetra, M. (2006) Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. Biodiversity and Conservation, 15, 587–612.

Floren, A. & Otto, S. (2002) Beeinflusst die Anwesenheit der Waldameise *Formica polyctena* Foerster die Artenzusammensetzung und Struktur von Spinnengemeinschaften auf Eichen?. Arachnologische Mitteilungen, 24, 1−18.

Floren, A. & Deeleman-Reinhold, C. (2005) Diversity of arboreal spiders in primary and disturbed tropical forests. Journal of Arachnology, 33, 323−333.

Frampton, G. K. (1999). Spatial variation in non-target effects of the insecticides chlorpyrifos, cypermethrin and pirimicarb on Collembola in winter wheat. Pesticide Science, 55, 875–886.

FWI/GFW (2002) The State of the Forest: Indonesia. Bogor, Indonesia: Forest Watch Indonesia, and Washington DC: Global Forest Watch.

Gilbert, B. & Lechowicz, M.J. (2004) Neutrality, niches, and dispersal in a temperate forest understory. PNAS, 101, 7651−7656.

Greenberg, R., Perfecto, I. & Philpott, S.M. (2008) Agroforests as model systems for tropical ecology. Ecology, 89, 913–914.

Greenstone, M.H. (1990) Meteorological determinants of spider ballooning: the roles of thermals v. the vertical windspeed gradient in becoming airborne. Oecologia, 84, 164–168.

Gunnarsson, B. (1990) Vegetation structure and the abundance and size distribution of spruce-living spiders. Journal of Animal Ecology, 59, 743–752.

Halaj, J., Ross, D. & Moldenke, A. (1997) Negative effects of ant foraging on spiders in Douglas-fir canopies. Oecologia, 109, 313−322.

Halaj, J.D. & Wise, D.H. (2002) Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. Ecology, 83, 3141–3151.

Halaj, J., Halpern, C.B. & Yi, H.B. (2008) Responses of litter-dwelling spiders and carabid beetles to varying levels and patterns of green-tree retention. Forest Ecology and Management, 255, 887–900.

Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio, 42, 47–58.

Höfer, H. & Brescovit, A. (2001) Species and guild structure of a Neotropical spider assemblage (Araneae) from Reserva Ducke, Amazonas, Brazil. Andrias, 15, 99−119.

Hore, U. & Uniyal, V. (2008) Diversity and composition of spider assemblages in five vegetation types of the Terai Conservation Area, India. Journal of Arachnology, 36, 251−258.

Hubbell, S.P. (2001) The unified neutral theory of biodiversity and biogography. Princeton University Press.

International Cocoa Organization (ICCO) (2009) Update of the annual forecasts of production and consumption and estimates of production levels to achieve equilibrium in the world cocoa market as of 21 may 2009. <http://www.icco.org/statistics/statistics%20PDFs/EX-139-CRP1-FORECAST-UPDATES.pdf.>

Jiménez-Valverde, A. & Lobo, J. (2007) Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. Ecological Entomology, 32, 113−122.

Jiménez-Valverde, A., Baselga, A., Melic, A. & Txasko, N. (2010) Climate and regional beta-diversity gradients in spiders: dispersal capacity has nothing to say? Insect Conservation and Diversity, 3, 51−60.

Jocqué, R. & Dippenaar-Schoeman, A. (2007) Spider families of the world. , 2nd ed. Royal Musuem for Central Africa, Tervuren.

Johnson, M. D. (2000) Effects of shade tree species and crop structure on the arthropod and bird communities in a Jamaican coffee plantations. Biotropica, 32, 133–145.

Kajak, A., Andrzejewska, L. & Wojcik, Z. (1968) The role of spiders in the decrease of damages caused by Acridoidea on meadows: experimental investigations. Ekologia Polska (A), 16, 755−764.

Kessler, M., Kessler, P.J.A., Gradstein, S.R., Bach, K., Schmull, M. & Pitopang, R. (2005) Tree diversity in primary forest and different land use systems in Central Sulawesi, Indonesia. Biodiversity and Conservation, 14, 547−560.

