Diversity and ecology of spider assemblages in secondary forests of the southern Mata Atlântica, Brazil

Implications for environmental conservation

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Inhalt

1 – Introduction

Biodiversity and its function in tropical forests

Tropical forests are among the most species rich ecosystems on earth (Bradshaw et al., 2009; Gibson et al., 2011; Pimm & Raven, 2000; Wilson, 1992) and they have therefore repeatedly been in the focus of science. First, during the era of biodiversity inventories to answer the question of how many species may exist on earth (Stork, 1993), later, when the studies on the function (or redundancy) of species richness (Loreau et al., 2001) gained more attention. Finally, the ecosystem services linked to species richness and the threat to loose many of them due to the ongoing loss of species (Rey Benayas et al., 2009) became a key aspect of studies of (tropical) ecology. For a long time vertebrate species have attracted the main attention of scientists and conservation managers and were used to provide arguments to preserve diversity. Recently more research effort has been put into the analysis of arthropod communities, of their function, and of the impact of land use on their diversity and distribution (Barlow et al., 2007; Lawton et al., 1998).

Numerous globally important ecosystem services are offered or at least strongly influenced by arthropods, e.g. biocontrol or decomposition (Feld et al., 2009; Nelson et al., 2009). So these organisms sustain also the proper function of tropical forest ecosystems, which cover 7% of the land area of our planet but host two-thirds of the terrestrial diversity (Raven, 1980; Wilson, 1992). The fertility of tropical soils and therewith the basis for the maintenance and use of tropical forest ecosystems relies on the recycling of nutrients during the decomposition of leaf and wood litter and the stock of organic matter in the soil. The deeply weathered soils cannot provide nutrients from deeper layers (Vitousek & Sanford, 1986) as in most temperate ecosystems. Soil arthropods initiate the remobilization of nutrients fixed in the litter (Martius et al., 2004a; Schmidt et al., 2008; Wardle, 1999). They foster the generation of organo-mineral structures and therewith the nutrient availability for plants (Brussaard & Juma, 1996; Rossi et al., 2010). As "ecosystem engineers" some arthropods can also visibly form ecosystems. Their presence is overall crucial for ecosystems persistence (Giller & O´Donovan, 2002; Milton & Kaspari, 2007): Via direct and indirect interactions in the food web dynamics they help to maintain the sensitive nutrition balance of tropical forest ecosystems (Abrams et al., 1996).

Nowadays it is well known that a disturbance of the ecological cycles in tropical regions by traditional agricultural land-use increases plant biomass but on the other hand decreases species richness (Juo & Manu, 1996; Rossi et al., 2010) and so breaks functional relationships. During the transformation of natural ecosystems to agriculturally used areas numerous environmental conditions, like soil humidity, temperature, litter quantity and quality, are considerably altered. These changes often lead to a decrease of soil fauna abundance and diversity and a negative impact on soil processes, driven by these organisms (Martius et al., 2004a, b, c; Rossi et al., 2010). In extreme cases these processes can result in a loss of the entire upper organic soil layer, dissolution of the plant cover till desertification, followed by physical erosion. A natural regeneration of such fallow land is very slow, if not impossible.

In tropical regions, agriculture is traditionally based on early abandonment of the areas under cultivation due to the rapidly decreasing soil fertility and productivity after slash-and-burn (Juo & Manu, 1996). This inevitably leads to the clearing of ever new forest areas and is the main cause of the loss of huge forest areas during the last decades. While in the Amazonian region a vast area of primary forest still remains, only about 7 % of the original extension of the Atlantic forests of Brazil (see below) are yet remaining. Practically no primary forest, i.e. without any anthropogenic influence, is left. At most, so called old-growth forests with a low degree of human impact during the last 100 years survived. Due to the lack of real primary forests without any anthropogenic influence, regrowing (secondary) forest habitats and their potential for hosting the regional biodiversity are of particular interest not only in the Atlantic forest region. The importance of secondary forest for the conservation of the tropical (arthropod) biodiversity, however, is a controversial topic (Gardner et al., 2007; Laurance, 2006; Wright & Muller-Landau, 2006). To what extent these secondary forests can sustain the biodiversity of natural forests is up to now poorly analyzed and therefore an important topic for biodiversity science and conservation planning.

The SOLOBIOMA project and spider study

The studies presented here have been conducted during the bilateral scientific project SOLOBIOMA[1] (Höfer at al., 2007). During the two phases of this project, analogous to the recommendations of the OECD, an evaluation of soil functioning and biodiversity was done. Especially in such a highly diverse and also threatened ecosystem like the Atlantic forest, a better scientific knowledge of the soil biodiversity is important (Höfer et al., 2007). The main task of the first project phase was the description of the development of the soil faunal

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community in the course of forest regeneration, its bio-geo-chemical interactions, and its influence on soil function. To reach this goal, plots of different successional stages from young secondary to old-growth forests were implemented in two protection areas of the Brazilian Non-Governmental-Organization SPVS ("Society for wildlife research and environmental education") comprising 8,600 and 6,700 ha. These plots were sampled in a multi-taxon approach (Kotze & Samways, 1999; Vellend et al., 2008) to evaluate the contribution of the different stages to the conservation of the regional biodiversity. The results of this phase allowed the evaluation of a soil biological classification for secondary forests, based on biodiversity and measures of soil functionality. During the second phase of the project, an in-depth evaluation of the secondary forests and their value for biodiversity conservation and the maintenance of ecosystem services was launched. The gathered knowledge on the local biodiversity structures and its ecological interactions led to the identification of possible indicators for the state of secondary forests systems supporting decisions in regional forest and land use management. In the long term this can help to maintain a sustainable use of natural resources and foster ecologic as well as economic stability.

Part of this project was a diversity survey of the spider fauna in (regrowing) neotropical forest habitats to address questions of environmental management and protection: Are there indicatory spider species for young and old-growth forest stages? Is there a directional development of the spider community along forest succession? Can the conservation value of a system be evaluated by assessing (parts of) the spider assemblage?

However, not only the diversity of spiders, but also their role/importance as part of the soil fauna was addressed during this study to gain inside into the interaction pathways in the investigated ecosystems. In the frame of diversity conservation and regional management strategies all facets have to be integrated to achieve an evaluation of the whole range of services which an ecosystem can offer. Due to the complex interactions of spiders with their biotic and abiotic environment, a combination of the results of the spider diversity survey with an experimental study on arthropod community ecology seemed reasonable to enable a profound assessment of the different forest stages. Therefore we performed an experimental study on bottom-up influences and the effect of artificial habitat structures on the soil faunal community in secondary forest of 10-15 years and an old-growth forest. The integration of the results of the diversity study and of the experimental study should shed light on the complex interactions of spiders and the ecosystem they live in.

Diversity and ecology of spiders – their use as indicators

Spiders constitute about 2 % to 10 % of the abundance of the soil arthropods in neotropical forests (for Atlantic forests in the study region: Schmidt et al., 2008; for Amazonian forests: Adis et al., 1987; Adis & de Morais, 1987; Harada & Bandeira, 1994). A moderate to high species richness, the relatively good taxonomic knowledge (Agnarsson et al., 2013; Gasnier & Höfer, 2001; Höfer & Brescovit, 1994, 2001) and their large absolute and relative abundance within the soil arthropod community in tropical ecosystems make spiders an interesting group.

Spiders play an important role as predators of insects in terrestrial decomposition food webs (Lawrence & Wise, 2000; Schmitz, 2009; Wise et al., 1999). Their exclusively predatory way of life determines their position in the food web. As predators, spiders are not only directly influenced by environmental conditions (and changes) but also indirectly via prey diversity and abundance (Birkhofer et al., 2013; Bultman et al., 1982; Bultman & Uetz, 1982; Höfer et al., 1996; Uetz, 1979, 1991). This position in the food web enables spiders to integrate on a variety of influential factors in the lower levels (Chen & Wise, 1999). So the abundance and biodiversity of spiders might reflect already small changes in habitat characteristics via indirect effects, shown to represent an important part of food web interactions (Abrams et al., 1996): The generalist predatory spiders need a highly structured habitat to hide for capturing prey, to build webs or hunt, to reduce competition and to avoid intra-guild predation. As most tropical forest ecosystems are considered to be nutrient-limited an increase in food (nutrient) availability should lead to an increase in decomposer abundance and in consequence also their predators (a bottom-up effect).

Based on the high diversity of spiders, assemblages can change in species composition, dominance structures or relative abundances analogous to variations in habitat variables or prey availability (Birkhofer et al., 2013; Ekschmitt et al., 2001; Ekschmitt et al., 2003; Giller & O´Donovan, 2002). Changes should mirror changes in the ecosystem (e.g. perturbations). Especially guild structure are hereby considered to be able to reflect these changes (Uetz et al., 1999) and are of great interest for comparing different succession stages and old-growth forests.

A multitude of ecological and experimental research on spiders is already available (Alderweireldt, 1994; Bultman et al., 1982; Bultman & Uetz, 1982, 1984; Chen & Wise, 1997, 1999; Clarke, 1968; Fagan & Hurd, 1991; Gunnarsson, 1990; Gurevitch et al., 1992; Halaj et al., 1998; Hatley & Macmahon, 1980; Herberstein, 1997; Höfer et al., 1996; Hunter

& Price, 1992; Jones, 1941; Lawrence & Wise, 2004; Pollierer et al., 2007; Rinaldi & Forti, 2007; Robinson, 1981; Scheidler, 1990; Scheu & Schaefer, 1998; Scheu, 2002; Sunderland & Samu, 2000; Uetz et al., 1999; Vargas, 2000; Wise et al., 1999). The position of spiders in the complex net of ecological relations and their interrelations in the frame of top-down and bottom-up interactions is of great interest, concerning the already mentioned identification of indicator groups for changes in an ecosystem and its performance (Billeter et al., 2008; Churchill, 1997; Clausen, 1986; Lawton et al., 1998; Lindenmayer et al., 2000; Neet, 1996). Such an evaluation of ecosystems (and provided ecosystem services) using indicator organisms can reduce sampling effort considerably because they are potentially able to integrate over many habitat variables, some of which are fairly difficult to identify and to measure directly.

Study areas

The field studies for this thesis have been performed in the southern Mata Atlântica of the state of Paraná in Brazil. The Atlantic forest is a hotspot of biological diversity (Myers et al., 2000) extending over a range of 3,500 km along the coast of Brazil. The occurrence of endemic species in these forests is exceptionally high (Bihn, 2008; Laurance, 2009; Myers et al., 2000). But also the anthropogenic pressure is very high. Three of the biggest cities of Brazil (São Paulo, Rio de Janeiro and Curitiba) are situated in the area of the Atlantic forest and the anthropogenic pressure is constantly increasing (Rodrigues et al., 2009). Therefore profound land management and protection strategies for the local biodiversity are urgently needed (Antonelli Filho & Antunes Ferreira, 2012; Höfer et al., 2011; Ferretti & Britez, 2006).

The studied areas are part of an ecological restoration program (Ferretti & Britez, 2006) and are located in the two private nature reserves (RPPN) “Reserva Natural do Rio Cachoeira” and “Reserva Natural Serra do Itaqui” of the SPVS. In the region the climate is classified as humid subtropical (Köppen´s Cfa, Strahler & Strahler, 2005) with mean temperatures between 16.2 °C in July and 24.5 °C in February (IPARDES, 2001). Average precipitation ranges between 2000 and 3000 mm year-1 (Roderjan & Kunyoshi, 1988). Rainfall is more or less evenly distributed throughout the year, although with some seasonality (low rainfall from April to August).

The NGO SPVS strongly promotes the regeneration of degraded land in its projects and the acquisition of ancient farmland for this purpose (Höfer et al., 2011). Since 1991 the SPVS has been working on biodiversity conservation, ultimately founding “InBioVeritas – the Competence Centre for the Conservation of Biodiversity in the Atlantic Forest” in 2007 (Höfer et al., 2011) with different stakeholders, amongst others the State Museum of Natural History Karlsruhe (SMNK), following the cooperation during the SOLOBIOMA project.

Outline of this dissertation

For this thesis the diversity of spiders in different forest stages of the Mata Atlântica in Brazil (Chapter 2) has been sampled, described and estimated and the spatial distribution of spider diversity (Chapter 3) analyzed. Both with regard to the role and importance of secondary forests for the conservation of biodiversity. The functional relationships of predatory arthropods within the soil faunal community (Chapter 4) was experimentally studied with regard to the direct and indirect interactions of spiders and their potential indicatory value:

Chapter 2: The conservation value of secondary forests in the southern Brazilian Mata Atlântica from a spider perspective

To assess the conservation value of secondary forests I compared the diversity of spiders in differently aged secondary forests with old-growth forests. I sampled spiders using a standard protocol in 24 sites of three successional stages and old-growth forests in two nature reserves. I describe the diversity and structure of the spider assemblages using morphospecies and genera and analyze “richness” at the genus level, a surrogate for the species level. A total of 4,495 adult individuals were collected from 539 samples and identified to 43 families, 192 genera and 440 morphospecies. Generic richness and diversity show no differences between successional stages but guild diversity does. High alpha diversity, high turnover among sites and the lack of differences in richness between stages support the value of secondary forests for species conservation in the studied region.

Chapter 3: Conserving landscape structure – conclusions from partitioning of spider diversity in southern Atlantic forests of Brazil

In this chapter I addressed the contribution of different stages of secondary forest to total diversity in two reserves by analyzing the patterns with additive partitioning of beta diversity on the genera and morphospecies level and for different sampling methods. The study took place in a relatively good preserved region of the Mata Atlântica, where the matrix of the patchy landscape is still forest. Mean alpha diversity was 47 genera and 62 morphospecies, beta diversity added up to 192 respectively 440. Beta diversity is driven by turnover, not by gain/losses (nestedness). All spatial levels contribute more to beta diversity than expected, without strong influence of the forest stage. Patterns are consistent for both identification levels and all methods, so that one of two main sampling protocols and identification to genera seem sufficient to assess diversity of spiders for conservation. In this mosaic landscape the protection of large areas encompassing all forest stages, without special attention to old-growth, is the best way to conserve the high regional species richness.

Chapter 4: No bottom-up effects of food limitation on predators in a tropical forest.

I investigated the ecologic interactions within the arthropod community by studying the response of decomposers and predators to increased food resources and space in an early succession stage of secondary forest and an old-growth forest using an experimental approach. I added organic material, artificial litter of no nutritional value and a combination of both to the soil surface to evaluate the effects of habitat space and food on soil food webs. I sampled litter- and soil-dwelling arthropods with three methods to analyze effects of the experimental treatments on the richness and diversity of the soil faunal community. Adding artificial litter has no effect on the analyzed taxa, adding food has a positive effect on decomposers, but not on predators. The lack of a bottom-up effect on predators suggests that they are not predominantly regulated by the abundance of prey.

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2 – The conservation value of secondary forests in the southern Brazilian Mata Atlântica from a spider perspective.

with Hubert Höfer, Ludger Scheuermann & Roland Brandl, Published in Journal of Arachnology, 2014

Abstract

In many tropical areas of the world, pristine forests have become rare. Nevertheless, due to shifts in the human population the area covered by secondary forests is increasing. These forests may harbour a rich flora and fauna and are considered to be main refuges for species of primary forests. However, this issue is far from clear. To assess the conservation value of secondary forests in the Atlantic Forest of Brazil, we compared the diversity of spiders in differently aged secondary forests with old-growth forests. Within a larger project treating several invertebrate taxa, we sampled spiders using a standard protocol in 24 sites of three successional stages (5-8, 15-20, 30-50 years old) and old-growth forests (> 100 years untouched) in two nature reserves. We describe the diversity and structure of the assemblages using morphospecies and genera and analyze richness at the genus level. Generic richness and diversity showed no differences between successional stages, i.e. did not increase from the youngest to older forests, but guild diversity did. The youngest stage shows the highest variability in generic composition and the turnover of genera (species) is strong between the younger forests (5-20 years old) and forests older than 30 years. High alpha diversity, high turnover among sites and the lack of differences in richness between stages support the value of secondary forests for species conservation in the studied region.

Introduction

The Brazilian Atlantic forest biome (Mata Atlântica) is one of the ‘‘hottest hotspots’’ of biodiversity (Laurance, 2009), due to the exceptional species richness and high number of endemic taxa in the various forest types (Forzza et al., 2012). However, the coastal region of Brazil has also experienced an exceptionally high degree of forest conversion and deforestation (Myers et al., 2000; Ribeiro et al., 2009) for more than 500 years. In contrast to the more strongly deforested areas of the Atlantic coast, in the state of Paraná in southern Brazil large remnants of Atlantic forests still exist, forming a mosaic of patches of old-growth forests (sensu Clark, 1996; see also Wirth et al., 2009) and secondary forests in various stages of succession. These secondary forests originate mainly from abandoned buffalo pastures.

Recently the issue of the importance of these secondary forests for the conservation of biodiversity initiated a controversial discussion (see Bihn et al., 2008b).

Conservation strategies and management in the tropics are often based on large, exotic and beautiful or rare, endangered vertebrate species. However, the overwhelming part of biodiversity consists of invertebrates. Furthermore invertebrates are involved in numerous important ecosystem functions (e.g. nutrient cycling or pollination). The analyses of invertebrate diversity for conservation are usually restricted to species numbers or lists of species of selected taxa. Although the number of species is not a quality measure *per se*, richness and diversity measures, which include the relative abundance of species, are valuable approximations to biodiversity and the conservation value of a habitat (Brose et al., 2003; Gaston, 1996; Gotelli & Colwell, 2001; Magurran, 2004), especially when autecological data are lacking, i.e. knowledge on the distribution, natural history traits and habitat preferences for most of the species is sparse. However, to evaluate the richness of an assemblage a reference is needed. Comparing species numbers of assemblages in secondary vegetation with the original (primary) vegetation seems to be a meaningful approach to estimate degradation, to recognize the loss of functional diversity (Bihn et al., 2008b, 2010) and to classify areas with regard to their conservation value (Dunn, 2004), although there is some evidence of functional redundancy (Lawton et al., 1998; Loreau et al., 2001).

The Brazilian-German cooperative project SOLOBIOMA (Höfer et al., 2007, 2011) studied the biogeochemistry and - in a multi-taxon approach - the diversity of earthworms (Römbke et al., 2009), enchytraeids (Schmelz et al., 2009, 2011), ants (Bihn et al., 2008a,b), beetles (Hopp et al., 2010, 2011; Ottermanns et al., 2011) and spiders in order to evaluate the conservation value of secondary forests in the Mata Atlântica. The overall aim of this project was to check the possibility of classifying secondary forest stages by their soil fauna and comparing that with the "traditional" classification by age and vegetation. In the absence of true primary vegetation in this region, we had to rely on "old-growth" forests as a reference.

Spiders are a species-rich taxon in the tropics. In Brazil the taxonomy is comparatively well studied (Brescovit et al., 2011) and meaningful faunistic inventories are available (Bonaldo et al., 2009; Höfer, 1990, 1997; Höfer & Brescovit, 2001; Rego et al., 2007; Silva, 1996; Silva & Coddington, 1996; Venticinque et al., 2008). However, in these studies there is a strong bias towards the Amazonian region. During the last years and based on taxonomic advances and faunistic knowledge, several studies in the Mata Atlântica, focussing on spiders, approached ecological questions (effects of disturbance, fragmentation and vegetation type;

Benati et al., 2005; Candiani et al., 2005; Oliveira-Alves et al., 2005; Podgaiski et al., 2007). However studies with well-replicated designs are still rare (Bonaldo et al., 2007; Dias et al., 2005; Lo-Man-Hung et al., 2008; Pinto-Leite et al., 2008; Ricetti & Bonaldo, 2008). To assess the conservation value of secondary forests, we sampled spiders on the ground and in the lower vegetation in three different stages of secondary and old-growth forests, appraising the changes in richness and composition of genera across the successional gradient.

Material and Methods

Study area

The study was conducted in the coastal region of the Paraná state in south-eastern Brazil. Originally the region was covered by dense ombrophilous lowland and submontane forests (IBGE, 1992), but these ecosystems suffered massive exploitation and were largely converted to buffalo pastures (IPARDES, 1995). Today, the landscape is characterized by a mosaic of open land, secondary forests and few, but compared to the rest of the Atlantic Forest relatively large patches of old-growth forests. The regional climate is humid subtropical (Köppen´s Cfa, Strahler & Strahler, 2005) with mean temperatures between 16.2 °C in July and 24.5 °C in February (IPARDES, 2001). Average precipitation ranges between 2000 and 3000 mm year^{-1} (Roderjan & Kunyoshi, 1988). Rainfall is more or less evenly distributed throughout the year, although with some seasonality (low rainfall from April to August).

The studied areas are part of an ecological restoration program (Ferretti & Britez, 2006). Sampled sites were located in two private nature reserves (RPPN) “Reserva Natural do Rio Cachoeira” and “Reserva Natural Serra do Itaqui” (Fig. 1). Both are owned and managed by the Brazilian NGO “Society for wildlife research and environmental education” (SPVS) and are part of the Environmental Protection Area (EPA) of Guaraqueçaba and also the Mata Atlântica Biosphere Reserve. Within their areas of 12,000 resp. 6,700 ha, ranging from sea level to elevations of 700 m a.s.l., different successional stages from pasture to forest were categorized *a-priori* by the SPVS using age and vegetational structure, based on ortho-photos from 1952, 1980 and 2002 and knowledge of the residents on historical use.

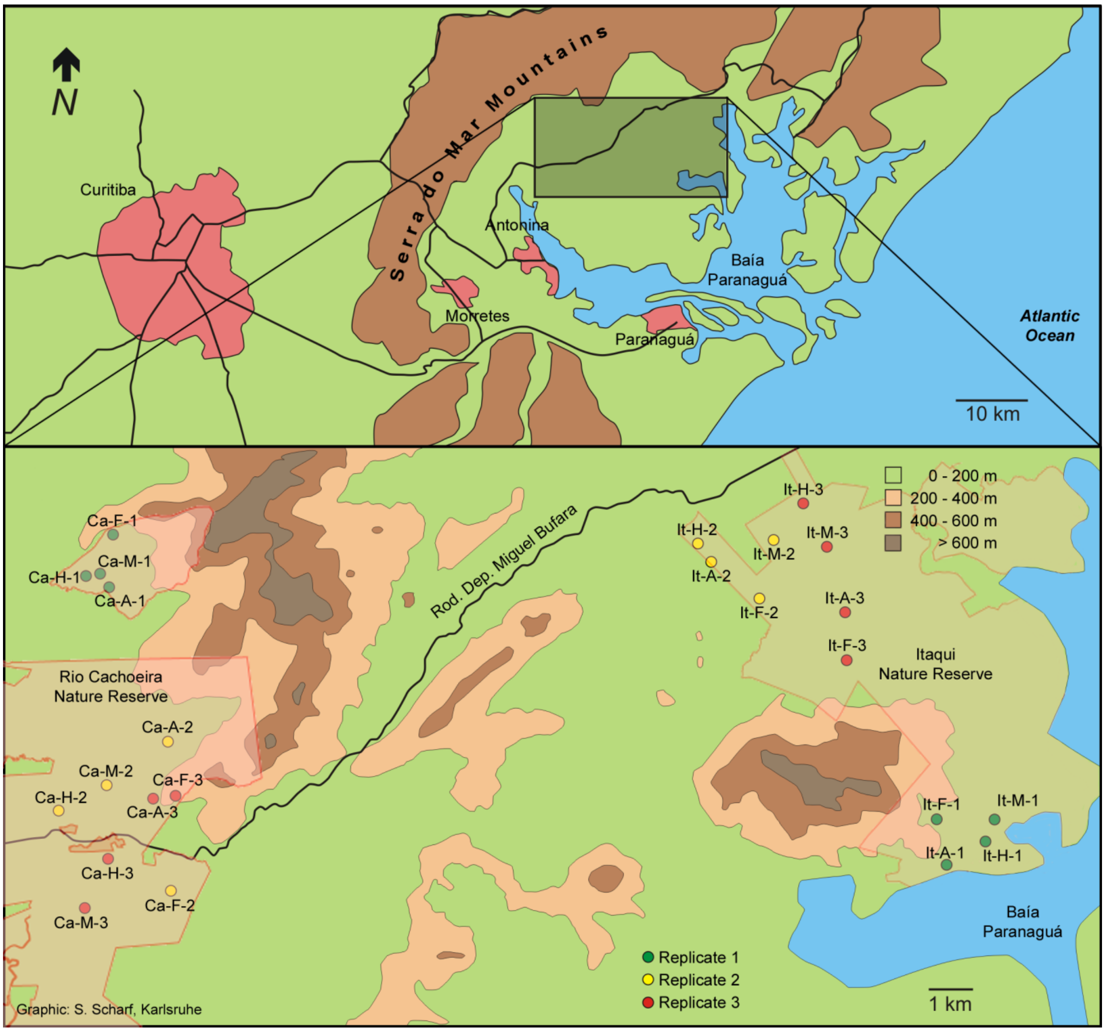

Figure 1. Location of the study region in Paraná state, Brazil and the sampling sites in the two Nature Reserves Rio Cachoeira (Ca) and Itaqui (It); successional stages: H – herbaceous, A – arboreal, M – medium, F – old-growth forest.