Klein, A., Steffan-Dewenter, I. & Tscharntke, T. (2002) Predator-prey ratios on cacao along a land-use gradient in Indonesia. Biodiversity and Conservation, 11, 683−693.

Koh, J.K.H. (1989) A Guide to Common Singapore Spiders. Singapore Science Centre, Singapore.

Korinus, L (2007) Diversity and Seasonality of Tropical Spiders in Cacao Agroforestry Systems of North Sulawesi, Indonesia., Diploma thesis, University of Alberta.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology, 45, 175−201.

Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia, 139, 1–10.

Larrivée, M. & Buddle, C.M. (2009) Diversity of canopy and understorey spiders in north-temperate hardwood forests. Agricultural and Forest Entomology, 11, 225–237.

Lawrence, K.L. & Wise, D.H. (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44, 33–39.

Leibold, M.A., Chase, J.M., Shurin, J.B. & Downing, A.L. (1997) Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics, 28, 467–494.

Maeyama, T. & Matsumoto, T. (2000) Colonial system of *Philidris* ants (Formicidae, Dolichoderinae) occupying epiphytic myrmecophytes in a tropical mangrove forest. Tropical Ecology, 41, 209−216

Majer, J.D., Delabie, J.H.C. & Smith, M.R.B. (1994) Arboreal ant community patterns in Brazilian cocoa farms. Biotropica, 26, 73–83.

Maloney, D., Drummond, F., Alford, R., Agricultural, M. & Station, F. (2003) Spider predation in agroecosystems: can spiders effectively control pest populations?. Technical Bulletin, 190, University of Maine.

Mansour, F., Rosen, D. & Shulov, A. (1980) A survey of spider populations (Araneae) in sprayed and unsprayed apple orchards in Israel and their ability to feed on larvae of *Spodoptera littoralis* (Boisd.). Acta Oecologica, 1, 189−197.

MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. Ecology, 42, 594−598.

Marc, P. & Canard, A. (1997) Maintaining spider biodiversity in agroecosystems as a tool in pest control. Agriculture Ecosystems and Environment, 62, 229−235.

Marc, P., Canard, A. & Ysnel, F. (1999) Spiders (Araneae) useful for pest limitation and bioindication. Agriculture, Ecosystems and Environment, 74, 229−273.

McNeely, J.A. (2004) Nature vs. nurture: managing relationships between forests, agroforestry and wild biodiversity. Agroforestry Systems, 61, 155−165.

McNeely, J. A., Schroth, G., 2006. Agroforestry and biodiversity conservation – traditional practices, present dynamics, and lessons for the future. Biodiversity and Conservation, 15, 549–554.

McNett, B.J. & Rypstra, A.L. (2000) Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. Ecological Entomology, 25, 423–432.

Metzner, J. (1981) Palu (Sulawesi): Problematik der Landnutzung in einem klimatischen Trockental am Äquator. Erdkunde, 35, 42−54.

Misnawi & Teguh, W. (2008) Potential uses of cacao bean infested by *Conopomorpha cramerella* for polyphenol extraction. ASEAN Food Journal, 15, 27−34.

Murphy, F. & Murphy, J. (2000) An introduction to the spiders of South East Asia. Malaysian Nature Society, Kuala Lumpur.

Myers, N., Mittelmeier, R.A., Mittelmeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. Nature, 493, 853−858.

Nakasuji, F., Yamanaka, H. & Korotani, K. (1973) The disturbing effect of micryphantid spiders on the larval aggregation of the tobacco cutworm *Spodoptera litura* (Lepidoptera: Noctuidae). Japanese Journal of Entomology, 41, 220−227.

Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. Journal of Biogeography, 26, 867–878.

Novotny, V. & Weiblen, G.D. (2005) From communities to continents: beta-diversity of herbivorous insects. Annales Zoologici Fennici, 42, 463–475.

Nyffeler, M. & Sunderland, K.D. (2003) Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. Agriculture, Ecosystems and Environment, 95, 579–612.

Oksanen, J. & Minchin, P.R. (1997) Instability of ordination results under changes in input data order: explanations and remedies. Journal of Vegetation Science, 8, 447–454.

Oksanen, J., Kindt, R., Legendre, P., O’Hara B. & Stevens, M.H.H. (2007) Vegan: Community ecology package. R package, version 1.8–8. Website <http://r-forge.r project.org/projects/vegan/>.

Ovtcharenko, V. (2009) Diversity of Dominican spiders: Oonopidae on cacao plantations. 25th European Congress of Arachnology, Alexandroupoli

Pekár, S. (2005) Horizontal and vertical distribution of spiders (Araneae) in sunflowers. Journal of Arachnology, 33, 197–204.

Pérez-de La Cruz, M., Sanchez-Soto, S., Ortiz-Garcia, C., Zapata-Mata, R. & Cruz-Pérez, A. d. L. (2007) Diversidad de insectos capturados por arañas tejedoras (Arachnida: Araneae) en el agroecosistema cacao en Tabasco, México. Neotropical Entomology, 36, 90−101.

Perfecto, I. & Snelling, R., (1995) Biodiversity and the transformation of a tropical agroecosystem – ants in coffee plantations. Ecological Application, 5, 1084–1097.

Perfecto, I., Armbrecht, I., Philpott, S.M., Soto-Pinto, L. & Dietsch, T.V. (2007) Shaded coffee and the stability of rainforest margins in northern Latin America, in: Tscharntke, T., Leuschner, C., Zeller, M., Guhadja, E. &. Bidin, A. (Eds.), Stability of tropical rainforest margins, linking ecological, economic and social constraints of land use and conservation. Springer, Berlin, pp. 227−264.

Perfecto, I. & Vandermeer, J. (2008) Biodiversity conservation in tropical agroecosystems – a new conservation paradigm. Annals of the New York Academy of Sciences, 1134, 173−200.

Philpott, S.M. (2005) Changes in arboreal ant populations following pruning of coffee shade-trees in Chiapas, Mexico. Agroforestry Systems, 64, 219−224.

Philpott, S. & Armbrecht, I. (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecological Entomology, 31, 369–377.

Platnick, N. I. (2010) The world spider catalog, version 10.5. American Museum of Natural History, <http://research.amnh.org/entomology/spiders/catalog/index.html>.

Potter, L. (2001) Agricultural intensification in Indonesia: outside pressures and indigenous strategies. Asia Pacific Viewpoint, 42, 305−324.

Preston, F.W. (1960) Time and space and variation of species. Ecology, 41, 611-627.

Prinzing, A. (2001) Use of shifting microclimatic mosaics by arthropods on exposed tree trunks. Annals of the Entomological Society of America, 94, 210−218.

Proszynski, J. (2007) Monograph of the Salticidae (Araneae) of the world. <http://salticidae.org/salticid/main.htm>

R Development Core Team (2008) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, <http:// www.r-project.org>.

Rice, R. & Greenberg, R. (2000) Cacao cultivation and the conservation of biological diversity. AMBIO: A Journal of the Human Environment, 29, 1679−173.

Riechert, S. & Tracy, C. (1975) Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology, 56, 265−284.

Riechert, S.E. & Lockley, T. (1984) Spiders as biological control agents. Annual Review of Entomology, 29, 299-320.

Rodrigues, A.S.L., Gregory, R.D. & Gaston, K.J. (2000) Robustness of reserve selection procedures under temporal species turnover. Proceedings of the Royal Society of London B Biological Sciences, 167, 49-55.

Rosenzweig, M.L. (1995) Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.

Russell-Smith, A. & Stork, N.E. (1994) Abundance and diversity of spiders from the canopy of tropical rainforests with particular references to Sulawesi, Indonesia. Journal of Tropical Ecology, 10, 545–558.