Study design

In both reserves (further called localities), which are located approximately 25 km apart (Cachoeira: 25.3142°S, 48.6958°W; Itaqui: 25.2733°S, 48.4872°W; WGS84), we sampled spiders along a chronosequence of four forest stages: 5-8 years old (H – herbaceous stage), 10-15 years old (A – arboreal stage), 35-50 years old (M – medium stage) and > 100 years old (F – old-growth); the latter was used as a reference stage. In each stage we sampled three spatially separated replicate sites of 30 x 50 m² each. In total 12 sites (3 replicates x 4 stages) were studied in each of the two localities (Fig. 1) during several days of sampling (see below) in springtime (October/November) of 2005 (Cachoeira) resp. 2007 (Itaqui). The springtime period has been shown to lead to a high degree of sampling completeness without the necessity of resampling throughout the year (Baldissera et al., 2003; Podgaiski et al., 2007; Rodrigues, 2005).

Sampling methods and identification

A structured sampling, following a widely accepted standard protocol (Coddington et al., 1991) was applied to sample spider diversity in these forests:

(a) Ground hand sampling ("looking down" of Coddington et al., 1991): Two (experienced) persons sampled during one hour at night (with headlights), exploring all structures below knee level – resulting in 1 sample per person, 2 samples per site.

(b) Aerial hand sampling ("looking up" of Coddington et al., 1991): One person sampled for one hour at night, exploring all structures from knee height upwards to overhead arm's reach, i.e. lower vegetation – resulting in 1 sample per site.

(c) Beating: three persons striking vegetation at any reachable level (i.e. lower vegetation) with a stick, collecting the spiders falling on a 50 X 50 cm^2 tray held below, during one hour. Twenty beating points made one sample. Depending on the person sampling, a different number of samples per site (3-9) resulted.

(d) Pitfall trapping: 10 traps per site were installed to capture active ground spiders during one week – resulting in usually 10 samples per site, with a few failures. Traps were 330 ml PE cups with an opening diameter of 7.5 cm, filled with 100 ml of 4% formaldehyde solution and protected against rain by transparent plastic plates.

The sampled spiders were stored in 75% ethanol. All adult spiders were determined to (morpho-) species or to (morpho-) genera if possible, using a conservative approach to delimit morphospecies and -genera. All analyses are based on adult spiders. Notwithstanding the progress in spider taxonomy in the Neotropics, severe shortcomings in the analyses of the diversity of tropical faunas remains a prime difficulty in identifying specimens to the species level or to sort all (adult) specimens to the level of morphospecies. This is due to the high number of not (adequately) described species and the lack of identification keys (Uehara-Prado et al., 2009). We therefore used genera as a surrogate for the comparison of species richness and diversity, which has been shown to be a successful strategy even at local scales (Andersen & Hauge, 1995; Baldissera et al., 2008; Balmford et al., 1996; Bihn et al., 2008b).

Identification was done by the first and third author with help from Brazilian experts at Butantan Institute (São Paulo, IBSP) and Museu de Ciências Naturais da Fundação Zoobotânica (Porto Alegre, MCN). Morphospecies numbers (in the appendix) were assigned according to ISBN and MCN numeration to assure future comparability. Voucher material is deposited at the entomological department of Universidade Federal do Paraná in Curitiba (UFPR), at IBSP and MCN.

Data analysis

For all analyses we pooled the complementary captures from the different methods and strata. Richness and diversity of the spider assemblages per site (alpha diversity) were described by the (observed) numbers of genera (G), the ratio genera/individuals (G/N), the Shannon index (H), the Shannon evenness measure (E) and Log series α (Magurran, 2004). For the direct comparison of genus richness between the single sites, we used rarefaction (Coleman, 1982; Gotelli & Entsminger, 2004; Hurlbert, 1971; Magurran, 2004). It was calculated with R version 2.10.2 (R Development Core Team, 2009), using the rarefy function of the package VEGAN 1.17-2 (Oksanen et al., 2009). To evaluate the portion of rare genera at the single site, we calculated the relative abundance of singletons (portion of genera with one individual from the total genera number per site; Magurran, 2004). Furthermore we calculated the nonparametric (sample-based) estimators Chao 2 and ICE (Magurran, 2004) with EstimateS 8.0 (Colwell, 2005). A coverage measure for each site was calculated using the number of observed genera in percent of the estimated richness.

Similarity across stages (beta diversity) was analyzed with qualitative presence/absence (Sørensen index) and quantitative (abundance) data for assemblage structure (NESS = Normalized Expected Species Shared, Grassle & Smith, 1976). In contrast to the Sørensen Index, NESS is a quantitative similarity measure, which accounts for the individual numbers of the shared species in the compared sites or assemblages (as in the Renkonen or Bray-Curtis qualitative index), but weights the rare species with ascending values for the sample size. Therefore it seems to be a good measure for tropical communities, where rare species account for a considerable part of the recorded species (Chazdon et al., 1998; Novotny & Basset, 2000). We calculated the NESS with the program BIODIV 97 for Excel.

To visualize differences in spider assemblages of the forest stages and localities, we used a three-dimensional ordination based on a non-metric multidimensional scaling (nMDS) analysis, calculated on Bray-Curtis similarities of square-root transformed abundances of genera using Winkyst 1.0 (100 random perturbations) and Canoco for Windows 4.53 (Ter Braak, 2002). The similarity matrix was tested for spatial autocorrelation using the mantel function of the R package ECODIST. The spatial distribution of the study sites had no effect on the patterns of beta diversity ($P = 0.98$).

To complete the comparison of the forest stages, we used available guild classifications for the Neotropical spider fauna (Dias et al., 2010; Höfer & Brescovit, 2001). We assigned the specimens to 16 distinct guilds. The assignment of a species to a guild is usually based on the family, in some cases on the genus, which was possible for almost all specimens in our samples. In a few cases we had to apply personal knowledge on the biology of a taxon based on our own observations in the field, the sampling method and information in literature (Álvares et al., 2004; Silva & Coddington, 1996). Only the Amaurobiidae (18 individuals) were not assigned to a guild due to the unclear taxonomic status and lack of ecological information for Neotropical species. For the comparison of guild structure in the different stages, data from the two localities were pooled.

The rarefied genera numbers, the estimated richness and the alpha diversity values were tested for significant effects of the stage (4 levels) and the locality (2 levels) with two-way ANOVAs using Statistica 8.0 (StatSoft, 2007). Permutational multivariate analysis of variance (Permanova, Version 1.6, Anderson 2001, 2005) was used to analyze the generic turn-over in the spider assemblage of different forest stages and to underpin the ordination with a statistical analysis. We tested the main factors of the residuals and their interaction terms with 9999 permutations using Bray-Curtis dissimilarities between the study sites.

Indicator analysis was done with R, version 2.10.1 (R Development Core Team, 2009) and the packages MASS (Venables & Ripley, 2002) and labdsv (Roberts, 2007). Because indicators of single stages were weak, we pooled the beating tray data of the two younger and the two older stages to one group each (stages H and A = young, “Y”, stages M and F = old, “O”) in order to achieve a distinctive separation with indicator genera of high indicator values for younger and older forests respectively.

Results

A total of 11,293 individuals were collected from 539 samples, of which only the 4,495 (39.8%) adults were identified and sorted to 43 families, 192 genera and 440 morphospecies (Appendix 1). We were able to identify and name 155 species according to the available literature. Although the two localities were sampled during two campaigns in different years, similar numbers of spiders were collected: 2,116 individuals of 33 families and 157 genera in Cachoeira (2005) and 2,379 individuals of 37 families and 154 genera in Itaqui (2007). The ratios females/males (0.941, 0.948) and adults/juveniles (0.673, 0.669) were also similar.

Overall, Theridiidae ranked first in abundance, accounting for 27% of all adults, and also in species richness with 117 morphospecies in 34 genera. The theridiid genera *Dipoena* (19 morphospecies), *Theridion* (16), *Cryptachaea* (13) and *Thymoites* (10) showed the highest species richness. Only the araneid genus *Mangora* was represented by a comparably high number of morphospecies (10). Zoridae ranked second with 19% of the individuals, but only eight morphospecies. The spider assemblages in Cachoeira and Itaqui showed a similar ranking (Spearman r = 0.36) of family abundance values, but Theridiidae and Linyphiidae were nearly twice as abundant in Itaqui as in Cachoeira. The Araneidae (58 mspp./21 gen.), Salticidae (55/29) and Linyphiidae (43/15) accounted together for more than 35% of all species and 34% of all genera collected.

As expected, sampling in different strata (ground/vegetation) yielded strongly complementary sets of lineages. In the vegetation 74% of all spiders captured were web-builders. Theridiidae and Linyphiidae alone accounted for more than 50% (Table 1), with more than 100 species.

The only abundant hunting spiders in the vegetation were Salticidae (55 morphospecies) and Anyphaenidae (10 species). There was no dominant (10% criterion) species or genus in the vegetation and the 316 morphospecies (148 genera) collected showed that this stratum houses a large part of the total diversity. In strong contrast, half of all spiders captured on the ground belong to one genus of the small hunting zorids and 70% of all were hunting spiders (Table 2). All abundant hunting-spider families (Zoridae, Ctenidae, Lycosidae, Pisauridae) were represented by few genera and species and thus overall richness (216 mspp., 116 genera) was lower than in the vegetation. Only very few mygalomorphs (i.e. Nemesiidae, Dipluridae) were collected.

Table 1. Absolute and relative abundance and richness of the spider families captured on lower vegetation (by beating and looking up). N = number of individuals, G = number of genera, S = number of morphospecies.

Family	**N**	**% N**	**G**	**% G**	**S**	**% S**
Theridiidae	1010	37.4	29	19.6	96	30.2
Linyphiidae	374	13.8	9	6.1	23	7.2
Salticidae	370	13.7	29	19.6	52	16.4
Araneidae	234	8.7	21	14.2	53	16.7
Anyphaenidae	148	5.5	8	5.4	10	3.1
Thomisidae	119	4.4	7	4.7	10	3.1
Pholcidae	98	3.6	3	2.0	12	3.8
Uloboridae	69	2.6	3	2.0	5	1.6
Tetragnathidae	60	2.2	5	3.4	9	2.8
Dictynidae	58	2.2	1	0.7	1	0.3
Mimetidae	33	1.2	3	2.0	4	1.3
Scytodidae	32	1.2	1	0.7	2	0.6
Oonopidae	24	0.9	5	3.4	5	1.6
Theridiosomatidae	24	0.9	5	3.4	12	3.8
Corinnidae	10	0.4	4	2.7	7	2.2
Oxyopidae	9	0.3	3	2.0	4	1.3
Hahniidae	8	0.3	1	0.7	1	0.3
Zoridae	5	0.2	1	0.7	2	0.6
Miturgidae	4	0.2	2	1.4	2	0.6
Lycosidae	3	0.1	1	0.7	1	0.3
Deinopidae	2	0.1	1	0.7	1	0.3
Hersiliidae	2	0.1	1	0.7	1	0.3
Sparassidae	2	0.1	1	0.7	1	0.3
Amaurobiidae	1	0.0	1	0.7	1	0.3
Ctenidae	1	0.0	1	0.7	1	0.3
Philodromidae	1	0.0	1	0.7	1	0.3
Synotaxidae	1	0.0	1	0.7	1	0.3
Sum: 27	2702		148		318	

Table 2. Absolute and relative abundance and richness of the spider families captured on the ground (by pitfall traps and looking down). N = number of individuals, G = number of genera, S = number of morphospecies.

Family	**N**	**% N**	**G**	**% G**	**S**	**% S**
Zoridae	855	47.7	1	0.9	8	3.6
Theridiidae	210	11.7	25	21.6	48	21.6
Linyphiidae	126	7.0	12	10.3	29	13.1
Ctenidae	121	6.8	2	1.7	6	2.7
Pholcidae	69	3.9	5	4.3	13	5.9
Lycosidae	62	3.5	5	4.3	9	4.1
Pisauridae	54	3.0	1	0.9	2	0.9
Araneidae	49	2.7	10	8.6	22	9.9
Mysmenidae	40	2.2	3	2.6	4	1.8
Hahniidae	26	1.5	1	0.9	7	3.2
Salticidae	25	1.4	8	6.9	14	6.3
Corinnidae	18	1.0	3	2.6	6	2.7
Amaurobiidae	17	1.0	1	0.9	3	1.4
Oonopidae	16	0.9	4	3.5	5	2.3
Ochyroceratidae	14	0.8	1	0.9	3	1.4
Theridiosomatidae	12	0.7	2	1.7	4	1.8
Tetragnathidae	11	0.6	5	4.3	7	3.2
Thomisidae	11	0.6	3	2.6	6	2.7
Anyphaenidae	10	0.6	3	2.6	3	1.4
Scytodidae	10	0.6	1	0.9	2	0.9
Nemesiidae	8	0.5	2	1.7	2	0.9
Titanoecidae	7	0.4	1	0.9	1	0.5
Mimetidae	4	0.2	1	0.9	2	0.9
Gnaphosidae	2	0.1	1	0.9	1	0.5
Palpimanidae	2	0.1	2	1.7	2	0.9
Prodidomidae	2	0.1	1	0.9	1	0.5
Anapidae	1	0.1	1	0.9	1	0.5
Caponiidae	1	0.1	1	0.9	1	0.5
Deinopidae	1	0.1	1	0.9	1	0.5
Dipluridae	1	0.1	1	0.9	1	0.5
Liocranidae	1	0.1	1	0.9	1	0.5
Miturgidae	1	0.1	1	0.9	1	0.5
Nesticidae	1	0.1	1	0.9	1	0.5
Symphytognathidae	1	0.1	1	0.9	1	0.5
Synotaxidae	1	0.1	1	0.9	1	0.5
Trechaleidae	1	0.1	1	0.9	1	0.5
Uloboridae	1	0.1	1	0.9	1	0.5
Zodariidae	1	0.1	1	0.9	1	0.5
Sum: 38	1793		116		222	

Alpha diversity

The number of individuals ranged from 134 to 241, representing 37 to 57 genera, in Cachoeira and from 121 to 277, representing 33 to 60 genera, in Itaqui. Means of all generic richness values were very close and coefficient of variation rarely exceeded 20% (Tables 3, 4). The same applies for the diversity indices. Typical for nonrecurring sampling of tropical habitats, nearly half of the morphospecies or genera were represented by only one adult specimen per site of a stage (singletons; Tables 3, 4, Appendix 1). Both estimators came to very similar values (mean of 81 genera in Cachoeira, 76 in Itaqui), corresponding to a coverage of over 60%. The richness of genera (total, mean rarefied, estimated) was very similar across the stages of forest succession (see means in Table 5).

After correcting for the sampling effort (number of samples, individuals), no differences between the stages were found. None of the statistical tests (two-way ANOVAs with stage and locality as factors and rarefied and estimated generic richness and the two diversity indices as dependent variable) showed a significant effect of stage or locality. The spider assemblages in younger stages are obviously as rich in genera and as diverse as in the old-growth forests. At the stage level the portion of singletons was 33% or higher, the estimated number of genera, based on the Chao 2 and ICE estimators, was mostly less than twice the number of observed genera and, consequently, coverage was higher than 66% (Table 5). At the morphospecies level the portion of singletons in the stages was even higher.

Table 3. Alpha diversity of spiders in the Cachoeira sites (genera based, samples from all methods pooled). Site codes: Ca H1–3 = Cachoeira sites of herbaceous stage, Ca A1–3 of arboreal stage, Ca M1–3 of medium stage, Ca F1–3 of old-growth. N = number of individuals, G = number of genera, H = Shannon Index, E = evenness, α = Fishers's alpha index, Ra = rarefied genera number, Sg = portion of singletons, Chao 2 = estimated generic richness, ICE = sample-based richness estimate, Coverage = number of observed genera as a percentage of Chao 2-estimated richness, SD = standard deviation, CV = coefficient of variation.

Site	N	G	G/N	H	E	A	Ra (SD)	Sg	Chao 2 (SD)	ICE	Coverage
Ca H1	165	51	0.31	3.5	0.66	25.3	44.0 (2.1)	0.39	61.6 (6.2)	73.5	82.8
Ca H2	139	40	0.29	3.1	0.57	18.8	36.4 (1.6)	0.55	69.0 (16.1)	86.8	58
Ca H3	194	51	0.26	3.3	0.52	22.5	40.5 (2.4)	0.45	79.0 (14.8)	83.0	64.6
Ca A1	169	37	0.22	2.6	0.36	14.6	30.7 (2.0)	0.49	53.3 (10.2)	62.1	69.4
Ca A2	134	50	0.37	3.4	0.59	28.9	46.4 (1.6)	0.54	94.4 (22.0)	119.7	53
Ca A3	185	52	0.28	3.4	0.58	24.0	41.5 (2.4)	0.46	100.6 (25.4)	103.7	51.7
Ca M1	137	49	0.36	3.2	0.51	27.3	44.5 (1.7)	0.61	86.9 (18.8)	115.0	56.4
Ca M2	155	46	0.30	3.4	0.56	22.1	39.8 (2.0)	0.52	94.1 (26.2)	93.1	48.9
Ca M3	169	44	0.26	3.0	0.45	19.3	36.4 (2.1)	0.50	70.3 (14.5)	78.1	62.6
Ca F1	216	54	0.25	3.3	0.50	23.1	40.6 (2.5)	0.46	95.7 (22.5)	88.4	56.4
Ca F2	212	49	0.23	3.2	0.51	20.0	36.7 (2.5)	0.47	83.7 (18.6)	89.5	58.5
Ca F3	241	57	0.24	3.3	0.48	23.6	39.9 (2.7)	0.46	79.6 (11.3)	92.8	71.6
Total	**2116**	**157**							**220.4 (25.2)**	**200.0**	**71.3**
Mean	**176.3**	**49.3**	**0.28**	**3.2**	**0.52**	**22.5**	**39.8**	**0.49**	**80.7**	**90.5**	**61.2**
CV	**19%**	**12%**	**17%**	**8%**	**15%**	**17%**	**11%**	**12%**	**18%**	**18%**	**16%**

Table 4. Alpha diversity of spiders in the Itaqui sites (genera based, samples from all methods pooled). Site codes: It H1-3 = Itaqui sites of herbaceous stage, It A1-3 of arboreal stage, It M1-3 of medium stage, It F1-3 of old-growth. N = number of individuals, G = number of genera, H = Shannon index, E = evenness, α = Fishers's alpha index, Ra = rarefied genera number, Sg = portion of singletons, Chao 2 = estimated generic richness, ICE = sample-based richness estimate, Coverage = number of observed genera as a percentage of Chao 2-estimated richness, SD = standard deviation, CV = coefficient of variation.

Site	N	G	G/N	H	E	A	Ra (SD)	Sg	Chao2 (SD)	ICE	Coverage
It H1	121	38	0.31	3.2	0.64	19.0	37.5 (0.7)	0.42	51.6 (8.3)	64.7	73.6
It H2	253	54	0.21	3.2	0.45	21.0	37.1 (2.7)	0.48	97.2 (22.2)	103.3	55.6
It H3	125	34	0.28	2.4	0.31	15.4	32.5 (1.1)	0.68	71.7 (21.4)	128.6	47.4
It A1	150	44	0.29	3.2	0.53	21.0	38.6 (1.9)	0.52	75.7 (17.3)	90.6	58.1
It A2	230	50	0.22	2.5	0.26	18.5	32.7 (2.6)	0.54	117.3 (37.4)	101.8	42.6
It A3	160	42	0.26	3.1	0.54	17.8	35.4 (1.9)	0.46	61.1 (12.0)	71.1	68.7
It M1	205	43	0.21	3.0	0.49	16.6	33.4 (2.3)	0.44	70.7 (16.1)	79.7	60.8
It M2	277	54	0.20	3.2	0.46	20.0	37.3 (2.7)	0.37	78.2 (13.6)	77.3	69.1
It M3	281	57	0.20	3.3	0.46	21.6	38.7 (2.8)	0.37	73.5 (8.9)	85.2	77.6
It F1	123	33	0.27	3.1	0.69	14.8	32.4 (0.7)	0.36	47.3 (9.9)	51.3	69.8
It F2	274	60	0.22	3.4	0.47	23.7	39.4 (2.9)	0.45	109.2 (24.7)	105.5	54.9
It F3	180	44	0.24	3.2	0.58	18.6	37.2 (2.0)	0.36	60.4 (9.7)	67.0	72.8
Total	**2379**	**154**							**196.8 (17.3)**	**191.5**	**78.3**
Mean	**198.3**	**46.1**	**0.24**	**3.1**	**0.49**	**19.0**	**36.0**	**0.45**	**76.2**	**85.5**	**62.6**
CV	**32%**	**19%**	**16%**	**10%**	**25%**	**14%**	**7%**	**21%**	**29%**	**25%**	**18%**

Table 5. Sampling effort, generic richness (observed and estimated) and diversity per stage (means and standard deviations from three replicates, all samples pooled). N = number of individuals, G = number of genera, α = Fishers's alpha index, Ra = rarefied genera number, Sg = portion of singletons (pooled data for the three replicates), Chao 2 = estimated generic richness, ICE = sample-based richness estimate, Coverage = number of observed genera as a percentage of Chao 2-estimated richness. SD = standard deviation.