Rypstra, A.L., Carter, P.E., Balfour, R.A. & Marshall, S.D. (1999) Architectural features of agricultural habitats and their impact on the spider inhabitants. Journal of Arachnology, 27, 371–377.

Sahari, B. (2004) Effect of isolation on temporal dynamic of insect community structure and parasitic hymenoptera diversity in cacao agroforestry systems at the margin of Lore Lindu National Park, Central Sulawesi. PhD-thesis, Bogor Agricultural University

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. Science, 287, 1770−1774.

Scales, B.R. & Marsden, S.J. (2008) Biodiversity in small-scale tropical agroforests: a review of species richness and abundance shifts and the factors influencing them. Environmental Conservation, 35, 160−172.

Schmidt, M., Thies, C., Nentwig, W. & Tscharntke, T. (2008) Contrasting responses of arable spiders to the landscape matrix at different spatial scales. Journal of Biogeography, 35, 157−166.

Schroth, G., da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, H.L. & Izac, A.-M.N. (2004) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington DC.

Schroth, G. & Harvey, C.A. (2007) Biodiversity conservation in cocoa production landscapes: an overview. Biodiversity and Conservation, 16, 2237–2244.

Schulz, W. (2006) Einfluss der Habitatstruktur auf die Prädatorengemeinschaft der Laubstreu entlang eines Landnutzungsgradienten (Kakaoplantage zu Naturwald) in Zentral Sulawesi. Diploma thesis, University of Göttingen.

Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. PloS Biology, 4, 2132-2137.

Shattuck, S. (1999) Australian ants: their biology and identification. CSIRO Publishing, Collingwood VIC.

Shurin, J.B. (2007) How is diversity related to species turnover through time? Oikos, 116, 957-965.

Siebert, S.F. (2002) From shade- to sun-grown perennial crops in Sulawesi, Indonesia: implications for biodiversity conservation and soil fertility. Biodiversity and Conservation, 11, 1889−1902.

Simanjuntak, H. (2001) Musuh alami hama dan penyakit tanaman Kakao. Direktorat Perlindungan, Departemen Petanian, Jakarta.

Simon, U., 1993: Spider and harvestmen fauna (Arachnida: Araneae, Opiliones) of pine trees (*Pinus silvestris* L.) and its stratification. Boll. Acc. Gioenia Sci. Nat., 26, 323–334.

Simon, U. (1995) Untersuchung der Stratozönosen von Spinnen und Weberknechten (Arachn.: Araneae, Opilionida) an der Waldkiefer (*Pinus sylvestris* L.). Wissenschaft und Technik Verlag, Berlin

Sørensen, L.L. (2003) Stratification of the spider fauna in a Tanzanian forest, in: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge, pp. 92–101.

Sørensen, L.L. (2004) Composition and diversity of the spider fauna in the canopy of a montane forest in Tanzania. Biodiversity and Conservation, 13, 437–452.

de Souza, A. & Martins, R. (2005) Foliage density of branches and distribution of plant-dwelling spiders. Biotropica, 37, 416−420.

Steffan-Dewenter, I. & Tscharntke, T. (2000) Butterfly community structure in fragmented habitats. Ecology Letters, 3, 449–456.

Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M., Buchori, D., Erasmi, S., Faust, H., Gerold, G., Glenk, K., Gradstein, S. & others (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proceedings of the National Academy of Sciences, 104, 4973−4978.

Sunderland, K. & Samu, F. (2000) Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. Entomologia Experimentalis et Applicata, 95, 1−13.

Suter, R. (1981) Behavioral thermoregulation: Solar orientation in *Frontinella communis* (Linyphiidae), a 6-mg spider. Behavioral Ecology and Sociobiology, 8, 77−81.

Tylianakis, J.M., Klein, A.-M. & Tscharntke, T. (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology, 86, 3296–3302.

Uetz, G., Halaj, J. & Cady, A. (1999) Guild structure of spiders in major crops. Journal of Arachnology, 27, 270−280.

Urones, C. & Puerto, A. (1988) Ecological study of the Clubionoidea and Thomisoidea (Araneae) in the Spanish Central System. Revue Arachnologique, 8, 1−32.