Stage	**Samples**	**Total N**	**Mean N (SD)**	**Total G**	**Ra (SD)**	**Sg**	**α (SD)**	**Chao 2 (SD)**	**ICE**	**Coverage**
Ca H	60	498	166 (28)	89	47.6 (3.4)	0.34	31.6 (2.3)	116.6 (12.5)	125.2	76.3
Ca A	69	488	163 (26)	85	43.7 (3.4)	0.34	29.8 (2.2)	111.3 (11.9)	126.2	76.3
Ca M	70	461	153 (16)	83	42.9 (3.3)	0.41	29.5 (2.3)	115.8 (14.3)	135.5	71.7
Ca F	72	669	223 (16)	84	40.9 (3.2)	0.36	25.4 (1.7)	119.3 (17.0)	113.6	70.4
It H	69	499	166 (75)	86	44.9 (3.4)	0.34	30.0 (2.2)	102.5 (8.0)	115.8	83.9
It A	65	540	180 (44)	82	39.3 (3.3)	0.43	26.9 (2.0)	116.5 (15.2)	132.2	70.4
It M	72	763	254 (43)	89	40.6 (3.3)	0.33	26.1 (1.7)	117.6 (13.9)	118.6	75.7
It F	62	577	192 (76)	81	41.4 (3.2)	0.40	25.7 (1.8)	123.5 (19.7)	127.4	65.6
Total	**539**	**4495**	**187 (51)**	**192**	**49.8 (3.8)**	**0.23**	**40.7 (1.4)**	**248.8 (22.3)**	**229.3**	**77.2**

Beta diversity

Qualitative similarity (Sørensen index) of the different stages at each locality ranged from 0.53 (youngest stage with older) to around 0.7 (between older stages) (Tables 6, 7), reflecting a turnover of genera (and species) along the successional gradient. Furthermore, within-stage similarities were not higher, ranging from 0.4 (stage H) to 0.7 (stage F) in Cachoeira and from 0.3 (H) to 0.6 (M) in Itaqui. Similarities of the same stages from the two reserves were usually higher (Tables 8, 9) than of the different stages within the same locality (Tables 6, 7). Similarities between stage H and other stages were always lowest, the spider assemblage of the herbaceous stage differed strongly from the older stages.

Quantitative (NESS) is generally higher than qualitative similarity (Tables 6-9), indicating that the dominant genera (i.e. species) were abundant in all stages. This is also obvious in the list of the ten most abundant genera (species) of the two localities, representing 49% resp. 50% of all adults (Tables 10, 11). One zorid genus clearly dominated in all stages and the positions of many abundant genera in the list are also very similar. Abundant spider species reflecting the turnover between younger (H, A) and older forests (M, F) are the linyphiids of the genus *Anodoration* and several theriidid genera (*Spintharus*, *Theridion*, *Thwaitesia*) in Itaqui and the dictynid *Thallumetus* and the pholcids of the genus *Mesabolivar* in Cachoeira. In Itaqui the latter was also exclusively found in the two older stages, but was not among the ten most abundant genera (see also indicator analysis).

Table 6. Qualitative (Sørensen index, upper right) and quantitative (NESS index, lower left, m = 228) similarities between the forest stages in Cachoeira reserve, based on genera data, all methods pooled.

	Ca H	**Ca A**	**Ca M**	**Ca F**
Ca H		0.58	0.56	0.53
Ca A	0.76		0.70	0.67
Ca M	0.72	0.93		0.71
Ca F	0.70	0.92	0.92	

Table 7. Qualitative (Sørensen index, upper right) and quantitative (NESS index, lower left, m = 248) similarities between the forest stages in Itaqui reserve, based on genera data, all methods pooled.

	It H	**It A**	**It M**	**It F**
It H		0.59	0.54	0.53
It A	0.82		0.65	0.58
It M	0.72	0.85		0.66
It F	0.67	0.76	0.91	

Table 8. Qualitative similarity (Sørensen) between the forest stages in both reserves, based on genera data, all methods pooled.

	It H	**It A**	**It M**	**It F**
Ca H	0.65	0.56	0.49	0.51
Ca A	0.58	0.62	0.65	0.66
Ca M	0.56	0.66	0.69	0.69
Ca F	0.50	0.64	0.68	0.68

Table 9. Quantitative similarity (NESS, m = 228) between the forest stages in both reserves, based on genera data, all methods pooled.

	It H	**It A**	**It M**	**It F**
Ca H	0.82	0.75	0.65	0.65
Ca A	0.76	0.85	0.91	0.85
Ca M	0.68	0.80	0.89	0.86
Ca F	0.57	0.80	0.91	0.92

Table 10. Assemblage structure (relative abundance of the ten most abundant genera) and total number of individuals (Ind.) in the four forest stages in Cachoeira reserve, pooled from all methods in all sites.

		Ca H	**Ca A**	**Ca M**	**Ca F**	**Ca total**	**Ca**
Family	**Genus**	**%**	**%**	**%**	**%**	**%**	**Ind.**
Zoridae	gen. 1	15.0	16.1	22.3	29.7	20.3	429
Salticidae	*Tariona*	5.1	6.7	3.8	4.1	5.1	108
Theridiidae	*Dipoena*	5.3	3.9	5.6	5.4	5.0	105
Linyphiidae	*Sphecozone*	6.4	3.3	0.4	7.6	4.3	90
Theridiidae	*Theridion*	3.1	2.4	0.8	6.7	3.1	66
Pholcidae	*Mesabolivar*	0.2	1.8	1.2	9.1	2.9	61
Araneidae	*Mangora*	2.0	0.9	2.8	6.5	2.8	60
Anyphaenidae	*Patrera*	0.0	1.5	3.8	3.9	2.2	47
Dictynidae	*Thallumetus*	0.0	0.0	4.0	5.4	2.1	45
Theridiidae	*Spintharus*	0.4	1.5	1.6	5.4	2.1	45

Table 11. Assemblage structure (relative abundance of the ten most abundant genera) and total number of individuals (Ind.) in the four forest stages in Itaqui reserve, pooled from all methods in all sites.

		It H	**It A**	**It M**	**It F**	**It total**	**It**
Family	**Genus**	**%**	**%**	**%**	**%**	**%**	**Ind.**
Zoridae	gen. 1	7.4	30.9	18.3	15.1	18.1	431
Theridiidae	*Dipoena*	2.4	6.1	7.9	3.6	5.3	126
Linyphiidae	*Sphecozone*	5.0	2.8	6.0	5.4	4.9	117
Theridiidae	*Spintharus*	0.2	1.9	9.7	5.2	4.8	115
Linyphiidae	*Anodoration*	16.2	2.8	0.0	0.0	4.0	96
Salticidae	*Tariona*	0.4	1.5	4.3	4.9	3.0	71
Theridiidae	*Thwaitesia*	0.4	1.3	1.6	7.1	2.6	62
Ctenidae	*Isoctenus*	0.8	2.4	2.9	3.8	2.6	61
Theridiidae	*Episinus*	6.4	1.3	2.2	0.9	2.6	61
Theridiidae	*Theridion*	9.2	0.2	0.1	1.9	2.5	59

Multivariate Analysis

The ordination (Stress = 0.12, Fig. 2) shows the stages of both localities arranged along the first axis. Especially the younger stages (H, A) are well separated from each other and from the older stages, with the exception of one herbaceous site in Cachoeira. A much higher variability of the youngest (H) stage is obvious. Sites of the two older stages (M, F) ordinate close to each other. Sites at the two localities Itaqui and Cachoeira separate along the second and third axis. Although the nMDS is based on Bray-Curtis distances, which are more biased to dominant species than the NESS measures, the ordination visualizes the same differences between sites than the NESS values (Tables 6, 7, 9). Several genera (mainly orb- and sheet-weavers, some anyphaenids) characterized the youngest herbaceous stage, whereas the older stages grouped apart from the younger by pholcids (*Mesabolivar* spp.), the anyphaenid genus *Patrera*, the uloborid genus *Miagrammopes* and the theridiid genus *Spintharus*. The nMDS ordination was confirmed by a Permanova analysis. The four stages showed highly significant differences concerning their composition of spider assemblages ($F = 2.34$; $P = 0.0007$).

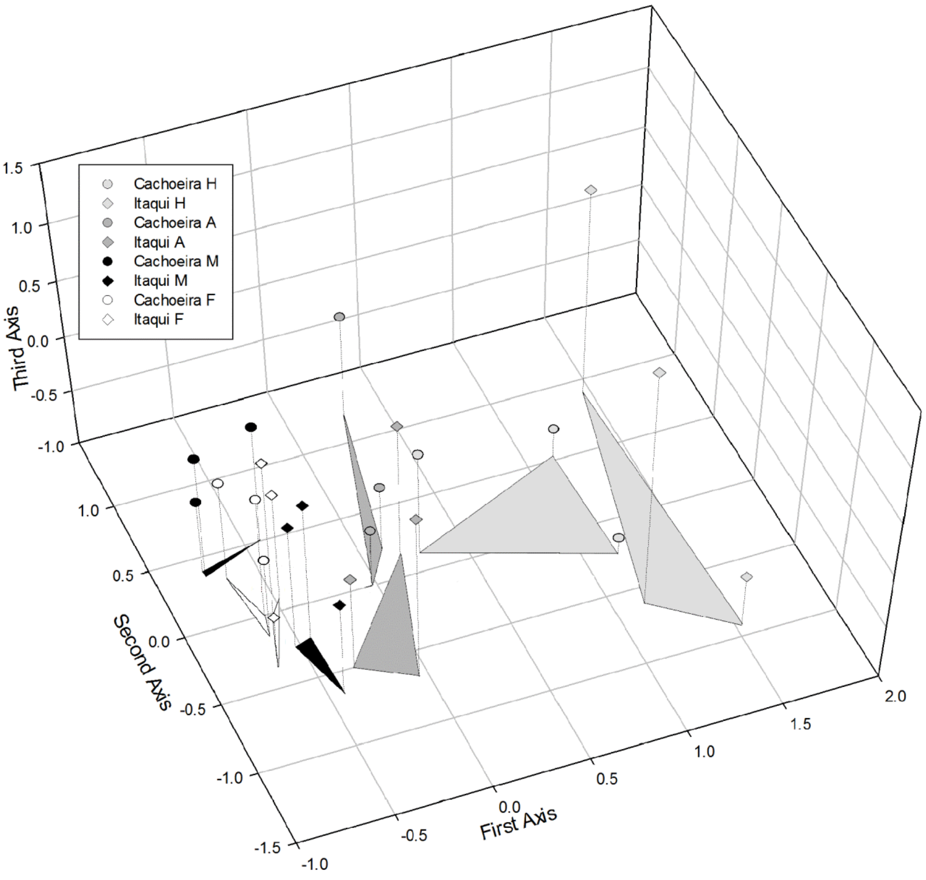

Figure 2. Three-dimensional representation of a non-metric multidimensional scaling analysis (nMDS), based on Bray-Curtis distances; generic data pooled from all methods and sites in Cachoeira and Itaqui and square-root transformed (stress = 0.12).

Functional diversity

Weavers were more abundant than hunting spiders in all stages (62/38% - 56/44%), with the exception of the young arboreal stage (49/51%). Most spiders (40%) belonged to the diurnal space-web weavers, and these were more abundant in the herbaceous stage than in the older ones. 21% were ground runners, most abundant in the young arboreal stage and less in the herbaceous. Spiders known to be diurnal dominated the collections with 44% of all individuals, while nocturnal spiders accounted for 20%. The portion of diurnal spiders decreased with the age of the stages from 53 to 41%. In older forests distinctly more orb weavers (e.g. near the ground), sedentary sheet-web weavers and nocturnal ground ambushers (i.e. ctenids) were caught than in the younger stages. Ground runners were most abundant in the more open young arboreal stage (due to a higher portion of lycosids). The number of guilds in the stages was nearly equal, but the diversity of guilds seems to increase from the young herbaceous to the old forest stages (Table 12).

Indicator analysis

Indicators of single stages were weak, so the two younger (H + A) and the two older (M + F) stages were pooled to show a clear separation by the genera (Table 13). *Spintharus* and *Miagrammopes* showed high indicator values for the older forest stages, whereas *Anodoration* and *Titidius* were indicatory taxa for the younger forests. The same genera fitted best to the nMDS ordination space, but species arrows are not shown in Figure 2 for legibility.

Table 12. Guild structure of the spider assemblage in the four stages, data of both localities and all methods pooled. Taxa assigned to guilds following Dias (2010) or Höfer and Brescovit (2001) [a].

Guild	**Stages**				**Assigned families (genera)**
	H	**A**	**M**	**F**	
Diurnal aerial ambushers	32	46	34	19	Thomisidae, Philodromidae
Diurnal aerial hunters	5	4	2	1	Miturgidae 2 (*Radulphius*), Oxyopidae
Diurnal ground runners	1	0	0	0	Liocranidae
Nocturnal aerial ambushers	2	2	0	1	Hersiliidae, Sparassidae,Trechaleidae
Nocturnal aerial hunters	77	37	68	46	Anyphaenidae, Scytodidae, Corinnidae
Aerial runners	91	101	121	110	Salticidae, Mimetidae
Nocturnal ground ambushers	13	29	39	49	Ctenidae, Nemesiidae
Nocturnal ground hunters	10	15	20	12	Salticidae 2 (*Asaphobelis*), Oonopidae, Palpimanidae, Caponiidae, Zodariidae, Prodidomidae
Ground runners/Nocturnal ground hunters	34	13	0	20	Lycosidae 1, Gnaphosidae
Ground runners	111	276	251	224	Miturgidae 1 (*Teminius, Strotarchis*), Zoridae
Diurnal ground orb weavers [a]	3	8	5	25	Mysmenidae, Symphytognathidae
Diurnal space-web weavers	487	374	460	459	Dictynidae, Linyphiidae, Synotaxidae, Theridiidae, Nesticidae
Nocturnal ground weavers [a]	12	2	20	12	Deinopidae, Dipluridae, Titanoecidae, Anapidae, Hahniidae
Nocturnal space web weavers	1	2	4	7	Ochyroceratidae
Sedentary sheet weavers [a]	16	54	58	97	Pholcidae and Pisauridae 2 (*Architis*)
Orb weavers	103	65	138	154	Araneidae, Tetragnathidae, Theridiosomatidae, Uloboridae
Shannon Index H	1.75	1.83	1.87	1.94	
Evenness E	0.64	0.68	0.69	0.72	

Table 13. Indicator analysis of the vegetation-bound spiders (beating tray data): O = older stages (M & F); Y = younger stages (H & A).

	Cluster	Indicator value	Probability
Spintharus	O	0.82	0.003
Miagrammopes	O	0.82	0.003
Patrera	O	0.76	0.002
Mangora	O	0.69	0.007
Thallumetus	O	0.67	0.003
Mesabolivar	O	0.63	0.041
Faiditus	O	0.50	0.013
Chrosiothes	O	0.42	0.043
Onoculus	O	0.42	0.043
Anodoration	Y	0.92	0.001
Titidius	Y	0.77	0.003
Hetschkia	Y	0.59	0.027

Discussion

According to the project's approach, we put time and effort in the use of replicates to allow for a statistical analysis of biodiversity patterns of spiders in secondary forests rather than to attempt to inventory the entire spider assemblage. We therefore did not undertake special effort to sample cryptic, specialized or rare species, but rather used an accepted and widely used protocol to sample the spider assemblage on the ground and the lower vegetation. By doing so we also made our samples per site comparable within our study and to other studies in the Neotropics. Due to difficulties in identifying the species and to avoid a biased result by wrong morphospecification of the (partly undescribed) tropical species, we based our richness measures and estimates on genera. According to other studies genera serve as a reliable base for evaluating the species richness (Baldissera et al., 2008; Bihn et al., 2010).

The temporal distant sampling of the two localities obviously had no effect on any of the analyzed variables (total number of individuals, genera, families; ratios female/male and adult/juvenile). The absence of autocorrelation in the dataset indicates that neither the temporal distance of the two sampling campaigns nor the spatial distance between the two localities had significant effects on the sampled spider assemblages.

Shortcomings in the methods, sampling protocol and identification could have masked differences in richness between the stages. Most probably, old-growth forests offer more specific microhabitats (e.g. in bromeliads or dead wood) for specialized, cryptically living or rare (less abundant, not widely distributed, not active during the whole year) species. These species cannot be sampled by either strongly vision-based sampling or beating the well accessible lower vegetation (Dias et al., 2000; Rinaldi et al., 2002). Thus, to assess and evaluate the diversity of complex habitats such as an old-growth forest in an unbiased way, more effort might be necessary using special sampling techniques for specialized species. It might even be questionable whether the studied old-growth sites, although not strongly altered by humans, were suitable as a reference instead of primary forests. They could have obscured differences between stages or a directed succession, being an "old-growth successional state" in itself. The lack of any native earthworm species in the investigated sites and the high dominance of the invasive species *Pontoscolex corethrurus* in all, even the oldest forest sites (Römbke et al., 2009) at least shed some light on the long history of anthropogenic influence in the region.

Notwithstanding these possible constraints, our survey of spiders revealed a high richness at the genera and species level when compared to other studies in the realm of the Atlantic Forests. Some of them, however, had sampled in urban parks, plantations or small forest fragments (Benati et al., 2005; Candiani et al., 2005; Oliveira-Alves et al., 2005; Rinaldi & Ruiz, 2002). Comparably high richness values were recorded by Brescovit et al. (2004), Baldissera et al. (2008), Podgaiski et al. (2007) for Atlantic forests and Ricetti & Bonaldo (2008) for Amazonian forests. The differences in both sampled and estimated alpha-diversity values between sites (of all types) and also between the two sampled reserves of our study were low and not significant. Even the youngest successional stages in the study area house a considerable diversity of spiders. This is not unusual, because such habitats often show high structural heterogeneity, prey availability and ecotone characteristics, which increase species numbers (Baldissera et al., 2003; Kotze & Samways, 1999; Pétillon & Garbutt, 2008; Platen, 2006).

Interesting is the high turn-over of species between all sites, independent of the stage. Stages differ in their species composition, not in richness. Variability within the *a-priori* defined stages originates from the heterogeneity of structural and microclimatic conditions (openness, plant density), which in all stages is based on physical and pedological heterogeneity (exposition, inclination, soil type, groundwater level). The higher variability within the youngest stage (visible in the ordination) is probably caused by differences in the historical (largely unknown) land use (e. g. the use of machines, fertilizers or pesticides), which mainly influences early succession. During further succession, differences in biotic (prey availability, structure) and abiotic (climate) habitat parameters within and between the stages appear to decrease. An experimental manipulation of food and structure in one arboreal stage and the old-growth forest suggested food limitation of the decomposer fauna, but also revealed no effect of food or structure or any influence of stage on the spiders (Raub et al., 2014). Spiders are mostly generalist predators and seem to adapt easily to different food conditions and prey types (Uetz, 1992), as long as suitable habitat structures and climate are provided. Baldissera et al. (2008) also found no differences in family, generic and species composition of the spider assemblages of natural *Araucaria* forest fragments and *Eucalyptus* monocultures, when appropriate habitat structures where provided.

Richness in our sites is comparable to other studies in Atlantic forests (see above), but some studies showed a different (family) composition of the assemblages (Rinaldi & Ruiz, 2002; Rinaldi et al., 2002) and also significant differences in richness between young secondary and old-growth forest sites (Pinto-Leite et al., 2008; Uehara-Prado et al., 2009). We assume such differences to be caused by different usages of the sampled areas, for example the use of pesticides or heavy machinery, and by the influence of the matrix of a forest fragment (see above).

Studies from tropical forest regions in Brazil (i.e. in the Amazon) revealed distinctly lower species richness of spiders in anthropogenic altered landscapes with forest patches in comparison to a continuous forest cover (Lo-Man-Hung et al., 2011). However, as shown by Rego et al. (2005), taxa-specific responses can also lead to opposite responses in Neotropical forest fragments. High spider richness in the younger secondary sites should be regarded carefully in the context of conservation issues and not be taken as an absolute measure of habitat quality. Other investigated invertebrate groups in the same area showed an increase in richness along the successional gradient (Bihn et al., 2008b; Hopp et al., 2010).

The use of indicator taxa is becoming more and more important in the context of the growing anthropogenic pressure on highly diverse and threatened tropical ecosystems. For the evaluation of the conservation potential and state of secondary and old-growth tropical forests, precise but quick and cheap tools such as indicators are needed (Uehara-Prado et al., 2009). However the use of indicator taxa in the evaluation of ecosystems is a controversial topic, especially because of the indirect effects in food webs (Abrams et al., 1996) together with the lack of knowledge of the interrelations between the taxa. Therefore a multi-taxon approach with a carefully selected set of organisms (Cabra-García et al., 2012; Kotze & Samways, 1999) should be used. Nonetheless, the results of our indicator analysis can be used for evaluations of secondary forest areas in the southern Mata Atlântica region. The identified genera can serve as indicator taxa for the evaluation of priority areas for forest conservation. For future evaluations they should be combined with the outcomes of other arthropod studies (Bihn et al., 2008b; Hopp et al., 2011; Ottermanns et al., 2011) and also ecological traits should be included to establish a reliable multi-taxon approach for the implementation of conservation strategies (Kotze & Samways, 1999; Uehara-Prado et al., 2009).

Recovery of (species) richness can be relatively fast. Dunn (2004) reported a time span of 20-40 years for ant and bird richness recovery, which is comparable to the age of our medium-aged secondary forests. But the regeneration of the original forest community often needs much more time (Bihn et al., 2008b; Dunn, 2004). Regarding spiders, some forest dwelling Lycosidae still do not seem to find adequate habitat in the oldest secondary stage. We therefore assume that mature secondary forests can host a highly diverse spider community, but do not serve as surrogate habitats for all old/primary forest dwelling genera (species). A classification of forests by the diversity and structure of spider assemblages would separate young (< 20 years) from median to old forests (> 30 years), in good accordance with results on beetles (Hopp et al., 2010), but not on ants (Bihn et al., 2008a).

Our study did not show a succession of the spider diversity from species-poor young secondary vegetation towards a species-rich old-growth fauna, but rather a turnover of spider genera along the successional gradient, strongest between the two young and the two older stages, i.e. between an age of 20-30 years. We interpret the high alpha diversity and turnover between sites of the same stage as an expression of a rich regional spider fauna, maintained by the mosaic landscape of forests of different ages and mainly stochastic processes in the establishment of spider assemblages in early successional stages. Our study region presents a highly diverse mosaic texture with large patches of old-growth forest acting as refuges for spiders (Rodrigues et al., 2009), never far away even from the youngest secondary stages. This variation in vegetation complexity and the large set of microhabitats provided is able to host highly diverse spider assemblages (Ricetti & Bonaldo, 2008). We assume that ideal preconditions for colonization and repopulation of secondary habitats have been met in the region. Spiders survived the deforestation and fragmentation of the coastal forests in Paraná due to the constant availability of retreat habitats for a later resettlement.

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Appendix – Supporting Material Chapter 2: Morphospecies list of adult spiders captured in the forest stages of the two reserves Cachoeira and Itaqui (specimens from all methods and replicate sites pooled). Page 94 ff

3 – Conserving landscape structure - conclusions from the partitioning of spider diversity in southern Atlantic forests of Brazil.

with Hubert Höfer, Ludger Scheuermann, Ricardo Miranda de Britez, Roland Brandl, Published in Studies on Neotropical Fauna and Environment, 2015

Abstract

In the Atlantic Forest in Brazil, where no more primary forests exist, the value of secondary forests for biodiversity conservation is becoming more and more important. We studied the spiders in a relatively well preserved region of the Mata Atlântica, where the matrix of the landscape is still forest. We addressed the contribution of different spatial levels including forest stages to total diversity and analyzed the patterns by additive partitioning of beta diversity on genus and morphospecies level and for different sampling methods. Beta diversity was strongly based on turnover, not on gain/loss. All spatial levels (sample, stage, area, locality) contributed more to beta diversity than expected, without stronger influence of stage. Patterns were consistent for both identification levels and all methods. We conclude that in this landscape the protection of large areas encompassing all forest stages, without special attention to old-growth, is the best way to conserve the regional species richness.

Introduction

Secondary forests are becoming ever more important for biodiversity conservation (see debate summarized in Bihn et al., 2008) although their specific contribution (value) – i.e. which part of the diversity they house – is not always known (for the region and the taxon; Barlow et al., 2007; Gardner et al., 2007). This is especially true for the Brazilian Mata Atlântica (Ribeiro et al., 2009), a region regarded as “one of the hottest biodiversity hotspots” (Laurance, 2009) of the world, due to the high degrees of species richness and endemism, but also forest loss and fragmentation. Anthropogenic impact started early here in comparison with Amazonia and some of the biggest cities of Brazil (São Paulo, Rio de Janeiro) are situated in this region.

Matrix permeability is a key connectivity component (Fonseca et al., 2009). In the Atlantic Forest, small forest fragments (< 50 ha) are very important, because they constitute the largest fraction of the remaining forests (> 80% of all patches, but not area) and are essential for connectivity (Kauano et al., 2012; Ribeiro et al., 2009). Clusters of neighboring fragments (< 200m distance) that form large tracts of forest (> 50,000 ha) are common and form important potential mosaics for conservation (Ribeiro et al., 2009).

Our study concerned the best preserved and less fragmented biogeographic subregion of the Atlantic Forest, at the flanks and base of the mountain ridge (Serra do Mar) in the Environmental Protection Area (EPA) Guaraqueçaba (Kauano et al., 2012). This protected area comprises 83% of forests in different successional stages, of which 73% are Submontane Forest (slopes) and 27% are Lowland Forest. The remaining 17% of the EPA consist of pastures, grassland, anthropogenic areas, beach and water. Slopes were even less fragmented and better preserved than lowlands (Kauano et al., 2012). The studied sites are located in a landscape mosaic of differently sized forest patches resulting mainly from the regeneration of forest from abandoned (buffalo) pastures under a restoration and conservation program of the Brazilian non-governmental organization (NGO) SPVS (Society for wildlife research and environmental education) (Ferretti & Britez, 2006). Secondary forests of different successional stages are in this region embedded in a forest matrix with a still high presence of large forest patches (Kauano et al., 2012), compared to the rest of the Atlantic Forests (Ribeiro et al., 2009). All studied sites were surrounded or at least neighbored by forest, often with old-growth forest within a small distance.

To study the effect of land-use change in biological communities it is necessary to understand how the different components of diversity are distributed in space (Cardoso et al., 2009). For a regional conservation strategy it is most important to know which site or stage should have priority and if protection of old-growth (source areas) should have priority over restoration efforts (Rodrigues et al., 2009; Scarano 2009). Under these aspects a multi-taxon study was undertaken by the Brazilian-German cooperation project SOLOBIOMA from 2003 to 2009 (Höfer et al., 2007, 2011).

Important questions of the SOLOBIOMA project were:

(1) Is there a directional change in species richness or species composition (**turnover**) from younger to older stages, e.g. a succession paralleling the succession during the restoration of forest in the region?

(2) By how much does the number of species in the region exceed the average number of species per sampling? How large is the **variation** in species in different stages and two localities (reserves)?

In this respect the relative contribution of stages (especially old-growth) and the change among the two reserves in the richness/diversity of the region are of special interest.

Spiders are an abundant and species rich group in forests. They contribute considerably to the overall diversity and represent a well-studied taxon even in the Neotropics, sharing broadly similar community responses to land-use change with other species-rich taxa (Barlow et al., 2007). As predatory arthropods and mostly generalists, they occupy an important position in the food web and respond to environmental changes making them potential bioindicators (Cardoso et al., 2004; Scott et al., 2006). Several studies have shown their influence on decomposition dynamics and on plant community structure by mediating herbivore abundance and feeding (Griffiths et al., 2008; Lawrence & Wise, 2004; Pringle & Fox-Dobbs, 2008; Schmitz, 2009). This is why they are often included in experimental studies of trophic interactions and effects on ecosystem functioning, e.g. with respect to bottom-up (Chen & Wise, 1999; Raub et al., 2014a; Scherber et al., 2010) as well as top-down effects (Lawrence & Wise, 2004). However, there seem to be differences between (species poor) temperate and (species rich) subtropical and tropical forests (Raub et al., 2014a; Schuldt et al., 2011).

We aimed to sample a considerable portion of the spider diversity present in the different stages of forests in the two protected areas in the region. This species richness is to be conserved for its function in the existing systems and also as a source for colonization of "new forests", planted by the NGO SPVS or emerging by natural regrowth, both undergoing a succession during decades. It is difficult to differentiate between old-growth and secondary forest in the entire Atlantic forest region (Ribeiro et al., 2009) and also in the study region.

For an inclusion of invertebrate taxa in future conservation management planning it also seemed important to check at least for exemplary or surrogate taxa whether the used classification of forests based on the combination of age and vegetation is of equal relevance for arthropods and also how much work (for sampling and identification) must be invested for these groups.

We expected a directional change of richness along the age/vegetation gradient based on more structural diversity (vegetation) and bottom-up effects through the food web. In ants, genus richness (as a surrogate for species richness) increased with successional stage (Bihn et al., 2008); likewise the beetle species density increased (Hopp et al., 2010), but not spider species density (Raub et al., 2014b). For spiders however, we observed a strong turnover (exchange of genera/species) starting from a high alpha diversity in all forest types, with higher variance in the youngest stages. The a priori classified stages could be differentiated and for older forests as well as younger forests some indicator species were found (Raub et al., 2014b). So it seems that the hitherto used classification is a valid approach for invertebrate diversity and conservation agencies could use these classes (stages) for planning efforts. However, a deeper understanding of biological mechanisms acting during natural succession or anthropogenic restoration would be helpful in deciding upon protection of specific sites, selection of sites for restoration, necessary management activities and large scale planning of conservation, especially with restricted resources and the ongoing pressure of forest use.

Due to our sampling design we were able to calculate alpha (assemblage) diversity, beta diversity (turnover or degree of difference between assemblages) and gamma (regional) diversity for the lowland forest ecosystem. Recognizing the relationship between the alpha and beta components of diversity at multiple scales can help to understand the processes that control diversity over the whole range of scales (Loreau, 2001). We wanted to infer biological mechanisms from the patterns of species occurrences, to understand the relative contribution of alpha (within-community) and beta (between-community) components of diversity to the total regional (gamma) diversity. Objectives of the study were:

(1) To compare the patterns resulting from additive partitioning on genus and morphospecies bases to reveal whether genera can serve as surrogate for species.
(2) To compare the patterns resulting from the different methods to reveal if they are similar and decide on the best method and its use:
    (a) number of sites (areas)
    (b) relative contribution of methods (different strata, activity based sampling versus not activity based sampling).
(3) To interpret the patterns with respect to the project questions. How is regional diversity distributed? Which level contributes most: area (the number of sites of the same stage, i.e. an increase in sampled area), stage (forests of different age and with different vegetation structure and diversity within an area), or the expansion of the study to another reserve (locality under biogeographic influence, different climatic conditions and mosaic structures).
(4) To draw conclusions for priorities in conservation management and environmental protection planning in the region.

Materials and Methods

Study area

The study was conducted in the coastal region of the Paraná state in southeastern Brazil. The regional climate there is humid subtropical (Köppen´s Cfa, Strahler & Strahler, 2005), with mean temperatures between 16.2°C in July and 24.5°C in February (IPARDES, 2001). Average precipitation ranges between 2000 and 3000 mm year-1 (Roderjan & Kunyoshi, 1988). Rainfall is more or less evenly distributed throughout the year, although with some seasonality (low rainfall from April to August). Originally the region was covered by dense ombrophilous lowland and submontane forests (Veloso et al., 2012), but these ecosystems were largely converted to buffalo pastures up to the 1980s. After that, the logging practically stopped and during recent years most of the pastures and other used areas were abandoned (IPARDES, 1995).

In 1999 the Brazilian NGO SPVS started an ecological restoration program (Ferretti & Britez, 2006) and created the two private nature reserves (RPPNs) "Reserva Natural do Rio Cachoeira" and "Reserva Natural Serra do Itaqui" (Cachoeira: 25.3142°S, 48.6958°W; Itaqui: 25.2733°S, 48.4872°W; WGS84) with areas of 8600 and 6700 ha, ranging from sea level to elevations of 700 m asl. They are part of the Environmental Protection Area (EPA) Guaraqueçaba and belong to the Mata Atlântica Biosphere Reserve thus forming part of a larger mosaic landscape (Figure 1). The municipal area of Guaraqueçaba (2020.093 km²) is sparsely populated with around four habitants per square kilometer and the local population mainly depends on subsistence agriculture (by slash and burn) and forestry (Antonelli Filho & Antunes Ferreira, 2012). These practices (mainly before 1970) configured a landscape with a mosaic of small open areas of less than one hectare. Due to economic constraints the agricultural use is constantly decreasing since the logging stopped and due to the (planting and protecting) activities of the SPVS and the abandonment of agricultural use, the two reserves themselves today represent a patchy landscape of small open areas and secondary vegetation in a forest matrix.

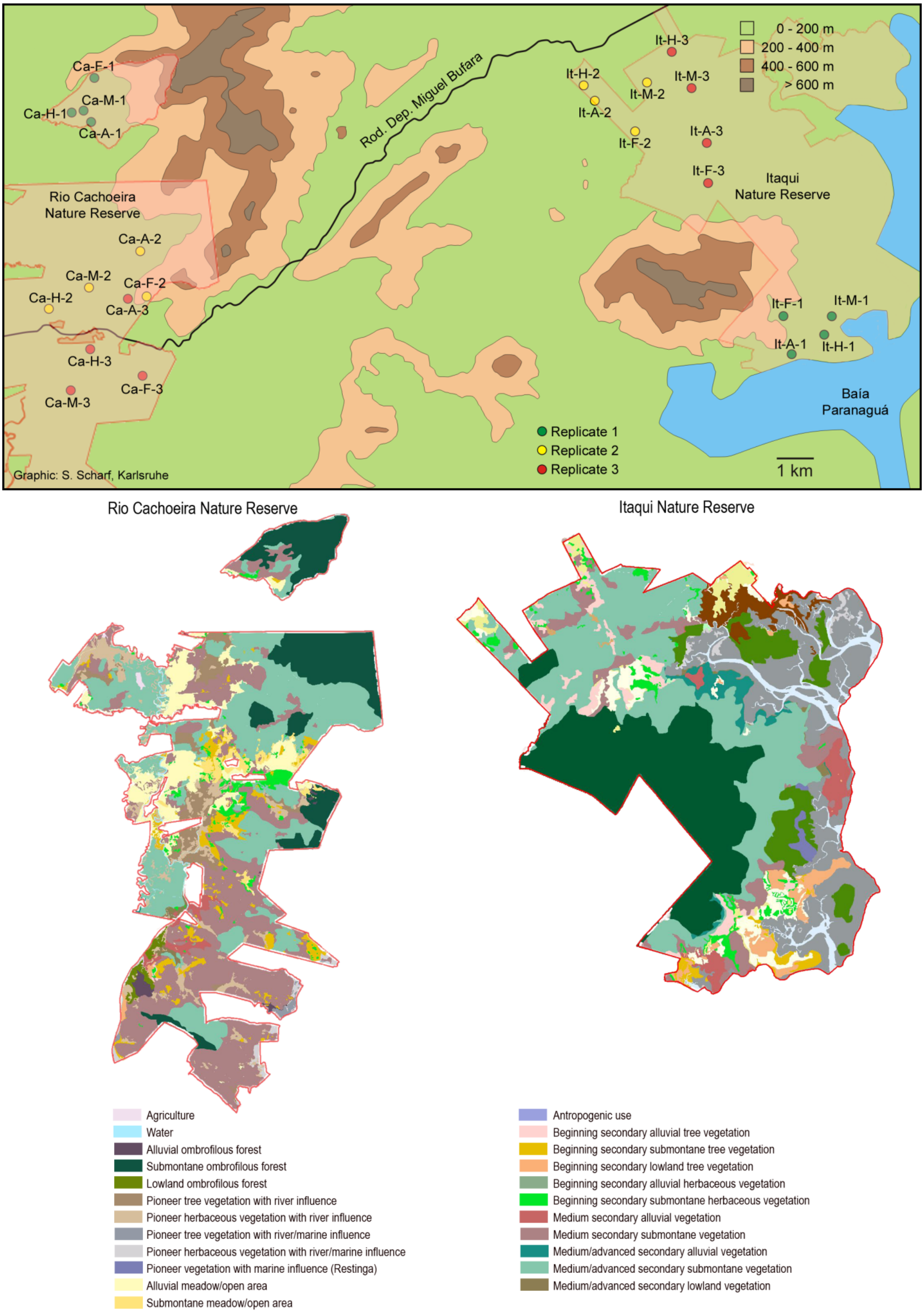

Figure 1. Location of the Sampling sites in the two Nature Reserves Rio Cachoeira (Ca) and Itaqui (It) (upper part) and vegetation types of the Reserves (lower part). Vegetation maps provided by the SPVS

The reserve areas comprise 20 different terrestrial vegetation and land use types (for Brazilian land use classification see Roderjan & Kunyoshi, 1988) with portions of less than 1% up to 28% of the overall area (Figure 1) of which the different successional stages (from pasture to forest) were categorized a priori by the SPVS using age and vegetation structure, based on orthophotographs from 1952, 1980 and 2002 and knowledge of residents on historical use. The herbaceous stage (H) is characterized by herb-rich secondary regrowth of 5-8 years with few small trees of one or two pioneer species (IPARDES, 1995). The arboreal stage (A) with a stand age of 10-15 years is characterized by a tree layer of few species with an initial, but low and still translucent canopy closure and the lack of a well-defined stratification, still with a dense herb layer near the ground (IPARDES, 1995). In contrast, the medium stage (M) is an advanced secondary forest of 35-50 years with a higher tree diversity (IPARDES, 1995; Schmidt et al., 2008), some large trees and an already nearly closed canopy resulting in insufficient light on the ground for a pronounced herbaceous layer. Finally, the old-growth stage (F) appears as a mature, species-rich forest older than 100 years, with several large and tall trees and without visible anthropogenic influence. Here the canopy is high and closed and undergrowth vegetation poor.

Sampling design

In these successional stages the spiders were sampled in 24 sites (30 m x 50 m) based on a fully orthogonal hierarchical design with three spatial levels: locality (two reserves, *c*.25 km apart), area (thee areas, nested within each locality, originally defined by road access, *c*.5-10 km apart) and forest stage (the four stages H, A, M and F, nested within each area, *c*.0.5-3 km apart).

Sampling and sample processing

Sampling was done in springtime (October/November) of 2005 (Cachoeira) and 2007 (Itaqui) and followed a standardized sampling protocol (Coddington et al., 1991; see Raub et al., 2014b) including:

(a) Nocturnal hand sampling. Two (experienced) persons sampled for 1 h at night (with headlights), exploring all structures below (“looking down”) or above (“looking up”) knee level.

(b) Beating. Three persons struck vegetation at any reachable level (i.e. lower vegetation) with a stick, collecting the spiders falling on a 50 x 50 cm tray held below, for 1 h. Twenty beating points made one sample.

(c) Pitfall trapping. 10 traps per site were installed to capture active ground spiders for one week. Traps were 330 ml PE cups with an opening diameter of 7.5 cm, filled with 100 ml of 4% formaldehyde solution and protected against rain by transparent plastic plates.

The sampled spiders were stored in 75% ethanol. All adult spiders were determined to (morpho-) genera or to (morpho-) species, further called recognizable taxonomic units (RTU) (see list in Raub et al., 2014b). Identification was done by the first and third author with help from Brazilian experts at Butantan Institute (São Paulo, Brazil, IBSP) and Museu de Ciências Naturais da Fundação Zoobotânica (Porto Alegre, Brazil, MCN). Voucher material was deposited in the collection of the entomological department of Universidade Federal do Paraná in Curitiba, Brazil (UFPR) and of IBSP and MCN.

Data analysis

We calculated species richness and abundance-based diversity measures for the entire sample and separately for the two localities (reserves), the three areas and the four stages: for each case pooled from all methods and separated by method. For direct comparison we used sample-based rarefaction and computed the corresponding individual-based Coleman curves (Gotelli & Colwell, 2001) with EstimateS 8.0 (Colwell, 2005).

We decomposed beta diversity (β_{cc} = Jaccard dissimilarity; Colwell & Coddington, 1994) into β_{-3} (dissimilarity due to species replacement) + β_{rich} (dissimilarity due to richness differences, species gain/loss) to evaluate the relative role of these components in generating the beta diversity patterns. Both β_{-3} (see Cardoso et al., 2009; Carvalho et al., 2013) and β_{rich} (Carvalho et al., 2013; Schmera & Podani, 2011) are supposed to be robust to undersampling (Cardoso et al., 2009).

We also decomposed beta diversity measures (Hill numbers: genera, morphospecies, exponential of Shannon, inverse Simpson) additively. Additive partitioning was done with the R 3.0.2 (R Development Core Team, 2009) function adipart of the package vegan 1.17-2 (Oksanen et al., 2009) using:

a) genus and RTU level;
b) three diversity measures: richness (all RTUs equally weighted), Shannon index (more weight to the more common species by the logarithm) and Simpson index (the dominant species are heavily weighted by squaring);

c) randomization on the individual basis to test the observed diversity pattern against the null hypothesis of random distribution of individuals;
d) the individual sample as the lowest level;
e) the data sets of the different sampling methods pooled (method as partitioning level) and also the methods separately.

The function *adipart* tests the statistical significance of observed level-specific alpha and beta to differ from the estimates based on a random distribution of individuals among higher level samples through randomization procedures.

We further calculated the multiplicative beta of the richness to quantify the effective number of completely distinct assemblages in comparison to the sample value of a partitioning level to get a measure of relative differentiation among assemblages.

Results

In total, 11,293 spiders with 4495 adults were sampled. Rarefaction curves for pooled data from all methods and stages are flattening and show only small differences between the two reserves (Figures 2, 3). The completeness for genera was 74% with observed genus richness between 81 and 89 and estimated richness (Chao 2) between 103 and 124 in the different stages.

In both reserves the youngest stage showed the highest genus richness (Figures 4, 6) with nearly 90 genera in stage H, compared to around 70 genera in stage F (rarefied for 450 individuals). At RTU level, the differences between stage H and F get smaller, especially in Itaqui, where all stages were very similar to each other in richness (Figures 5, 7). The youngest stage H is not the most species rich in Itaqui and confidence intervals strongly overlap between stages of adjacent age (Figures 4-7), illustrating the lack of significant differences. The curves of the different stages for each locality (Figures 4-7) are distinctly steeper than the curves from pooled data (Figures 2, 3).

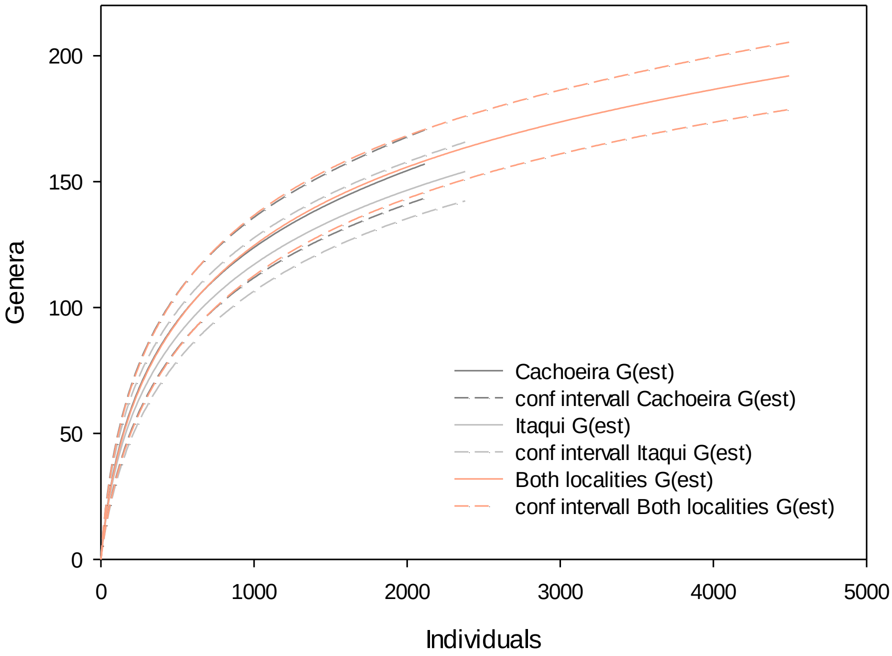

Figure 2. Genus richness (sample-based rarefaction, rescaled to individuals, G(est)) for Cachoeira and Itaqui, data from looking up, looking down, beating tray and pitfall traps as well as all forest stages pooled.

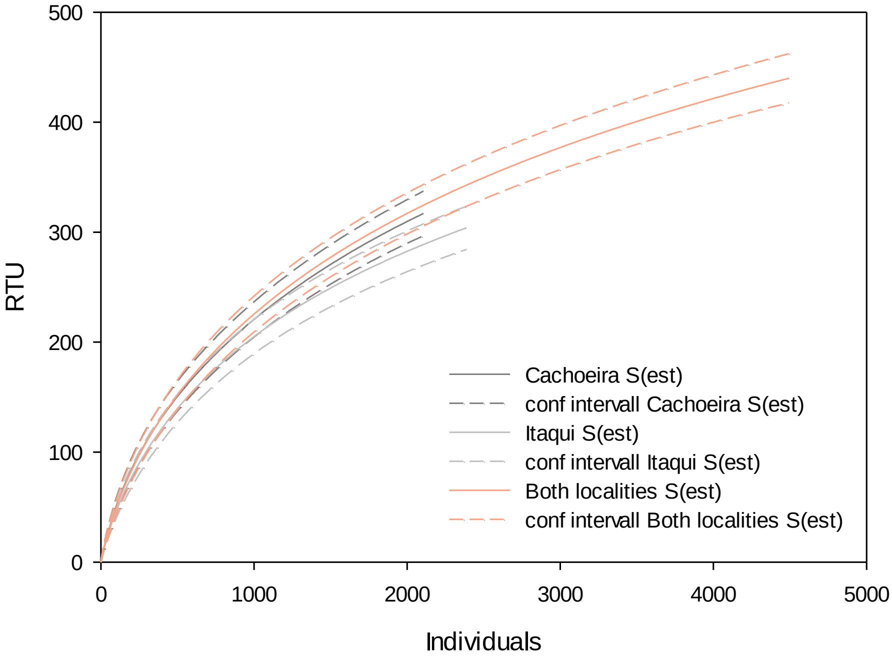

Figure 3. Recognizable taxonomic unit (RTU) richness (sample-based rarefaction, rescaled to individuals, S(est)) for Cachoeira and Itaqui, data from looking up, looking down, beating tray and pitfall traps as well as all forest stages pooled.