Vandermeer, I., Perfecto, I., Ibarra-Nunez, G., Philpott, S. & Garcia- Ballinas, I.A. (2002) Ants (Azteca sp.) as potential biological control agents in organic shade coffee production in Southern Chiapas, Mexico: complication of indirect effects. Agroforestry Systems, 56, 271–276.

Vollrath, F., Downes, M. & Krackow, S. (1997) Design variability in web geometry of an orb-weaving spider. Physiology & Behavior, 62, 735−743.

Wagner, J. D., Toft, S. & Wise, D.H. (2003) Spatial stratification in litter depth by forest-floor spiders. Journal of Arachnology, 31, 28–39.

Watt, A.D., Stork N.E. & Bolton B. (2002) The diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon. Journal of Applied Ecology, 39, 18−30.

Way, M.J. & Khoo, K.C. (1992) Role of ants in pest management. Annual Review of Entomology, 37, 479–503.

White, E. P., Adler, P. B., Lauenroth, W. K., Gill, R. A., Greenberg, D., Kaufman, D. M., Rassweiler, A., Rusak, J. A., Smith, M. D., Steinbeck, J. R., Waide, R. B. & Yao, J. (2006) A comparison of the species-time relationship across ecosystems and taxonomic groups. Oikos, 112, 185–195.

Whitmore, T.C. (1998) An Introduction to Tropical Rain Forests. Oxford University Press, Oxford.

Wunderle, J.M. & Jr., Latta, S. (1998) Avian resource use in Dominican shade coffee plantations. Wilson Bulletin, 110, 271–281.

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Appendix

Appendix 1 Spider species list of all studied cacao agroforestry systems (n = 22) in Kulawi valley with information to species occurrence.

Family / Genus	Species	Author	Occurrence		
			litter	herb	canopy
Agelenidae					
gen.?	sp.	—		x	
Araneidae					
Araneus	sp.	—		x	
Argiope	sp.	—			x
Bunocrania	sp.	—		x	
Gasteracantha	*kuhlii*	Doleschall, 1859	x	x	x
Gasteracantha	sp.1	—	x	x	
Gasteracantha	sp.2	—	x	x	
Gasteracantha	sp.3	—	x		
Gea	sp.	—		x	
Neoscona	sp.	—			x
gen.?	sp.1	—			
gen.?	sp.2	—		x	
gen.?	sp.3	—			x
gen.?	sp.4	—		x	
gen.?	sp.5	—			x
gen.?	sp.6	—			x
gen.?	sp.7	—			x
gen.?	sp.8	—			x
gen.?	sp.9	—		x	
Barychelidae					
gen.?	sp.1	—	x		
Clubionidae					
Calamoneta	sp.	—			x
Cheiracanthium	sp.	—			x
Clubiona	*(melanosticta)*	Thorell, 1890	x		
Clubiona	*(parconcinna)*	Deelemann-Reinhold, 2001			x
Clubiona	*(viridula)*	Ono, 1989			x
Clubiona	sp.1	—	x		
Clubiona	sp.2	—			x
Clubiona	sp.3	—			x
Pteroneta	*saltans* x *tertia*	Deelemann-Reinhold, 2001	x		x
gen.?	sp.1	—			x
gen.?	sp.2	—			x
gen.?	sp.3	—			x
gen.?	sp.4	—			x
gen.?	sp.5	—			x
Corinnidae					
Apochinomma	*(nitidum)*	(Thorell, 1895)	x		
Medmessa	sp.	—			x
Oedignatha	*spadix*	Deelemann-Reinhold, 2001	x		
Oedignatha	sp.	—	x		
Serendib	sp.	—			x
? *Trachelas*	sp.	—			x
Utivarachna	sp.	—			x

Appendix 1 continued.