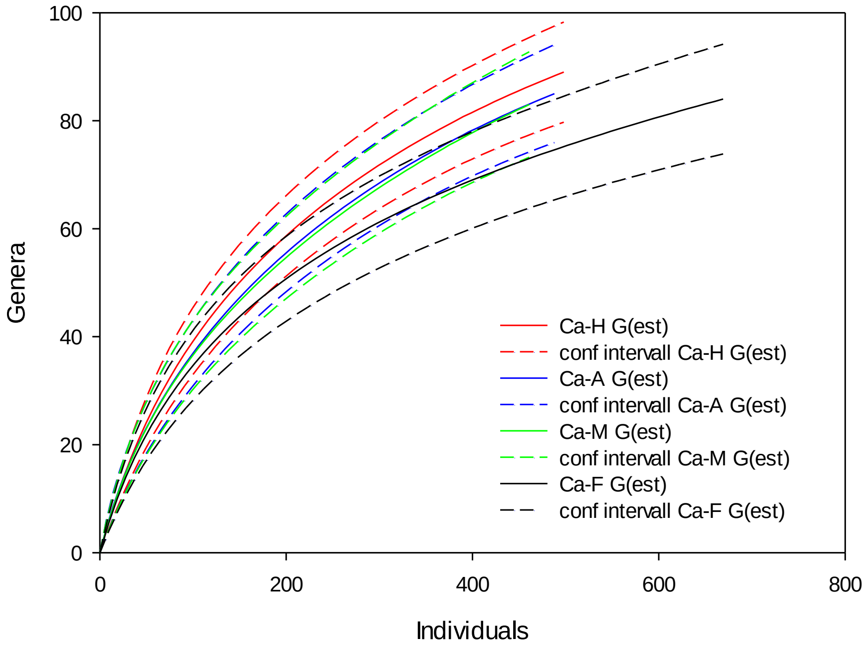

Figure 4. Genus richness (G(est), sample-based rarefaction, rescaled to individuals) for the stages (H – herbaceous stage, A – arboreal stage, M – medium stage, F – old-growth forest) in the Cachoeira reserve (Ca), data from looking up, looking down, beating tray and pitfall traps pooled.

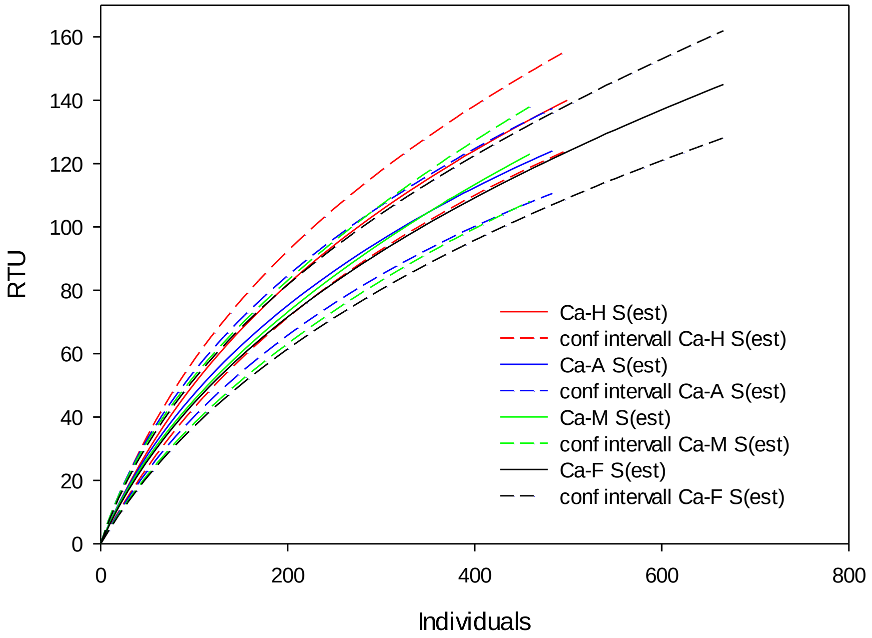

Figure 5. Recognizable taxonomic unit (RTU) richness (S(est), sample-based rarefaction, rescaled to individuals) for the stages (H – herbaceous stage, A – arboreal stage, M – medium stage, F – old-growth forest) in the Cachoeira reserve, data from looking up, looking down, beating tray and pitfall traps pooled.

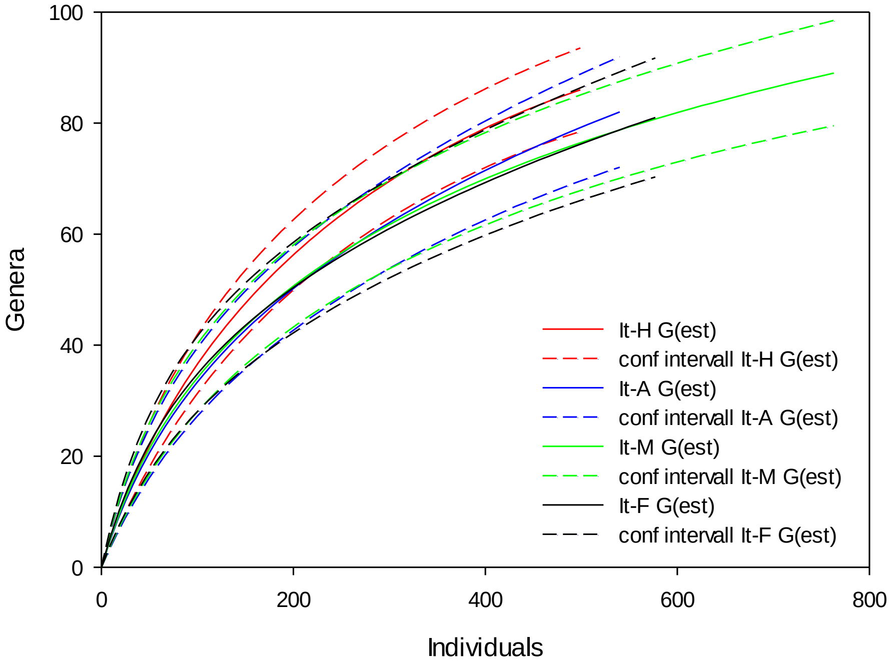

Figure 6. Genus richness (G(est), sample-based rarefaction, rescaled to individuals) for the stages (H – herbaceous stage, A – arboreal stage, M – medium stage, F – old-growth forest) in the Itaqui reserve, data from looking up, looking down, beating tray and pitfall traps pooled.

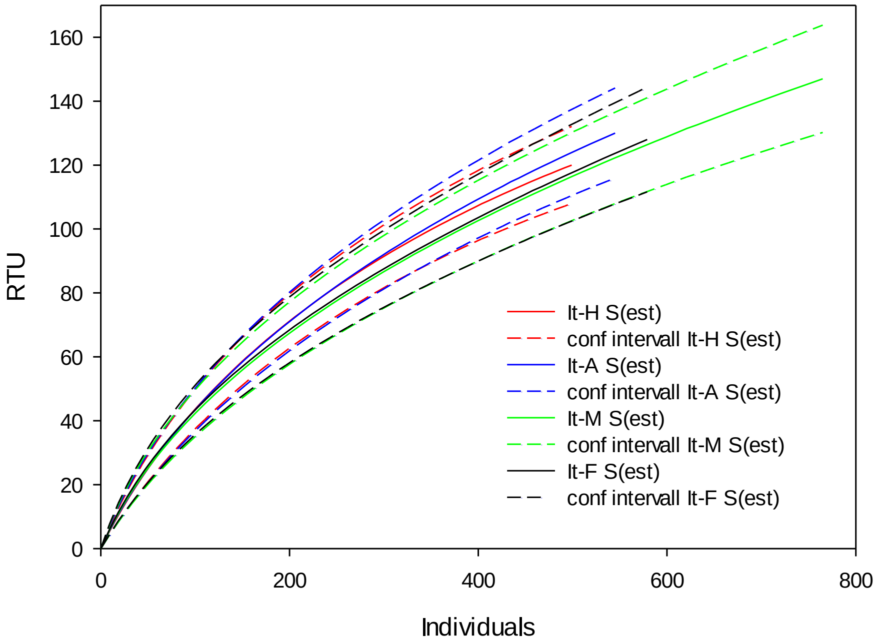

Figure 7. Recognizable taxonomic units (RTU) richness (S(est), sample-based rarefaction, rescaled to individuals) for the stages (H – herbaceous stage, A – arboreal stage, M – medium stage, F – old-growth forest) in the Itaqui reserve, data from looking up, looking down, beating tray and pitfall traps pooled.

General assemblage patterns

Mean observed alpha diversity was 49 genera in Cachoeira and 46 genera in Itaqui and 62 RTUs per site, with no significant differences between stages in both localities. Beta diversity is strongly based on turnover rather than on loss or gain during succession/regeneration (Table 1). The strongest turnover occurs between H and the other stages and there is clearly no gain in richness with increasing age. On RTU level the turnover is even higher, with the same pattern as in genera (Table 1).

Table 1. Beta diversity components (turnover (β_{-3}) = lower left versus gain/loss (β_{rich}) = upper right) for both identification levels Genera and Recognizable Taxonomic Units (RTU) in Cachoeira (Ca, upper part) and Itaqui (It, lower part).

	Genera				RTU			
	90	83	82	84	141	126	124	146
Turn/rich	**Ca-H**	**Ca-A**	**Ca-M**	**Ca-F**	**Ca-H**	**Ca-A**	**Ca-M**	**Ca-F**
Ca-H		0,06	0,06	0,05		0,07	0,08	0,02
Ca-A	0,54		0,01	0,01	0,75		0,01	0,09
Ca-M	0,58	0,52		0,02	0,78	0,70		0,11
Ca-F	0,59	0,59	0,50		0,82	0,73	0,64	
	86	83	90	80	120	128	146	129
Turn/rich	**It-H**	**It-A**	**It-M**	**It-F**	**It-H**	**It-A**	**It-M**	**It-F**
It-H		0,02	0,03	0,05		0,04	0,12	0,04
It-A	0,58		0,00	0,03	0,78		0,09	0,01
It-M	0,60	0,42		0,09	0,81	0,67		0,08
It-F	0,61	0,48	0,38		0,81	0,64	0,63	

H: herbaceous stage, A: arboreal stage, M: medium stage, F: old-growth forest, Turn: turnover, rich: gain/loss

Additive Partitioning

On the genera level deviations from expected values are all negative for alpha diversity and constantly positive for the highest beta level (locality) regarding richness and diversity (Table 2). Area and stage also contribute more than expected by chance to genus richness and diversity. Method contributed less than expected to richness, but more to Shannon and Simpson diversity. Generally, stage does not contribute more than sample and area to the beta diversity. Nearly the same pattern resulted from the identification level of RTU (Table 2 and Figures 8-9), with stage contributing even less than expected to richness. The observed patterns of relative contribution of the different levels of beta diversity appear very constant in the analyses of the different methods (Figure 9).

Multiplicative Partitioning

The average number of genera per sampling site (all methods pooled) was 47. Adding the four different stages at the next partition level resulted in 98.5 genera with a multiplier of 2.1. Further adding the three areas per locality and stage multiplied the number of genera by 1.6 resulting in 155.5 genera per sample unit. From the addition of the two localities a multiplier of 1.23 was calculated (192 genera for the whole region). Thus, the multiplier is always lower than the number of added units per level, meaning that there are not completely different assemblages for every unit.

Table 2. Deviance of observed partitions from expected values by individual-based randomization, for both identification levels Genera and Recognizable Taxonomic Units (RTU) and the different sampling methods.

			Genera			**RTU**		
Method	**Level**	**Among**	**Richness**	**Shannon**	**Simpson**	**Richness**	**Shannon**	**Simpson**
All	ß5	Locality	+	+	+	+	+	+
	ß4	Area	+	+	+	+	+	+
	ß3	Stage	+	+	+	-	+	+
	ß2	Method	-	+	+	-	+	+
	ß1	Sample	-	-	+	-	-	+
	ɑ		-	-	-	-	-	-
Pitfall traps	ß4	Locality	+	+	+	+	+	+
Active	ß3	Area	Ns	+	ns	ns	+	ns
Ground	ß2	Stage	-	+	+	-	+	+
Spiders	ß1	Sample	-	-	+	-	-	ns
	ɑ		-	-	-	-	-	-
Beating	ß4	Locality	+	+	+	+	+	+
Vegetation	ß3	Area	+	+	+	+	+	+
	ß2	Stage	Ns	+	+	-	+	+
	ß1	Sample	+	-	-	-	-	ns
	ɑ		-	-	-	-	-	-
Nocturnal looking	ß4	Locality	+	+	+	+	+	+
At ground	ß3	Area	Ns	+	+	ns	+	+
	ß2	Stage	Ns	+	+	-	+	+
	ß1	Sample	-	+	+	-	ns	+
	ɑ		-	-	-	-	-	-

+ = significantly larger; - = significantly smaller; ns = not significant at the 0.05 level

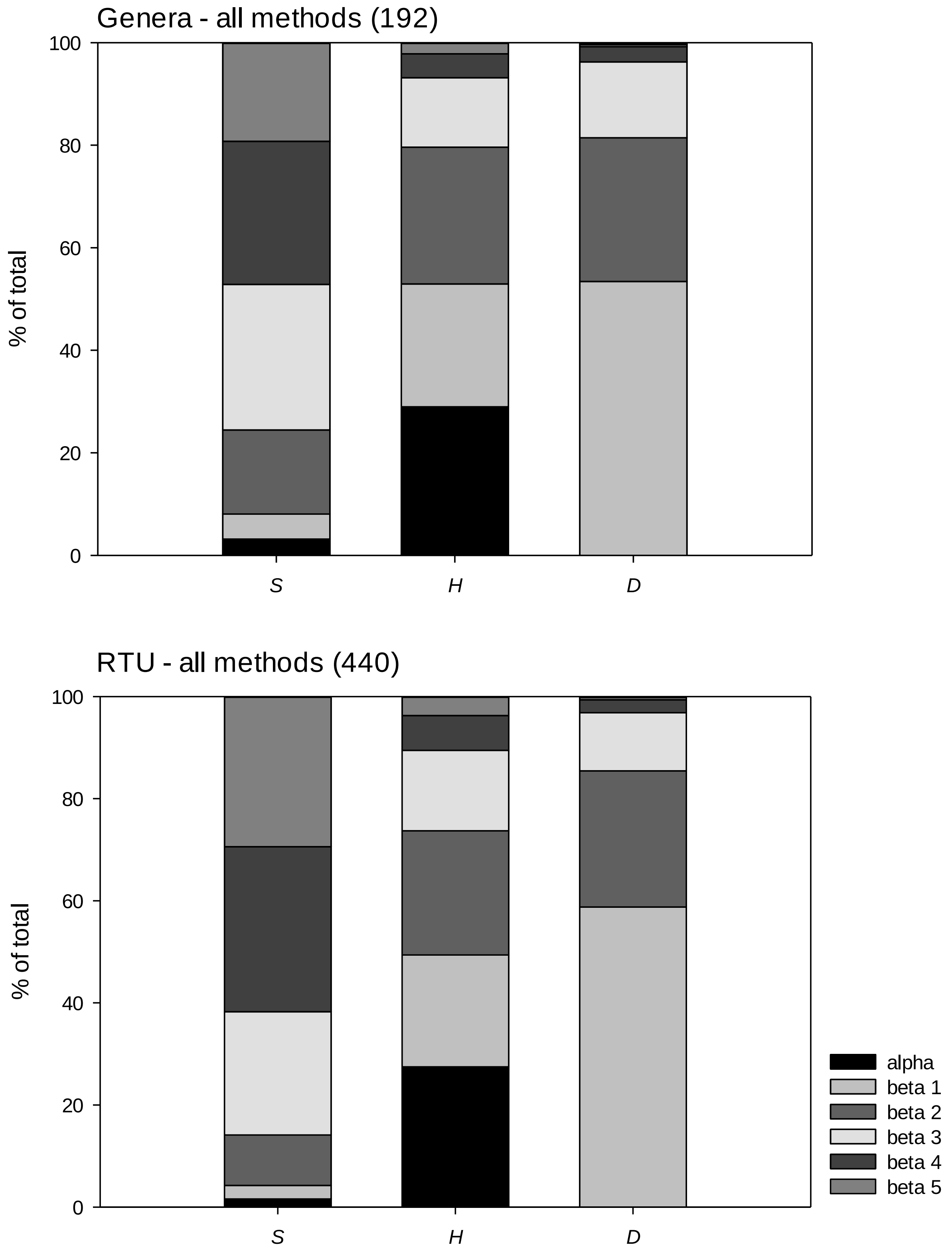

Figure 8. Contributions (in %) to total richness (*S*), Shannon (*H*) and Simpson (*D*) diversity for five spatial scales (all sampling methods included): ß1 samples, ß2 methods, ß3 stages, ß4 areas, ß5 localities, identification levels and total numbers of respective units are given in the titles.

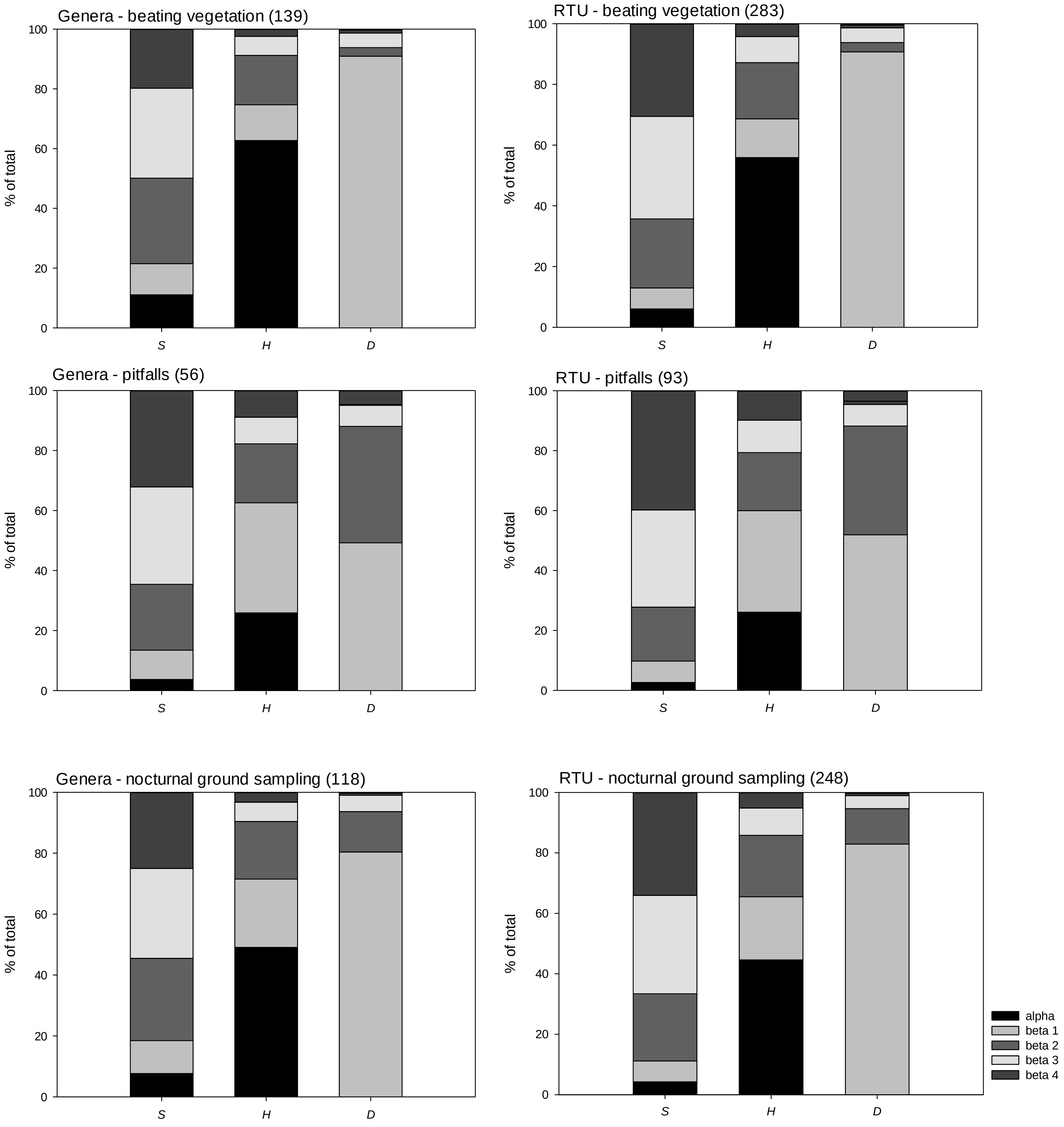

Figure 9. Contributions (in %) to total richness (*S*), Shannon (*H*) and Simpson (*D*) diversity for four spatial scales sampled by beating vegetation, pitfall trapping and nocturnal sampling: ß1 samples, ß2 stages, ß3 areas, ß4 localities, identification levels, the sampling method and total numbers of respective units are given in the titles.

Discussion

Richness and diversity

In a rough comparison with inventories from forests in the Neotropical region (e.g. Baldissera et al., 2008; Bonaldo et al., 2007; Fonseca et al., 2009; Dias & Bonaldo, 2012) as well as from other climates (Hövemeyer & Stippich, 2000 for German beech forests; Schuldt et al., 2011 for subtropical forests in China; Pryke & Samways, 2012 for South African forests; Samu et al., 2014 for Hungarian forests) the richness and diversity of spiders in the studied region can be considered high, especially as 47 genera and at least 62 species (RTU) per site and 192 genera and 440 RTU for the region resulted from singular sampling. The observed richness meets the expectations for the Brazilian Atlantic Forest.

Method and identification level

A completeness of the sampling of more than 75%, at least for genera, underlines the usefulness of the used sampling protocol for regional inventories, due to the involved complementarity of methods and sampled strata. These contributed more than expected by chance to beta diversity (Shannon, Simpson), but not very much to richness. Our interpretation is that every method sampled a comparable number of taxa, all including the common ones, although in different relative abundances. Most important, all methods showed the same patterns of beta diversity and therefore, in contrast to the experiences of Tourinho et al. (2014) with harvestman assemblages, did not sample different spider assemblages with different responses to the environment, obfuscating the patterns. Patterns (partitions) of beta diversity were also similar at both levels of identification (genus, RTU). Genera really seem to be a good surrogate for patterns of species composition (see also Baldissera et al., 2008; Cardoso et al., 2004). In practice this allows the use of only one of the principal methods – or nocturnal sampling or beating vegetation and identification to the genus level to reveal patterns of diversity in a region. This would reduce the number of visits and samples of each site as well as time for sorting and identifying and consequently lower the costs of such an investigation (compare Azevedo et al., 2014). Nocturnal sampling is an effective method for experienced arachnologists, but depends on accessibility of the sites at night. Beating, on the other hand can be done by unexperienced collectors after a short introduction. The activity based pitfall traps showed similar patterns as the other methods but sampled much fewer genera and RTU offering therefore no additional benefit justifying the increased effort.

Forest succession

The high beta diversity at all levels, caused by turnover does not point to a directed succession with a general gain/loss tendency from younger to older stages. Even young “forests” appear to offer suitable habitats for many species (from a large pool) and only few non-forest species disappear during succession. There is no change in richness but the variability of the assemblage composition changes. The variability within younger and older succession stages respectively originates in our opinion from the heterogeneity of biogeochemical, vegetational and microclimatic conditions. This assumption is supported by the results of Ottermanns et al., (2011), who showed a strong influence of vegetational (structural) and microclimatic conditions on beetles in the study region. During further forest succession the variance in biotic and abiotic habitat parameters within the stages seems to decrease (see also Raub et al., 2014b). A similar lack of influence of the age of forests and vegetation cover on spider diversity (but not on abundance) was observed in several studies: Baldissera et al. (2008) and Fonseca et al. (2009) for Araucaria forests in southern Brazil, Chen & Tso (2004) for four habitat types including forest on islands in Taiwan; Harris et al. (2003) for *Eucalyptus* forests in Australia. In 27 forest stands of different age and diversity in subtropical China Schuldt et al. (2011) observed that spider species richness decreased with increasing woody plant species richness and was not affected by structural variables of herb layer or litter. They detected some effects of forest age, but also no directed change in species richness along a succession from young (> 20 years) to old (> 80 years) stands. Positive effects of woody plant species richness were only detected on the rarefied number of spider guilds. Interestingly, variability in species richness and abundance increased with forest age and (Schuldt et al., 2012) relate this to successional changes in spider assemblages, in contrast to our observations. Not the number, but the diversity of guilds was observed to differ between the stages in our study (Raub et al., 2014b). In Chinese subtropical forests the horizontal plant structure of the herb layer had little impact on epigeic spiders compared to effects of the tree and shrub layer (Schuldt et al., 2011) and the lack of differences between the younger and older stages in our study, which differed most strongly in the herb layer, also points in this direction.

Spider distribution

At one extreme, the distribution of individual species can be considered to be purely dispersal limited; and at the other extreme to be limited purely by traits that influence the conditions in which they can survive and successfully reproduce (niche limitation) – see Gaston et al. (2007). As pure dispersal limitation means that all species have the potential to occur everywhere (no niche limitation), although they cannot reach many places, perfectly nested species distributions are unlikely to arise. Partially nested distributions are the most likely scenario to arise under dispersal limitation. Similarity between assemblages will decrease with distance, and gain/loss will increase with distance. We can see this in our data by the importance of an amplified sampled area (area and locality level) in additive partitioning, but after all it is difficult to infer the biological causes of dispersal limitation, niche limitation and species-area-relationships by pattern analysis.

Spiders have a high dispersal and colonization capacity due to their high agility and ballooning ability (Foelix, 2011) and therefore spider assemblages are potentially able to initiate rapid succession after disturbances and colonization of “new habitats” (Baldissera et al., 2013 from an experimental study in grassland in southern Brazil). Also their ability as generalist predators to feed on allochthonous prey (drifted insects) supports the high colonization ability. Therefore initial spider assemblage composition should largely be determined by the temporal order in which the species arrive and establish, irrespective of habitat size and vegetation and prey diversity. A continuous colonization process of forest patches from the regional pool of species is expected at least in a region with a forest matrix. The similar abundance and richness of spiders in more or less all patches (of initial succession stages) is interpreted as a response of the spider assemblage to non-diversity-related habitat structures (e.g. vegetation giving web support), which is equally provided in less diverse patches.

In canopy spider assemblages in SE Asia species richness correlated with forest fragment age, when fragments were not too isolated. But forest isolation was the strongest factor and habitat connectivity was of high importance (Floren et al., 2011). These authors emphasize the importance of neighboring primary forest for re-colonization of naturally regenerating forest fragments by spiders, contesting a high dispersal ability for the habitat specialists in primary forests.

The matrix structure strongly determines the pool of species able to colonize a habitat patch. In contrast to the situation in many tropical regions and also other states/subregions of the Atlantic Forest, in our study region the matrix is still forest (Antonelli Filho & Antunes Ferreira, 2012), explaining the high similarities among sites and stages. Most of the regionally occurring species are mobile and can reach the next suitable site (Baldissera et al., 2013) and most of the species examined can survive in all forest stages, encountering and occupying their proper niches. Only few species (sampled by our sampling protocol) seem to require a certain condition of forest stand age (especially old-growth forest) and only a low number of species of open land disappear when the forest grows higher and more dense vegetation appears.

The results of the additive partitioning approach support these assumptions with less contribution to the local diversity of the stage than expected by chance and more contribution of the area than expected. Rather than the stages, every sampled site independent of the stage contributed equally to beta diversity and an expansion of the sampled area (size) also contributed more than the stage as predicted by a dispersal limitation model. This highlights the importance of spatially replicated sampling efforts. Therefore sampling the different stages (stage level) did not add as much as we expected to the richness, but only to Shannon and Simpson diversity. The stages obviously differ stronger in the relative abundance of genera/species. In contrast, extending the sampling area (area and locality level) added more richness than expected by chance.

Further, the small contribution of the different methods to the richness demonstrates the overlapping of the used methods also shown by the similarity of graphical patterns. Only the contribution to the Shannon and Simpson diversity was higher than expected by chance. Our interpretation is that the abundant taxa stay the same, but relative abundance changes due to the unbalanced distribution of common genera/RTU in the methods/strata. The differences in additive partitioning for the identification levels genus and RTU are very small.

Additive and multiplicative partitioning

Regarding the multiplicative partitioning, the multipliers between the different levels were always lower than the number of added units per level, which means that there were no completely different assemblages sampled in every unit (Chao et al., 2012). Whereas this was expected for the area level, it sheds an important light on the importance of the stage and the locality level. For the four stages a multiplier of 2.1 is in accordance with the results of multivariate ordination and indicator species analysis (Raub et al., 2014b), indicating that only forests older than 30 years house a spider assemblage different to younger stages.

Recently there has been much debate upon partitioning diversity correctly – additive or multiplicative, replacement or species gain/loss (Anderson et al., 2011; Chao et al., 2012; Carvalho et al., 2013; Gering et al., 2003; Pereyra & Moreno, 2013; Schmera & Podani, 2011; Ulrich et al., 2009; Veech et al., 2002). The above results can contribute to highlight the usefulness of the different partitioning methods during ecological studies and present possible interpretation pathways to answer questions in the frame of biodiversity conservation and management.

Conclusion

As for other regions (Baldissera et al., 2008; Ziesche & Roth, 2008) maintaining the heterogeneity of a mosaic landscape (although anthropogenic) seems to be a good recommendation for conservation of the regional biodiversity (at least of the largest part represented by invertebrates) in the southern Mata Atlântica.

Our analyses point out the importance of a distinct mosaic pattern of different land use and regeneration types in protected areas for a maximized conservation of the regional biodiversity. Old-growth habitats usually are regarded to play an important role in conservation management as a pool of species for resettlement of secondary habitats. But to guarantee a sustainable protection of the widest range of the spider diversity the protection of large, contiguous areas (containing a mosaic of different succession stages) should be reached and, if a decision is obligate, preferred to the protection of small (mostly isolated) old-growth forest remnants. Although undisturbed primary forests often harbor more species than secondary forests, regenerating forests are not biological deserts (Barlow et al., 2007; Lo-Man-Hung et al., 2008).

We consider the used methods as suitable to reach a satisfying coverage/completeness of genus and RTU richness (about 70% of estimated richness, compare Azevedo et al., 2013) for biodiversity assessments in the frame of conservation management questions. Since the results of the different methods were very similar, we think that in terms of cost-effectiveness the use of part of the sampling protocol (night sampling or beating tray) is an adequate sampling effort for a fast inventory (compare Azevedo et al., 2013). Further, if identification effort is an issue, the genus level can be used as a surrogate for the RTU level without losing major parts of the explanatory power.

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Appendix – Supporting Material Chapter 3: Locality Information of the study sites Page 110

4 – No bottom-up effects of food limitation on predators in a tropical forest.

with Ludger Scheuermann, Hubert Höfer & Roland Brandl, Published in Basic and Applied Ecology, 2013

Abstract

Several studies in temperate forests have demonstrated effects of litter addition on decomposers and predators. However, adding litter does not allow separating the effects of food availability and habitat space. We investigated the response of decomposers and predators to increased food resources and space in forests of the southern Mata Atlântica of Brazil. In two forest ecosystems representing an early successional stage of secondary forests and old-growth forest, we added nutrient-rich organic material, artificial litter of no nutritional value, or a combination of both to the soil surface of 120 plots to separate the effects of habitat space and food on soil food webs. We sampled litter- and soil-dwelling arthropods after three months using pitfall traps, soil sample extraction, and sticky traps just above the soil. Adding artificial litter had no positive effect on any of the 17 analyzed arthropod groups. Combining all sampled arthropods the effect was even significantly negative. Adding food had a positive effect on the abundance of decomposers, but not predators. We found no interactions between added artificial litter and added organic material. Our results suggest that the soil fauna in tropical forests is food limited. The lack of a bottom-up effect on predators suggests that they are not predominantly regulated by the abundance of epigeic prey but rather by competition or predation.

Introduction

Most of the primary production ends up as litter, making litter decomposition an important process in terrestrial ecosystems (Anderson & Swift, 1983; Swift et al.,1979). Furthermore, forest litter is a complex habitat for a bewildering diversity of organisms (Bultman & Uetz, 1982, 1984; Lavelle et al., 2006; Uetz, 1979, 1991) with at least three principal roles for these organisms: first, litter with its three-dimensional structure provides living space for many organisms (Höfer et al., 1996; Langellotto & Denno, 2004; Spears & MacMahom, 2012; Uetz, 1991); second, litter generates a favorable and stable microclimate on the soil surface (David et al., 1991; Höfer et al., 1996); and third, litter is the substrate on which a complex food web is based (Rypstra, 1983; Scheu, 2002; Wise et al., 1999). Disentangling the importance of these three roles of litter has been one of the main aims of many experiments manipulating the amount and structure of litter over almost 150 years (e.g., Chen & Wise, 1997, 1999; Stippich, 1989; Scheu & Schaefer, 1998; Uetz, 1979, reviewed in Sayer, 2006).

The experimental removal of litter is generally followed by a decrease in the abundance of litter- and soil-dwelling organisms (Sayer, 2006). Based on this often dramatic decrease of litter-dwelling animals during removal experiments, one might expect also a dramatic increase in abundance when litter is added to experimental plots (Höfer et al., 1996). However, the response has often been much less than anticipated (Sayer, 2006). For example, the abundance of the predatory spiders increased when artificial litter was added, but the abundance of decomposers that depend on litter as a direct or indirect (via fungi) food resource did not (Bultman & Uetz, 1982). Irrespective of these asymmetric responses, adding or removing litter does not allow the various roles of the litter for animals to be distinguished because both treatments change habitat availability, microclimate, as well as resources.

Predators need a highly structured habitat to hide for capturing prey or in the case of spiders to build webs, to reduce competition and/or to avoid intra-guild predation (Bultman & Uetz, 1984; Finke & Denno, 2002; Wise & Wagner, 1992). Therefore, habitat space and structure should be of considerable importance for predators, particularly when food is not limiting (Bultman & Uetz, 1982; Duffey, 1966; Robinson, 1981; Rypstra, 1983, 1986; Scheidler, 1990; Stippich, 1989). Most tropical forest ecosystems are considered to be nutrient limited (Bazzaz & Pickett, 1980; Tiessen et al., 1994). Furthermore, in tropical climates decomposition is fast, leading to a rapid and effective recycling of resources (Anderson & Swift, 1983, Heneghan et al., 1999). Nutrient allocation by plants and the recycling of nutrients can result in food limitation for decomposers (Vitousek & Sanford Jr., 1986). This being so, an experimental increase in habitat availability should have little effect on the abundance of decomposers and also predators. In contrast, an increase in the food resource availability should lead to an increase of decomposers as well as predators, as long as these guilds are not controlled by higher trophic levels (Hunter & Price, 1992). Without food limitation the limitation of habitat should become important and increasing habitat space therefore lead to a further increase in the abundance of predators. In statistical terms, this means that one should find an interaction between these two treatments. We tested this hypothesis using an experimental approach where we manipulated food resource for decomposers by adding nutrient-rich organic material and space for litter-inhabiting soil animals by adding polystyrol snippets, both in secondary and old-growth forests of the Brazilian Atlantic Forest.

Materials and Methods

Study area

The experiment was conducted in the Rio Cachoeira Nature Reserve (-25.314, -48.696 WGS84), located near the city of Antonina, in the coastal state of Paraná in southeastern Brazil (see Appendix – Supporting Materials Chapter 4: Fig. 1). This private reserve, owned by the Brazilian NGO “Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental - SPVS”, covers 12,000 ha at elevations ranging from 0 to 600 m a.s.l. The regional climate is classified as Cfa (humid subtropical, mild with no dry season, hot summer) according to Köppen (Schröder, 2000; Strahler & Strahler, 2005), with mean temperatures between 16.2 °C in July and 24.5 °C in February (IPARDES, 2001) and an average annual precipitation between 2,000 and 3,000 mm (Roderjan & Kunyoshi, 1988). The area of the reserve was originally covered by dense ombrophilous lowland and submontane forests (IBGE, 1992). The intense exploitation of forests has transformed the landscape to a mosaic of pastures, successional stages of secondary forests, and few remnants of old-growth forest, mostly at higher elevations. From the 24 study sites of the German-Brazilian cooperation project SOLOBIOMA (Höfer et al., 2007; Höfer et al., 2011), we selected three sites of the youngest successional stage of secondary forests with a closed canopy and three sites representing old-growth forest on cambisol.

Experimental set-up

We added artificial litter of no nutritional value, nutrient-rich organic material, or a combination of both to 20 plots of 1.5 × 1.5 m² on each of the 6 sites (Appendix – Supporting Materials Chapter 4: Fig. 1) in a 5 × 4 arrangement of plots with a distance of 5 m between plots. To 5 randomly selected plots we added nutrient-rich organic material (treatment: Food) at the beginning and then every 2 weeks until the end of the experiment after 3 months. The organic material consisted of 110 g champignon mushrooms, 100 g potatoes, and 20 g fruit fly medium (*Drosophila* Zuchtkonzentrat, Nekton, Pforzheim, Germany) per m^2, following Chen & Wise (1997, 1999). The fungi and potatoes were chopped and stored at −20 °C before use. To 5 other randomly selected plots, we added 32 l of polystyrol snippets of no nutritional value (treatment: Space) at the beginning of the experiment to increase the available habitat space and habitat structure for arthropods. In comparison to this treatment the added food constituted only a minor manipulation of the available habitat space, due to its small quantity (volume) and low surface (structure). To 5 other randomly selected plots, we added both organic material and polystyrol snippets as described above. The remaining 5 plots served as a control.

Sampling of the fauna

After the third addition of organic material (end of week 4), we sampled small flying insects (mainly Diptera) for 24 h using vertical sticky traps (Gelb-Sticker, Neudorff, Emmerthalm Germany; 98.5 cm^2 of sticky surface) placed just above the litter layer and counted the number of insects on the traps.

During the last week of the experiment (week 11), we placed one pitfall trap in the middle of every plot; each pitfall trap consisted of a 330 ml plastic cup with an opening diameter of 7.5 cm, filled with 100 ml of 4% formaldehyde solution and protected against rain by a transparent plastic roof. At the end of the experiment (after 3 months), we took four cylindrical soil samples from each plot (core diameter 5 cm, height 5 cm), one from each corner of the plot, 10–15 cm from the edges. These four soil samples per plot were pooled together and extracted using a Berlese apparatus over 10 days. All extracted arthropods were stored in 75% ethanol.

The arthropods were sorted according to order, except for the Formicidae (family) and insect larvae; the latter were grouped together for pragmatic reasons. All sorted arthropods were then counted (see also Appendix Supporting Materials Chapter 4: Table 1, 2).

Statistical analysis

We analyzed abundance data using a generalized linear mixed model and the function *glmer* within the package *lme4* (Bates, 2010) in R (R Development Core Team, 2009). Sites and sampling methods were treated as random factors. We estimated the effects of forest successional stage, added organic material as well as artificial litter and all two-way interactions using a Poisson distribution with the standard link function (log). We accounted for over-dispersion as suggested in the help document of the function *glmer*. For the visual presentation of variation of the faunal composition between treatments and stages, we used the function *rda* provided by VEGAN 1.17-2 (Oksanen et al., 2009). We performed a constrained analysis using square root transformed abundance data as dependent variables, the two experimental treatments as factors including all interactions and the forest stage as independent environmental variables.

Results

We collected more than 70,000 arthropods with pitfall traps, 9,600 arthropods via Berlese extraction of soil samples (see also Appendix – Supporting Materials Chapter 4: Table 1, 2), and nearly 3,300 insects with sticky traps. The numbers of arthropods sampled with the different methods (log-transformed data) showed positive but low correlations across all sites ($r_{\text{pitfall-Berlese}} = 0.48$; $r_{\text{Berlese-sticky}} = 0.31$; $r_{\text{pitfall-sticky}} = 0.48$). This indicated that the three sampling methods provide complementary information on arthropod abundance. The soil and pitfall samples had roughly similar distributions of individuals across major invertebrate taxa (see Appendix A: Table 2; $r = 0.82$; with log(x+1)-transformed data). The most abundant group caught with these two methods was springtails (Collembola), which accounted for more than 84% of all individuals in pitfall and 30% in soil samples.

The abundance of 3 of the 17 groups significantly differed between the two forest stages; this corresponds to 18%, which is much higher than 0.85 groups (5%) expected to differ by chance (Table 1). Increased nutrient-rich organic material (Food) had a positive effect on the abundance of flying insects caught on sticky traps, on the abundance of all soil arthropods grouped together, on the abundance of decomposers, and on the abundance of 5 of the 17 groups (29% of all taxa, Table 1; see also Fig. 1, Fig. 2). When we grouped the sampled arthropods into the two functional groups of predators and decomposers, our analysis indicated that predators were significantly higher in abundance in old-growth forest plots than in secondary forest plots (Table 1, Fig. 2).

Table 1. Effects of forest stage, increased nutrient-rich organic material, or increased habitat space using artificial litter of no nutritional value on the abundance of taxonomic and two main functional groups (predator and decomposer). Only groups with at least one significant result in any of the factors are shown. Altogether we sampled 120 plots (3 sites in each successional stage; five replicates of each treatment within sites) using three methods. Data were analyzed using generalized mixed models using a Poisson distribution and the canonical link function including a correction for over-dispersion. Sites and methods were modeled as random factors (see Supporting Materials Chapter 4: Table 3 for separate analyses of the different methods). We present the *z*-values (= estimates/standard error) of the coefficients. Significant results are indicated in grey.

Taxon/Group	Functional group	Stage		Food		Space		Food*Space		Stage*Food		Stage*Space	
		z	P	z	P	z	P	z	P	z	P	z	P
Acari	Decomposer	1.33	0.18	4.22	<0.001	−0.50	0.62	0.48	0.63	1.20	0.23	0.82	0.41
Coleoptera	Polyphage	1.74	0.08	5.83	<0.001	−0.04	0.97	−1.08	0.28	−2.21	0.03	0.13	0.90
Collembola	Decomposer	−1.09	0.28	8.85	<0.001	−1.39	0.16	−0.97	0.33	−0.90	0.37	0.74	0.46
Formicidae	Polyphage	−2.42	0.02	0.55	0.58	−1.78	0.07	1.14	0.25	1.08	0.28	0.61	0.54
Hemiptera	Phytophage	0.35	0.73	3.18	0.001	−0.83	0.41	0.72	0.47	−0.88	0.38	0.73	0.47
Insect larvae	Polyphage	3.63	<0.001	6.36	<0.001	−1.11	0.27	0.06	0.95	−0.85	0.40	0.51	0.61
Opiliones	Predator	−2.27	0.02	−0.33	0.74	−1.01	0.31	−0.74	0.46	1.57	0.11	2.09	0.04
Symphyla	Decomposer	1.64	0.10	1.86	0.06	1.81	0.07	−0.71	0.48	−1.33	0.18	−2.72	0.006
Predators[1]		2.24	0.03	0.79	0.43	0.41	0.68	0.66	0.51	−0.41	0.68	−0.19	0.85
Decomposers[2]		0.09	0.93	8.03	<0.001	−0.79	0.43	−0.82	0.41	−1.04	0.30	0.48	0.62
All arthropods		−0.44	0.66	7.69	<0.001	−2.91	0.003	0.73	0.46	−0.49	0.62	0.33	0.75

[1] Sum of Araneae, Opiliones, Chilopoda, Pseudoscorpiones

[2] Sum of Acari, Collembola, Diplopoda, Isopoda, Blattodea, Symphyla

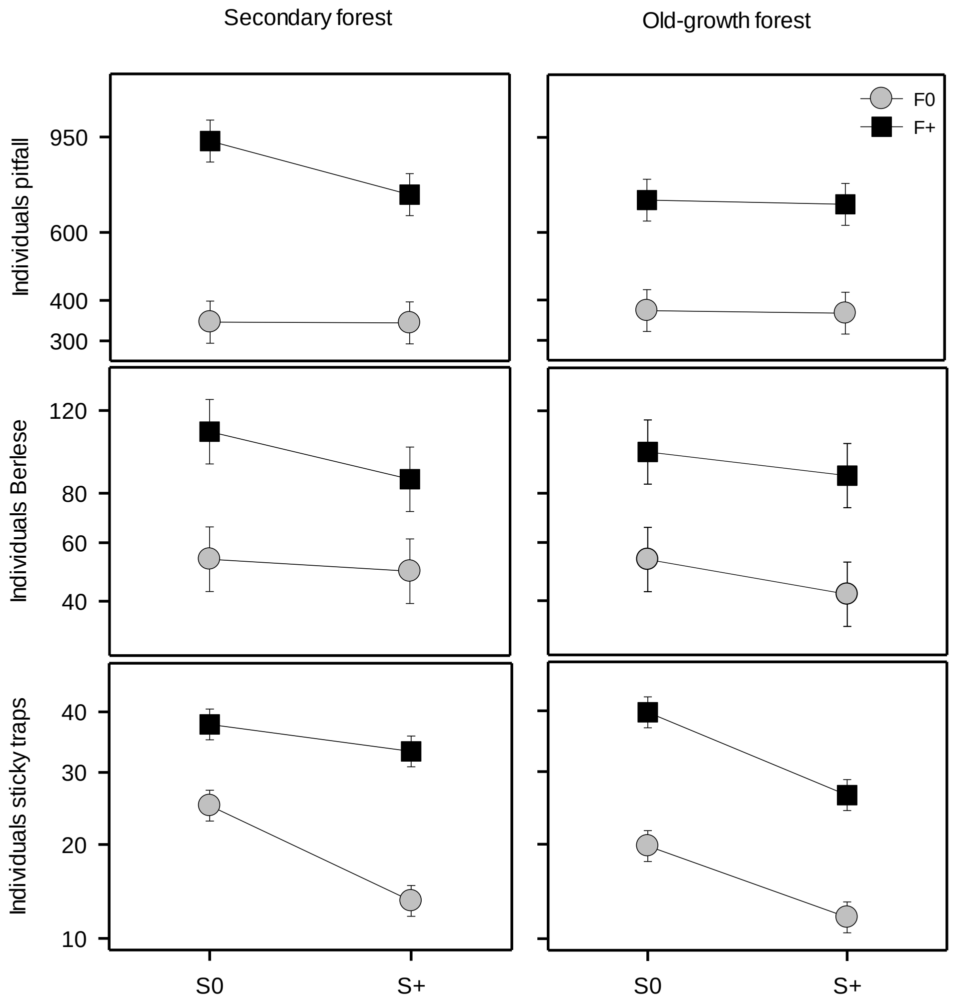

Figure 1. Mean number of all arthropods across samples for the three methods and two habitats for the treatments with/without Food (F+, F0) and with/without additional Space (S+, S0). Altogether we sampled 120 plots (3 sites in each successional stage; five replicates of each treatment within sites). We present the square root transformed means and the associated standard errors (note that the tick labels of the y-axes were back-transformed).