gen.?	sp.1	—	x		
gen.?	sp.2	—			x
gen.?	sp.3	—			x
gen.?	sp.4	—			x
Ctenidae					
Acantheis	sp.	—	x		
Ctenus	sp.	—	x		
gen.?	sp.1	—	x		
gen.?	sp.2	—	x		
? Cyatholipidae					
gen.?	sp.1	—			x
Dipluridae					
gen.?	sp.1	—	x		
Gnaphosidae					
Hongkongia	*(wuae)*	Song and Zhu, 1998	x		
Poecilchroa	*(dayamibrookiana)*	Barrion and Litsinger, 1995			x
Zelotes	*sarawakensis*	(Thorell, 1890)	x		
gen.?	sp.1	—			x
gen.?	sp.2	—	x		x
gen.?	sp.3	—			x
gen.?	sp.4	—			x
gen.?	sp.5	—	x		
gen.?	sp.6	—			x
gen.?	sp.7	—			x
Hahniidae					
Hahnia	sp.	—	x		
gen.?	sp.1	—			x
gen.?	sp.2	—			x
gen.?	sp.3	—			x
gen.?	sp.4	—			x
Linyphiidae					
Lepthyphantes	sp.	—	x		
gen.?	sp.1	—	x		x
gen.?	sp.2	—	x		
gen.?	sp.3	—	x		x
gen.?	sp.4	—	x		
gen.?	sp.5	—	x		
gen.?	sp.6	—			x
gen.?	sp.7	—		x	
gen.?	sp.8	—			x
Liocranidae					
Plynnon	*zborowskii*	Deelemann-Reinhold, 2001	x		
Sphingius	*punctatus/songi*	Deelemann-Reinhold, 2001	x		x
Sphingius	sp.	—	x		
Teutamus	*rothorum*	Deelemann-Reinhold, 2001	x		x
Teutamus	sp.	—	x		
gen.?	sp.1	—			x
gen.?	sp.2	—	x		
Lycosidae					
Artoria	*parvula*	Thorell, 1877	x		x

Appendix 1 continued.

Trochosa	*ruricoloides*	Schenkel, 1963	x		x
Trochosa	sp.	—	x		
Venonia	*coruscans*	Thorell, 1894	x		
Venonia	sp.1	—	x		x
Venonia	sp.2	—	x		
gen.?	sp.1	—	x		x
gen.?	sp.2	—	x		
gen.?	sp.3	—	x		
gen.?	sp.4	—	x		
gen.?	sp.5	—	x		
Mimetidae					
Ero	*(salittana)*	Barrion & Litsinger, 1995		x	
Nephilidae					
Nephila	sp.	—	x		x
Nephilengys	sp.	—			x
Oonopidae					
Orchestina	sp.	—			x
gen.?	sp.1	—	x		
gen.?	sp.2	—	x		
gen.?	sp.3	—			x
gen.?	sp.4	—	x		
Oxyopidae					
Hamataliwa	*(sanmenensis)*	Song and Zheng, 1992		x	
Oxyopes	sp.	—		x	
gen.?	sp.	—	x		
Psechridae					
gen.?	sp.	—		x	
Salticidae					
Bavia	*sexpunctata*	(Doleschall, 1859)			x
Brettus	sp.1	—			x
Brettus	sp.2	—			x
Chalcotropis	*(luceroi)*	Barrion & Litsinger, 1995			x
Epocilla	*calcarata*	(Karsch, 1880)	x		x
Evarcha	sp.	—		x	
Harmochirus	*brachiatus*	(Thorell, 1877)	x	x	x
Myrmarachne	sp.1		x		
Myrmarachne	sp.2	—			x
Myrmarachne	sp.3	—			x
Myrmarachne	sp.4	—			x
Myrmarachne	sp.5	—			x
Myrmarachne	sp.6	—			x
Myrmarachne	sp.7	—			x
Phaeacius	*(biramosus)*	Wijesinghe, 1991			x
Phaeacius	*(malayensis)*	Wanless, 1981			x
Phintella	sp.	—		x	
Plexippus	*setipes*	Karsch, 1879	x		x
Thorelliola	*ensifera*	(Thorell, 1877)		x	x
Viciria	*praemandibularis*	(Hasselt, 1893)			x
gen.?	sp.1	—			x
gen.?	sp.2	—			x