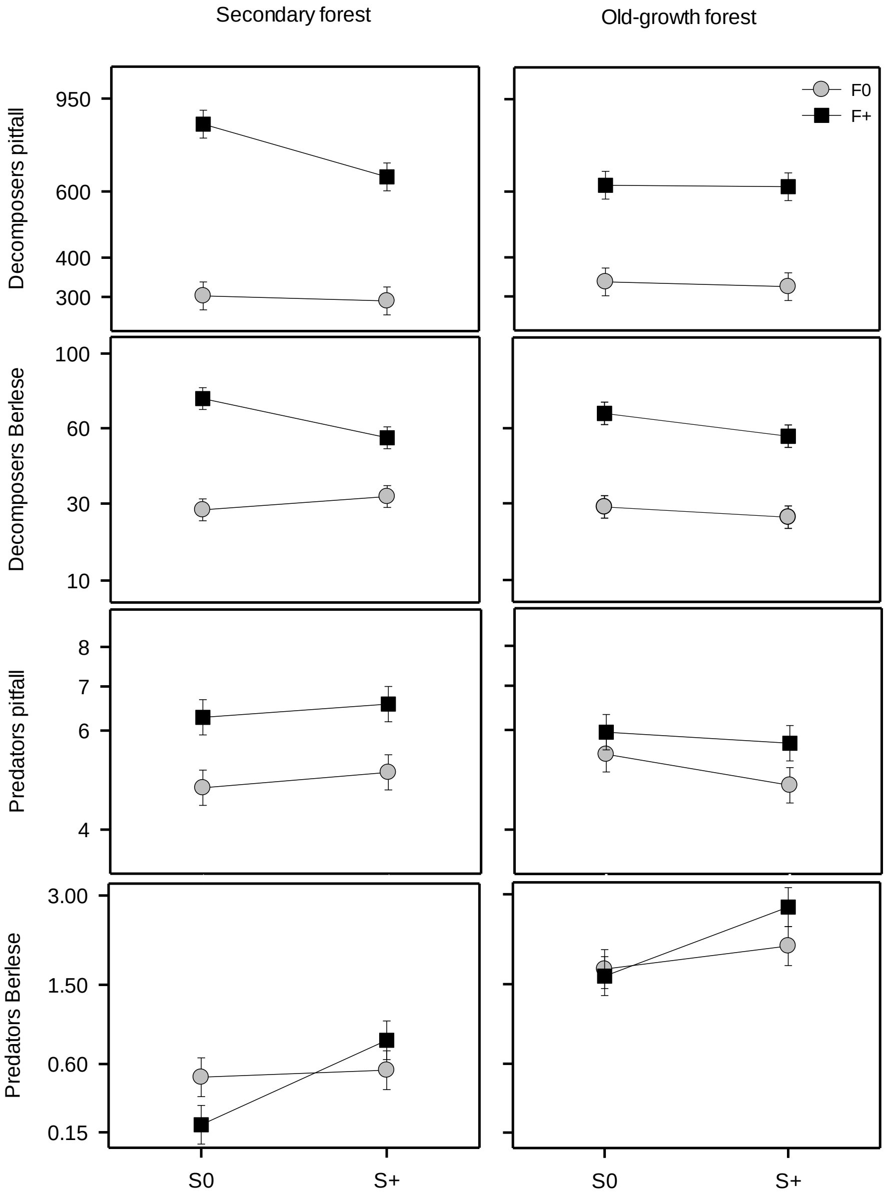

Figure 2. Mean number of decomposers and predators across samples for two methods and two habitats for the treatments with/without additional Food (F+, F0) and with/without additional Space (S+, S0). Altogether we sampled 120 plots (3 sites in each successional stage; five replicates of each treatment within sites). For the stick trap samples we were not able to classify species as decomposers or predators and therefore sticky traps are not shown (but see Fig. 1). We present the square root transformed mean and the associated standard error (note that the tick labels of the y-axes were back-transformed).

All significant coefficients had a positive sign, which indicated that abundance increased with the addition of nutrient-rich organic material to the plots (Table 1). Addition of organic material also consistently changed the composition of the fauna caught in pitfall traps and soil samples in both forest stages (Fig. 3). The dissimilarity of the communities following the food treatment is mainly based on changes in Acari and Collembola (see also Supporting Materials Chapter 4: Table 1). None of the groups responded to the increased habitat space provided by the artificial litter with increasing abundance (Fig. 2). The abundance of all arthropods was even negatively affected (Table 1).

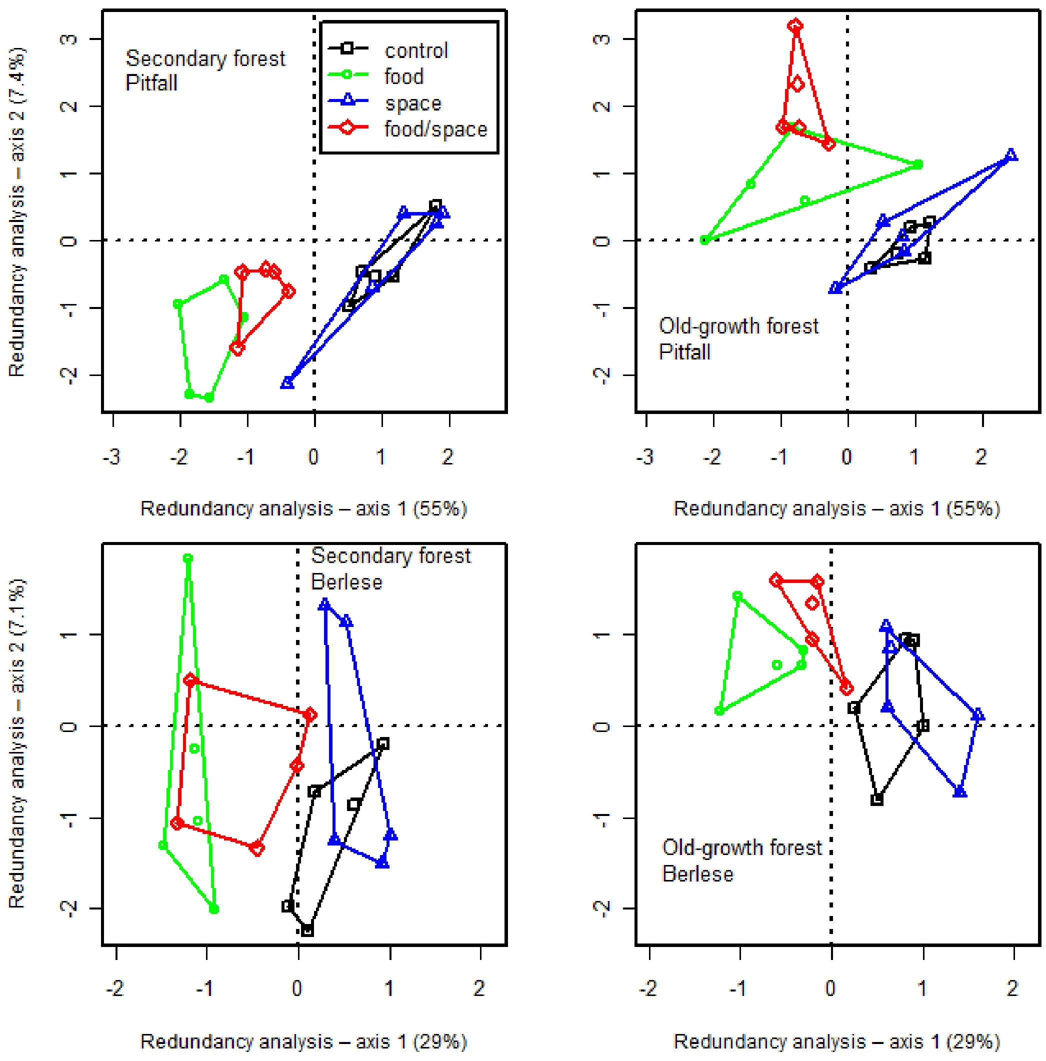

Figure 3. Results of redundancy analyses modeling the square root transformed abundance data (all arthropods) of the pitfall or soil samples using the two treatments and the forest stages as well as all interactions as independent variables. For each analysis the scores of the plots of the secondary and old-growth forests were plotted separately. Symbols: treatment Food - green circles; treatment Space - blue triangles; treatment Food and Space - red diamonds; controls – black squares. Altogether we sampled 120 plots (3 sites in each successional stage; five replicates of each treatment within sites).

Discussion

We found only minor differences in the abundance of decomposers between secondary and old-growth forests (see also Schmidt et al., 2008). Only the abundance of predators was higher in old-growth forests. As expected, the addition of nutrient-rich organic material to the plots had a positive effect on the abundance of litter- and soil-dwelling decomposers. This effect showed little variation between the two successional stages. This is an indication that decomposers are food-limited in the nutrient-poor Atlantic Forests of Brazil. However, our results suggest no simple bottom-up effect of the increase in food resources to higher trophic levels. Furthermore, neither the abundance of decomposers nor that of predators increased with increasing litter volume and therefore habitat space. Finally, our results did not support our prediction of an interaction between increased food resources and increased habitat space for predators.

In temperate, productive ecosystems, the positive effects of added neutral material and of added natural leaf litter are similar (Bultman & Uetz, 1982; Gill, 1969), which indicates that the habitat volume has at least some importance for litter-dwelling organisms. However, in our tropical sites, increasing habitat volume did not increase arthropod abundance. We used a biologically neutral material with no evidence of a chemically repellent effect (BASF, 1995) to increase habitat space without affecting food availability on the plots. Nevertheless, we cannot exclude the possibility that the material was not accepted as a living space by soil- and litter-inhabiting organisms due to its haptic character. The negative effect of the artificial litter on flying insects may have been caused by the chips covering the natural resources of these animals or by the possibly repulsive unnatural color of the chips (Greany et al., 1977). Despite these possibilities, our results allow us to tentatively conclude that the amount of habitat space in both investigated forest stages plays a minor role in determining the abundance of decomposers and predators of litter-dwelling animals. We therefore conclude that habitat space is not the limiting factor for both groups in the secondary as well as the old-growth forest. In our experiment, we manipulated the amount of litter but did not control its structure. Manipulating litter structure has mostly positive effects on the abundance of some animal groups (e.g., Uetz, 1979, 1991). For example, tying together branches to experimentally increase habitat complexity resulted in an eightfold increase in abundance of epigeic collembolans in a temperate forest ecosystem (Halaj et al., 2000).

In contrast to increased habitat space, the addition of nutrient-rich organic material clearly increased the abundance of soil animals and changed the composition of the assemblages. The most pronounced increase in abundance caused by adding nutrient-rich organic material was found for springtails. Since collembolans are a major component of the diet of spiders inhabiting litter (Chen & Wise, 1999; Lawrence & Wise, 2000; Wise et al., 1999), we expected to find effects of increased food resources also at higher trophic levels, as observed in temperate forests, where the addition of food resources often had positive effects on the abundance of predators (Chen & Wise, 1999; Wise et al., 1999). We even expected the response of predators in the nutrient-poor tropical forests to be stronger than that observed in productive temperate forests. Yet the increase in abundance was restricted to decomposers; predators showed no clear response.

Possible arguments for why we did not observe a response of increased food resources on predators are that the spatial scale may have been too small and the duration of our experiments may have been too short to produce a response at higher trophic levels. Compared to decomposers, predators are generally larger and forage across larger spatial scales (Chen & Wise, 1997, 1999; Uetz, 1991). However, even smaller plots were used by Bultman & Uetz (1982, 1984) and Höfer et al. (1996), and the length of our experiment was similar to that of other studies which observed a response of increased food resources on predators (Bultman & Uetz, 1982; Chen & Wise, 1999). Second, some of the sampled predators may feed not only on soil animals and, third, predators may be more affected by competition and intra-guild predation. Finally, the food addition may have also attracted small reptiles, birds and mammals to either feed on the rich food or on the arthropods that were attracted by the food treatment. These vertebrate predators feed also on invertebrate predators leading to complex food web interactions which are difficult to separate in simple field experiments.

The Atlantic Forests are a biodiversity hotspot (Laurance, 2009) but the region is also the most densely populated region of Brazil. Only small fragments of pristine forest remain, and therefore, as in many other regions of the world, secondary forests are becoming increasingly important as refuges for the conservation and survival of species of old-growth forests (Dunn, 2004). The successional stages of forest regeneration may harbor a surprisingly rich flora and fauna. Nevertheless, species composition and ecological processes in secondary forests and old-growth forests may differ (Bihn et al., 2008a; Bihn et al., 2008b; Liebsch et al., 2008; Schmidt et al. 2008 for the study region; Lo-Man-Hung et al., 2008 for Amazonia). We also found minor differences in the faunal composition between the two studied stages, but revealed no differences in the response of groups to our treatments. However, it would be premature to conclude from one single experiment that the processes influencing the soil and epigeic fauna are similar across successional stages and to rely on secondary forests for the conservation of forest species and associated ecological processes (see also Gießelmann et al., 2010).

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Appendix – Supporting Material Chapter 4: Additional figures and tables. Page 111 ff

5 – Outlook

Although we made considerable progress during our studies, further investigations need to address the following issues:

(1) The high degree of similarity of the used methods would suggest a restriction in the sampling protocol of such a broad diversity approach in order to be able to use a highly replicated sampling in a variety of different ecosystems. The use of only beating as a single method should lead to satisfactory assessment of biodiversity structures. Further, identification to the genera level seems adequate, is more economic and avoids biased results due to wrong species identification or a deficient morphospecification.

(2) The results of such a broadened diversity study should be included in a multi-taxon approach to identify “indicator communities” for different (states of) ecosystems, not only single indicator species.

(3) To be able to better assess the conservation value of secondary forests it seems reasonable to include further regional ecosystems in an expanded diversity evaluation approach of the spider fauna. Regarding the highly structured mosaic landscape in the region it would be interesting to compare the contribution of other forest types to the regional spider fauna (and its protection). Especially the Atlantic coastal restinga forests with a strong oceanic and tidal influence and the Araucaria forests are promising to host distinct and rich spider faunas. The inclusion of forest of the higher mountain range of the region and also agriculturally used areas of different types are important to be included to assess the whole range of biodiversity.

(4) For a better insight in the ecological interaction of spiders a replication and further experiments including more habitat types are recommended. The exclusion of predators (reptiles, birds, small mammals) of spiders could reveal a positive influence of prey abundance on the spiders, masked by predation. Such general principles (bottom-up versus top-down effects) should best be tested experimentally in different (tropical) regions with different soil nutritional conditions.

6 – Summary

Tropical forests have stimulated biodiversity research in the second half of the 20th century, when the overwhelming richness of arthropod species was discovered. Soon after the primary scientific interest to unravel and describe the biodiversity of the tropics, the concern of losing most of the newly identified diversity before it can be studied, directed the attention to conservation studies. However, for a long time vertebrate (flagship) species or groups were in the focus of conservation, being used also to underline the necessity of preserving the whole diversity of the ecosystem. Lately and under a more systemic and functional view of the species in ecosystems, attention shifted towards to the study of arthropod diversity, e.g. invertebrate communities in canopy and soil and their ecosystem functions. We had to learn that the productivity of tropical soils originates and depends on the recycling of organic matter and the remobilization of nutrients during the decomposition, for which a functional web of arthropods (invertebrates) and microorganisms is responsible. A broad range of globally important ecosystem services is offered or at least influenced by arthropods and an efficient protection of the biological and functional diversity of tropical forests is only possible by extensive conservation management strategies incorporating arthropods. A detailed knowledge of the diversity and ecological and functional interdependencies of the arthropod communities are an important prerequisite to accomplish this challenge.

To which degree secondary forests maintain the species diversity of natural forests is still controversially discussed and therefore an important topic for biodiversity science and conservation. Worldwide and also in the Atlantic Forest region of Brazil (Mata Atlântica) primary forests disappear and the few and often small remnants of old-growth forests suffer from strong and ongoing anthropogenic pressure. On the other hand international concern for environmental problems has led to an increasing quantity (number and size) of naturally regenerating or planted secondary forests and therefore these are becoming more and more relevant for conservation.

The objective of my thesis was to assess the diversity and the ecology of spider assemblages in secondary forests of the southern Mata Atlântica, with impact for environmental conservation and the protection of the regional biodiversity. My approach to address these questions was carried out in the frame of a multi-taxon approach of the bilateral cooperation project SOLOBIOMA. The aim of this project was the evaluation of the value of different secondary forest stages for the conservation of the local and regional biodiversity

and implications for soil function. Therefore my work addresses the diversity of spiders by describing and analyzing a large sampling carried out in different succesional stages of forest, as well as investigating the ecology of the predatory spider assemblage in an experimental approach of the interactions of spiders with habitat structures and nutritional resources in the soil food web.

To assess the conservation value of secondary forests and their contribution to maintain the regional diversity I compared the spider assemblages of secondary forests of different age (stage) and old-growth forests (chapter 2 & 3). We sampled spiders using a standard protocol in 24 sites of three successional stages and old-growth forests in two nature reserves in the state of Paraná in Brazil. The sampled region represents a relatively good preserved region of the Mata Atlântica, where the matrix of a patchy landscape is still forest.

Generic richness and diversity showed no differences between successional stages but guild diversity did. A high alpha diversity and a high turnover among sites as well as the lack of differences in richness between the stages support the value of secondary forests for species conservation in the studied region. Beta diversity turned out to be strongly based on turnover, not on gain/loss during succession. The spatial levels contributed more to beta diversity than expected, without the expected strong influence of the forest stage. Patterns were consistent for both identification levels and every method, leading to the conclusion that one of two parts of the sampling protocol and identification to genera are sufficient to assess the diversity of spiders under conservation interest.

During the experimental approach (chapter 4) I discovered that adding artificial litter had no effect on the studied taxa, adding food had a positive effect on decomposers independent from the forest stage, but not on predators. These results suggest that the soil fauna in tropical forests in general is food limited and the lack of a bottom-up effect on predators suggest that these organisms are not predominantly regulated by the abundance of prey but rather by competition or predation. However, it would be premature to conclude from one single experiment that the processes influencing the soil and epigeic fauna are generally similar across different successional stages, we can see evidence for distinct functional similarity. These results highlight the value of secondary forests for the conservation of forest species and associated ecological processes.

I conclude from the results of the biodiversity study and the experiment that maintaining the heterogeneity of a mosaic landscape seems to be a good recommendation for conservation of the regional invertebrate biodiversity and its ecosystem function in the southern Mata Atlântica. Our analyses from a spider perspective point out to the importance of a pattern of different land use and regeneration types as well as old-growth forest in protected areas to maximize conservation success. To guarantee a protection of the widest range of spider diversity on the long term the protection of large, contiguous areas of forest should be reached and, if a decision is obligate, preferred to the protection of small (mostly isolated) old-growth forest remnants.

7 – Zusammenfassung

Die Entdeckung der überwältigenden Artenvielfalt tropischer Wälder begründete im späten zwanzigsten Jahrhundert die Biodiversitätsforschung oder gab dieser zumindest einen enormen Schub. Nach dem ersten wissenschaftlichen Interesse an der umfassenden Beschreibung der tropischen Artenvielfalt, kamen sehr schnell Bedenken auf, ein Großteil dieser Biodiversität könnte verloren gehen, bevor er überhaupt erforscht werden konnte und der Forschungsschwerpunkt verschob sich in Richtung Natur- und Umweltschutz. Dabei waren lange Zeit Wirbeltiere im Fokus der wissenschaftlichen Aufmerksamkeit und wurden dazu benutzt die Notwendigkeit des Schutzes der gesamten Diversität tropischer Ökosysteme hervorzuheben. In den letzten Jahren wurde der Arthropodendiversität und ihrer ökosystemaren Funktion durch eine stärker systemisch und funktionell geprägte Betrachtung von Ökosystemen mehr Aufmerksamkeit zuteil. Ökosystemare Forschung hat gezeigt, dass die Produktivität tropischer Wälder auf nährstoffarmen Böden stark vom Recycling von organischem Material und der Wiederverfügbarmachung darin gebundener Nährstoffe abhängt. An diesem Prozess ist ein hochkomplexes funktionales Netz von Arthropoden und Mikroorganismen maßgeblich beteiligt. Ein breites Spektrum an global bedeutenden Ökosystemfunktionen wird damit von Arthropoden (Insekten, Spinnentieren) bereitgestellt oder zumindest maßgeblich beeinflusst und ein effizienter Schutz der biologischen und funktionellen Vielfalt tropischer Wälder ist nur durch (Umweltschutz-)Konzepte möglich, die Arthropoden mit einschließen. Dafür ist ein detailliertes Wissen über die Strukturen und Mechanismen der Biologie der Arten und die funktionellen Zusammenhänge in Arthropodengemeinschaften von großer Bedeutung.

Inwieweit Sekundarwälder zum Erhalt der Artenvielfalt von (Primär)Wäldern beitragen können, ist zur Zeit noch weitgehend unklar und deshalb ein wichtiger Schwerpunkt der Biodiversitätsforschung und des Naturschutzes. Auf der ganzen Welt, auch in der Region der

Atlantischen Wälder Brasiliens (Mata Atlântica), verschwinden mehr und mehr Primärwälder und die kleinen Reste alter, wenig vom Menschen beeinflusster Wälder unterliegen starkem anthropogenem Druck. Auf der anderen Seite hat aber das wachsende Bewusstsein für Umweltprobleme zu einer steigenden Zahl und einer größeren Fläche sich regenerierender oder angepflanzter Sekundärwälder geführt, die eine immer größere Rolle beim Naturschutz spielen.

Ziel meiner Dissertationsarbeit war die Erfassung der Artenvielfalt und Ökologie der Spinnengemeinschaften in Sekundärwäldern der Mata Atlântica um daraus Rückschlüsse für den Umweltschutz und den Schutz der regionalen Biodiversität zu ziehen. Mein Untersuchungsansatz gliederte sich in zwei Teile: Erstens eine umfangreiche Erfassung der Artenvielfalt der Spinnen (Diversitätsteil) und zweitens eine Untersuchung der ökologischen Zusammenhänge im Rahmen eines Feldexperiments (Experimentalteil).

Zur Erfassung des Beitrags der Sekundärwälder zum Erhalt der regionalen Diversität verglich ich die Spinnengemeinschaften unterschiedlich alter Waldsukzessionsstufen und eines alten, naturnahen Walds (Kapitel 2 & 3). Wir sammelten Spinnen mit Hilfe eines standardisierten Probenahme-Protokolls in 24 Untersuchungsflächen in zwei Naturschutzgebieten im brasilianischen Bundesstaat Paraná. Die untersuchten Wälder der Region sind relativ gut erhalten und die Matrix der kleinräumig strukturierten Landschaft ist noch Wald.

Arten- bzw. Gattungsreichtum und die Diversität der Waldstadien unterschieden sich nicht, wohl aber die Gildendiversität. Die hohe Alpha-Diversität und ein hoher Arten-Turnover zwischen allen Untersuchungsflächen betonen den hohen Wert der Sekundärwälder für den Schutz der Diversität in der untersuchten Region. Die Beta-Diversität basiert wesentlich auf dem turnover, nicht auf einem Zugewinn oder Verlust von Taxa. Die räumlichen Ebenen trugen mehr zur Betadiversität bei als erwartet und der zu erwartende, starke Beitrag der verschiedenen Waldstadien konnte nicht nachgewiesen werden. Diese Verteilungsmuster waren auf Gattungs- und Artniveau und auch über alle Methoden gleich. Daher kann bereits ein Teil des umfangreichen Probenahmeprotokolls sowie eine Identifikation auf Gattungsniveau für Fragestellungen im Rahmen von Umweltschutz-Untersuchungen ausreichend sein.