Appendix 1 continued.

gen.?	sp.3	—			x
gen.?	sp.4	—			x
gen.?	sp.5	—			x
gen.?	sp.6	—			x
gen.?	sp.7	—			x
gen.?	sp.8	—			x
gen.?	sp.9	—			x
gen.?	sp.10	—	x		
gen.?	sp.11	—	x		
gen.?	sp.12	—	x		
gen.?	sp.13	—			x
gen.?	sp.14	—			x
gen.?	sp.15	—	x		
gen.?	sp.16	—	x		
gen.?	sp.17	—	x		
gen.?	sp.18	—	x		
gen.?	sp.19	—		x	
gen.?	sp.20	—			x
gen.?	sp.21	—			x
gen.?	sp.22	—			x
gen.?	sp.23	—			x
gen.?	sp.24	—			x
Sparassidae					
Heteropoda	*laurae*	Jäger, 2008			x
(Olios)	sp.1	—			x
(Olios)	sp.2	—			x
gen.?	sp.1	—			x
gen.?	sp.2	—			x
Tetragnathidae					
Leucauge	*celbesiana*	(Walckenaer, 1842)		x	
Leucauge	*decorata*	(Blackwall, 1864)		x	x
Opadometa	*fastigata*	(Simon, 1877)	x	x	x
Tylorida	sp.	—		x	x
Tetragnatha	sp.	—		x	
gen.?	sp.1	—		x	
gen.?	sp.2	—		x	
Theraphosidae					
gen.?	sp.	—	x		
Theridiidae					
Acharanea	sp.	—	x	x	
Argyrodes	sp.	—		x	x
Chrysso	*(pulcherrima)*	(Mello-Leitão, 1917)	x		
Chrysso	*vesiculosa*	(Simon, 1895)	x	x	
Coleosoma	*blandum*	O. P.-Cambridge, 1882	x	x	
Coleosoma	*floridanum*	Banks, 1900	x	x	x
Euryopis	sp.	—	x		
Rhomphaea	sp.	—		x	
Steatoda	*cingulata*	(Thorell, 1890)	x		
Platnickina	*mneon*	(Bösenberg & Strand, 1906)			x

Appendix 1 continued.

Theridion	sp.	—	x		
gen.?	sp.1	—	x		
gen.?	sp.2	—	x		
gen.?	sp.3	—	x		
gen.?	sp.4	—	x		
gen.?	sp.5	—	x		
gen.?	sp.6	—	x		
gen.?	sp.7	—	x		
gen.?	sp.8	—	x		
gen.?	sp.9	—			x
gen.?	sp.10	—		x	
gen.?	sp.11	—		x	
Theridiosomatidae					
gen.?	sp.1	—			x
gen.?	sp.2	—			x
gen.?	sp.3	—			x
gen.?	sp.4	—			x
Thomisdae					
Boliscus	sp.	—		x	
Henriksenia	*hilaris*	(Thorell, 1877)		x	
Loxobates	sp.	—		x	
Misumena	sp.	—		x	
Thomisius	sp.	—		x	
? *Tmarus*	sp.	—	x		
gen.?	sp.1	—	x		
gen.?	sp.2	—			x
gen.?	sp.3	—			x
gen.?	sp.4	—			x
Uloboridae					
Miagrammopes	sp.	—		x	
Zodariidae					
Cryptothele	sp.	—	x		
gen.?	sp.1	—	x		
gen.?	sp.2	—	x		x
gen.?	sp.3	—			x
gen.?	sp.4	—	x		
gen.?	sp.5	—			x
Fam.?					
gen.?	sp.1	—	x		
gen.?	sp.2	—	x		
gen.?	sp.3	—		x	
gen.?	sp.4	—			x
gen.?	sp.5	—			x
gen.?	sp.6	—			x