Im Feldexperiment zeigte sich, dass die künstliche Erweiterung des Lebensraums nicht den erwarteten Einfluss auf die untersuchten Taxa hatte. Die Zugabe von Nahrung hatte einen positiven Effekt auf die Zersetzer, nicht aber auf deren Prädatoren. Diese Ergebnisse legen nahe, dass die Bodenfauna dieser tropischen Wälder durch eine eingeschränkte Nahrungsverfügbarkeit beeinflusst ist, jedoch zeigt der fehlende „bottom-up“-Effekt, dass die Räuber nicht in erster Linie durch die Abundanz ihrer Beute limitiert sind, sondern eher durch Wettbewerb oder ihrerseits durch Prädatoren.

Auch wurden keine Unterschiede zwischen den Sukzessionsstadien sichtbar. Diese Ergebnisse betonen den Wert der Sekundärwaldhabitate für den Schutz von Waldarten und den mit ihnen assoziierten ökologischen Prozessen.

Auf Basis der Ergebnisse der Biodiversitätaufnahmen und des Experimets komme ich zu dem Schluss, dass der Erhalt der Heterogenität des Landschaftsmosaiks ein guter Ansatz für den Erhalt der regionalen Biodiversität der Invertebratengemeinschaft in der südlichen Mata Atlântica zu sein scheint. Unsere Analysen belegen (aus Sicht der Spinnen) die große Bedeutung einer ausgeprägten kleinräumigen Mosaikstruktur verschiedener (Wald-) Regenerationsstadien sowie Landnutzungssystemen und naturnaher Wälder in Schutzgebieten für einen maximalen Schutz der Biodiversität. Um langfristig die Bewahrung eines möglichst breiten Spektrums der Spinnendiversität zu garantieren, sollte daher der Schutz möglichst großer, zusammenhängender Waldgebiete angestrebt werden und dieser ist, falls eine Entscheidung getroffen werden muss, dem Schutz kleiner (meist isoliert gelegener) Restflächen naturnaher, alter Wälder vorzuziehen.

8 – Appendix

Supporting Materials Chapter 2

Appendix Chapter 2 – Table 1. List of morphospecies of adult spiders recorded in the forest stages (H – herbaceous, A – arboreal, M – medium, F – old-growth forest) of the two nature reserves Cachoeira (Ca) and Itaqui (It) (specimens from all methods and replicate sites pooled).

	Locality and Stage							
Taxon	**Ca-H**	**Ca-A**	**Ca-M**	**Ca-F**	**It-H**	**It-A**	**It-M**	**It-F**
Amaurobiidae								
Amaurobiidae sp. 1	0	0	0	1	0	0	0	6
Amaurobiidae sp. 2	0	0	0	0	0	1	0	0
Amaurobiidae sp. 3	0	0	0	1	0	0	0	0
Amaurobiidae sp. 4	0	0	3	2	0	0	3	1
Anapidae								
Anapidae sp.	0	0	0	0	0	0	1	0
Anyphaenidae								
Amaurobioidinae sp. 1	1	0	0	0	0	0	0	0
Aysha sp. 1	11	2	0	1	7	1	1	1
Aysha sp. 2	1	0	0	0	0	0	0	0
Aysha sp. 4	0	0	0	1	0	0	0	0
Buckupiella imperatriz Brescovit, 1997	4	1	0	0	4	0	0	0
gen. 1 sp. 1	16	0	0	0	0	0	0	0
Patrera cita (Keyserling, 1891)	0	10	19	18	0	2	15	9
Temnida sp. 1	0	0	0	0	1	0	0	0
Wulfila sp. 1	0	0	0	0	0	1	0	0
Wulfilopsis sp. 1	2	1	1	3	8	2	10	4
Araneidae								
Araneidae sp. 8	0	1	0	0	0	0	0	0
Acacesia tenella (L. Koch,1871)	1	0	0	0	7	0	0	0

Acacesia yacuiensis Glueck, 1994	0	0	0	0	0	2	1	0
Alpaida biasii Levi, 1988	0	0	0	0	3	0	0	0
Alpaida canoa Levi, 1988	0	0	2	0	0	0	1	0
Alpaida rubellula (Keyserling, 1892)	0	0	0	1	0	0	0	0
Alpaida septemmammata (O. P.-Cambridge, 1889)	0	0	0	0	0	0	0	1
Alpaida sp. 3	0	0	0	1	0	0	0	0
Alpaida sp. 5	2	0	0	0	0	0	0	0
Alpaida tijuca Levi, 1988	1	0	1	0	0	1	3	0
Alpaida truncata (Keyserling, 1865)	0	0	1	0	0	0	0	0
Araneus iguacu Levi, 1991	0	1	0	2	0	2	3	3
Araneus tijuca Levi, 1991	0	0	2	1	2	1	1	0
Araneus unanimus (Keyserling, 1879)	0	0	0	1	0	0	0	0
Araneus uniformis (Keyserling, 1879)	0	0	0	0	1	0	0	0
Bertrana rufostriata Simon, 1893	1	0	0	0	7	0	0	0
Bertrana sp. 1	0	0	0	0	2	0	0	0
Cyclosa fililineata Hingston, 1932	1	0	4	8	1	2	1	2
Cyclosa morretes Levi, 1999	0	0	0	3	0	0	0	2
Enacrosoma anomalum (Taczanowski, 1873)	0	0	0	0	0	1	0	0
Eustala sp. 1	1	0	0	1	0	0	0	0
Eustala sp. 2	1	0	0	0	1	0	0	0
Eustala sp. 3	0	0	0	0	3	0	0	0
Eustala sp. 4	0	0	0	0	2	0	0	0
Eustala sp. 6	1	0	0	0	1	0	0	0
Eustala sp. 8	0	0	0	0	3	0	0	0
Hypognatha sp. 1	0	0	1	0	0	0	0	0
Kaira echinus (Simon, 1897)	0	1	0	0	0	0	0	0
Kapogea sellata (Simon, 1895)	0	0	1	0	1	0	0	0
Mangora blumenau Levi, 2007	4	0	2	14	0	4	6	2
Mangora bocaina Levi, 2007	0	1	0	0	1	4	1	0
Mangora botelho Levi, 2007	0	0	1	0	0	0	0	0
Mangora caparu Levi, 2007	1	0	1	3	0	0	3	1
Mangora chacobo Levi, 2007	0	0	0	0	0	1	0	0

Mangora manicore Levi, 2007	4	3	3	3	1	0	1	5
Mangora melanocephala (Taczanowski, 1874)	1	0	0	0	2	0	0	0
Mangora missa Levi, 2007	0	1	0	0	0	0	1	1
Mangora sp. 1	0	1	7	10	0	2	2	0
Mangora sp. 2	0	0	0	0	0	0	1	2
Metazygia manu Levi, 1995	0	0	0	0	1	0	1	0
Micrathena crassispina (C. L. Koch, 1836)	0	0	0	0	0	0	0	1
Micrathena excavata (C. L. Koch, 1836)	0	0	1	1	0	1	0	1
Micrathena sanctispiritus Brignoli, 1983	0	0	0	1	0	0	0	0
Micrathena triangularis (C. L. Koch, 1836)	1	2	0	0	0	0	1	0
Micrepeira albomaculata Schenkel, 1953	0	0	0	1	0	0	0	0
Parawixia audax (Blackwall, 1863)	3	0	0	0	2	0	1	2
Parawixia kochi (Taczanowski, 1873)	0	0	0	0	1	0	0	0
Parawixia monticola (Keyserling, 1892)	0	0	0	0	0	0	3	1
Scoloderus cordatus (Taczanowski, 1879)	0	0	1	0	2	0	0	4
Scoloderus gibber (O. P.-Cambridge, 1898)	1	1	0	0	0	0	0	0
Testudinaria gravatai Levi, 2005	0	0	0	1	0	2	0	0
Verrucosa sp. 1	0	1	1	2	0	1	1	3
Wagneriana eupalaestra (Mello-Leitão, 1943)	0	0	2	1	0	0	0	0
Wagneriana heteracantha (Mello-Leitão, 1943)	0	0	2	0	0	0	0	0
Wagneriana iguape Levi, 1991	0	1	1	1	0	1	2	1
Wagneriana janeiro Levi, 1991	0	1	1	6	0	1	3	1
Wagneriana taim Levi, 1991	3	0	0	0	2	0	0	1
Wixia sp. 1	0	1	0	0	0	0	0	0
Caponiidae								
Caponiidae sp.	0	0	0	0	0	0	1	0
Corinnidae								
Castianeira sp. 1	0	0	0	0	1	0	0	0
Castianeira sp. 2	0	1	0	0	0	0	0	0
Corinna sp. 1	0	1	0	1	0	0	1	0
Corinna sp. 2	1	1	0	0	0	0	0	0
Corinna sp. 3	0	1	0	0	0	0	0	0

Corinna sp. 4	0	0	0	0	0	0	1	0
Corinna sp. 5	1	0	0	0	2	0	1	0
Corinna sp. 6	0	0	0	0	0	1	0	0
Corinna sp. 7	0	0	0	0	0	0	1	0
Ianduba varia (Keyserling, 1891)	3	2	0	1	1	0	0	0
Myrmecium sp. 1	0	0	1	0	0	0	0	1
Trachelas sp. 1	0	1	0	1	0	0	1	0
Trachelas sp. 2	0	0	0	0	0	0	1	0
Ctenidae								
Ctenus medius Keyserling, 1891	1	3	4	4	0	1	3	2
Ctenus ornatus (Keyserling, 1877)	1	0	0	0	0	0	0	0
Ctenus sp. 1	0	0	0	1	0	0	0	0
Isoctenus janeirus (Walckenaer, 1837)	0	0	0	1	0	0	4	0
Isoctenus ordinario Polotow & Brescovit, 2009	0	0	0	1	0	2	4	1
Isoctenus strandi Mello-Leitão, 1936	7	11	4	16	4	11	15	21
Deinopidae								
Deinopis sp. 1	0	0	1	2	0	0	0	0
Dictynidae								
Thallumetus sp. 1	0	0	20	25	0	0	6	7
Dipluridae								
Trechona rufa Vellard, 1924	0	0	0	0	0	0	1	0
Gnaphosidae								
Gnaphosidae sp.	0	0	0	0	2	0	0	0
Hahniidae								
Hahniidae sp. 1	0	0	5	10	0	0	0	0
Hahniidae sp. 2	0	0	0	0	0	0	1	0
Hahniidae sp. 3	0	0	1	0	0	0	0	0
Hahniidae sp. 4	0	0	2	0	0	0	0	0
Hahniidae sp. 5	1	0	1	0	0	0	0	0
Hahniidae sp. 6	0	0	0	0	0	0	1	0
Hahniidae sp. 7	0	0	0	0	4	0	8	0

Hersiliidae								
Ypypuera crucifera (Vellard, 1924)	0	2	0	0	0	0	0	0
Linyphiidae								
Linyphiidae indet. 1	0	0	0	0	1	0	0	0
Linyphiidae indet. 2	0	0	0	0	3	0	0	0
Linyphiidae sp. 1	0	3	0	0	0	21	1	0
Linyphiidae sp. 2	2	0	0	0	0	1	0	0
Linyphiidae sp. 3	0	0	2	0	0	5	7	2
Anodoration claviferum Millidge, 1991	22	5	0	0	0	0	0	0
Anodoration sp. 1	2	0	0	0	81	15	0	0
Asemostera tacuapi Rodrigues, 2007	0	0	1	0	3	0	0	1
Dubiaranea sp.	0	0	1	0	0	0	0	0
Dubiaranea sp. 1	2	0	0	0	0	0	0	0
Dubiaranea sp. 2	0	0	0	0	0	1	0	0
Exechopsis conspicua Millidge, 1991	0	0	0	0	0	0	0	2
Exechopsis sp.	1	6	2	0	0	16	5	0
Exechopsis sp. 1	0	1	0	0	0	0	1	2
Exechopsis sp. 2	1	0	0	0	0	0	0	0
Exocora sp.	0	0	0	2	0	3	0	0
Exocora sp. 1	0	0	2	0	0	0	0	1
Labicymbium sp.	3	0	0	0	0	0	0	0
Labicymbium sp. 1	0	3	0	0	0	1	0	0
Lepthyphantes sp.	0	0	1	0	0	0	0	0
Lepthyphantes sp. 2	1	0	0	0	0	0	0	0
Linyphiinae indet. 1	0	0	0	1	0	0	0	0
Linyphiinae indet. 2	2	0	0	0	0	0	0	0
Meioneta sp.	0	0	0	0	0	0	0	1
Meioneta sp. 1	0	2	0	0	1	1	8	8
Meioneta sp. 2	0	0	0	0	0	0	8	0
Meioneta sp. 3	0	0	0	0	3	0	0	0
Meioneta sp. B	0	3	0	0	0	0	0	0
Moyosi prativaga (Keyserling, 1886)	0	1	0	0	0	0	0	0

Moyosi sp.	0	1	0	0	0	0	0	0
Moyosi sp. 1	1	0	0	0	0	1	0	0
Psilocymbium sp.	5	0	0	0	0	0	0	0
Psilocymbium sp. 1	6	0	1	0	0	0	0	0
Psilocymbium sp. 2	1	0	0	0	0	0	0	0
Scolecura sp.	1	0	0	0	0	0	0	0
Sphecozone diversicolor (Keyserling, 1886)	17	0	0	0	19	0	0	0
*Sphecozone labiata (*Keyserling, 1886)	0	3	0	0	0	0	0	5
Sphecozone personata (Simon, 1894)	10	13	2	1	0	5	7	7
Sphecozone sp.	1	0	0	0	0	0	0	0
Sphecozone sp. 1	3	5	0	0	6	0	0	0
Sphecozone tumidosa (Keyserling, 1886)	0	1	0	0	0	2	0	0
Sphecozone venialis (Keyserling, 1886)	0	0	0	34	0	8	39	19
Vesicapalpus simplex Millidge, 1991	0	0	0	0	0	0	1	0
Liocranidae								
Gen. 1 sp. 1	1	0	0	0	0	0	0	0
Lycosidae								
Agalenocosa sp. 1	7	0	0	0	0	0	0	0
Hogna sp. 1	0	2	0	0	2	0	0	0
Hogna sp. 2	4	2	0	0	0	0	0	0
Hogna sternalis (Bertkau, 1880)	0	5	0	0	3	0	0	0
Lobizon sp. 1	0	0	0	9	0	0	0	3
Lobizon sp. 2	0	4	0	3	11	0	0	0
Lycosa erythrognatha Lucas, 1836	0	0	0	0	1	0	0	0
Lycosa inornata Blackwall, 1862	3	0	0	0	1	0	0	0
Lycosinae sp. 1	0	0	0	5	0	0	0	0
Mimetidae								
Ero sp. 1	2	2	8	7	2	2	3	5
Ero sp. 2	2	0	0	0	0	1	0	0
Gelanor sp. 1	0	0	0	1	0	0	0	1
Mimetinae sp. 1	0	0	1	0	0	0	0	0

Miturgidae								
Radulphius sp. 1	1	1	0	0	0	0	0	1
Strotarchus sp. 1	0	1	0	0	0	0	0	0
Teminius insularis (Lucas, 1857)	0	0	0	0	1	0	0	0
Mysmenidae								
Mysmenidae sp. 1	0	0	0	1	0	0	0	0
Itapua sp.	1	2	1	0	0	0	0	0
Itapua sp. 1	0	0	1	0	0	0	0	0
Microdipoena sp. 1	0	0	0	0	2	6	2	24
Nemesiidae								
Acanthogonatus sp. 1	0	0	1	1	0	1	2	0
Pycnothele sp. 1	0	0	2	1	0	0	0	0
Nesticidae								
Eidmanella sp.	0	0	0	1	0	0	0	0
Ochyroceratidae								
Ochyrocera sp. 1	0	0	0	0	1	1	3	1
Ochyrocera sp. 2	0	0	0	3	0	0	1	3
Ochyrocera sp. 3	0	0	0	0	0	1	0	0
Oonopidae								
Gamasomorpha sp.	0	0	1	0	0	0	0	0
gen. 2 sp. 1	0	0	0	0	0	1	0	0
Neoxyphinus sp. 1	0	0	0	3	0	1	0	0
Oonops sp. 1	2	2	1	1	3	3	3	1
Oonops sp. 2	0	0	0	0	0	4	2	0
Orchestina sp. 1	0	0	0	0	0	0	4	0
Predatoroonops sp. 1	0	1	0	3	0	0	2	1
Triaeris stenaspis Simon, 1891	0	0	0	0	1	0	0	0
Oxyopidae								
Hamataliwa sp. 1	0	2	1	0	0	0	0	0
Hamataliwa sp. 2	0	1	0	0	2	0	1	0
Oxyopes salticus Hentz, 1845	1	0	0	0	0	0	0	0

Peucetia flava Keyserling, 1877	0	0	0	0	1	0	0	0
Palpimanidae								
Palpimanidae sp.	0	0	1	0	0	0	0	0
Notiothops birabeni (Zapfe, 1961)	0	0	0	0	0	0	0	1
Philodromidae								
Cleocnemis sp. 1	0	0	0	0	0	1	0	0
Pholcidae								
Pholcidae sp. 1	11	5	3	3	0	0	0	0
Mesabolivar aff. *brasiliensis* (Moenkhaus, 1898)	0	0	0	1	0	0	0	0
Mesabolivar aff. *cyaneotaeniatus* (Keyserling, 1891)	0	0	0	3	0	0	0	0
Mesabolivar aff. *guapiara* Huber, 2000	0	0	0	1	0	4	1	6
Mesabolivar brasiliensis (Moenkhaus, 1898)	0	1	3	11	0	0	0	0
Mesabolivar cyaneotaeniatus (Keyserling, 1891)	0	0	0	2	0	0	0	0
Mesabolivar luteus (Keyserling, 1891)	0	9	1	24	0	4	7	4
Mesabolivar rudilapsi Machado, Brescovit & Francisco, 2007	1	0	2	0	0	6	1	2
Mesabolivar sp. 1	0	0	0	0	1	0	3	0
Mesabolivar sp. 2	0	2	0	0	0	3	0	2
Metagonia aff. *bonaldoi* Huber, 2000	0	1	0	1	0	0	0	0
Metagonia furcata Huber, 2000	0	0	1	1	0	1	0	0
Metagonia sp. 1	0	3	2	5	0	5	4	0
Metagonia sp. 2	0	0	0	0	0	1	0	0
Ninetines sp. 1	0	0	0	0	0	0	0	2
Ninetines sp. 2	0	1	1	0	0	0	1	1
Tupigea nadleri Huber, 2000	0	2	0	1	0	0	6	0
Tupigea sp. 1	0	1	3	0	0	0	0	0
Pisauridae								
Architis brasiliensis (Mello-Leitão, 1940)	2	2	18	20	0	3	1	7
Architis capricorna Carico, 1981	1	0	0	0	0	0	0	0
Prodidomidae								
gen. sp.	0	0	0	0	0	0	2	0
Salticidae								
Salticidae sp. 26	1	0	0	0	0	0	0	0

Salticidae sp. 38	0	0	0	0	1	0	0	0
Salticidae sp. 45	0	0	0	0	0	1	0	0
Salticidae sp. 46	0	0	0	0	0	1	0	0
Salticidae sp. 54	0	0	0	0	0	0	3	0
Salticidae sp.	0	0	0	0	0	0	2	0
Amphidraus sp. 1	0	1	1	0	0	0	0	0
Amycinae sp.1	0	0	2	0	0	0	1	1
Amycinae sp.2	0	1	0	0	0	1	0	0
Arnoliseus graciosa Braul & Lise, 2002	0	4	1	4	0	0	2	3
Asaphobelis physonychus Simon, 1902	3	2	2	1	1	1	0	1
Atelurius sp. 1	1	0	0	0	0	0	1	0
Chira spinosa Mello-Leitão, 1945	1	0	0	0	1	0	0	0
Chira thysbe Simon, 1902	2	0	0	0	0	0	0	0
Coryphasia sp. 1	0	0	0	1	0	0	0	0
Coryphasia sp. 2	0	2	3	0	0	1	1	0
Cotinusa sp. 1	2	1	2	0	0	0	0	1
Cotinusa sp. 2	0	0	0	0	0	1	1	0
Cylistella sp. 1	0	0	1	1	0	3	2	0
Cyllodania sp. 1	0	0	0	0	1	0	0	0
Dendryphantinae sp.1	1	0	0	0	0	0	0	0
Dendryphantinae sp.2	0	0	0	0	1	0	0	0
Euophryinae sp. 2	0	0	0	2	0	0	1	0
Euophryinae sp. 3	2	0	0	0	0	0	0	0
Euophryinae sp. 4	0	0	0	2	0	0	0	0
Euophryinae sp. 5	1	0	0	0	0	0	0	0
Euophryinae sp. 6	0	3	0	0	1	1	0	0
Euophryinae sp. 7	0	0	1	0	0	1	1	2
Euophryinae sp. 8	1	0	0	0	1	0	0	0
Euophryinae sp. 9	1	0	0	1	0	0	0	0
Euophryinae sp. 10	0	0	1	0	0	0	1	2
Euophryinae sp. 11	0	0	0	0	0	0	0	1
Euophryinae sp. 12	0	0	0	0	0	0	1	0

Euophryinae sp. 13	0	0	0	0	0	1	0	0
Euophryinae sp. 14	0	0	0	0	0	1	0	0
gen. n. sp. 1	0	0	1	0	0	0	0	0
Hyetussinae sp. 1	0	0	1	3	0	0	0	2
Ilargus sp. 1	0	0	0	0	1	0	0	0
Itata sp. 1	0	0	0	1	0	0	0	0
Lyssomanes sp. 1	0	0	0	0	0	0	0	1
Lyssomanes sp. 2	0	0	0	0	0	0	1	0
Maeota dichrura Simon, 1901	0	1	0	0	5	1	0	1
Noegus sp. 1	8	9	11	7	5	4	7	10
Ramboia sp. 1	3	0	0	0	2	0	4	0
Romitia sp. 1	2	0	0	0	1	1	0	0
Semnolius sp. 1	0	1	0	0	1	0	0	1
Semora napaea Peckham & Peckham, 1892	0	0	0	0	4	0	0	0
Synemosyna lauretta Peckham & Peckham, 1892	1	0	0	0	3	0	0	0
Synemosyninae sp. 1	0	0	0	1	0	2	3	0
Tanybelus aeneiceps Simon, 1902	0	0	0	0	0	0	0	1
Tariona sp. 1	18	38	19	19	1	7	33	28
Tariona sp. 3	0	3	0	0	0	0	0	0
Tariona sp. 4	5	4	0	0	0	0	0	0
Tariona sp. 5	2	0	0	0	0	0	0	0
Tariona sp. 6	0	0	0	0	1	1	0	0
Vinnius uncatus Simon, 1902	3	0	0	0	0	0	0	0
Scytodidae								
Scytodes antonina Rheims & Brescovit, 2009	6	2	9	0	7	6	3	3
Scytodes globula Nicolet, 1849	0	0	0	1	0	0	0	0
Scytodes sp. 1	0	0	2	1	0	1	1	0
Sparassidae								
Olios sp. 1	1	0	0	1	0	0	0	0
Symphytognathidae								
Anapistula sp. 1	0	0	1	0	0	0	0	0
Synotaxidae								

Synotaxus sp. 1	0	0	0	0	0	1	0	1
Tetragnathidae								
Azilia histrio Simon, 1895	1	0	0	0	0	0	0	1
Chrysometa boraceia Levi, 1986	0	0	0	0	2	0	2	0
Chrysometa ludibunda (Keyserling, 1893)	0	2	1	2	1	1	13	2
Chrysometa sp.	0	0	0	1	0	0	3	0
Cyrtognatha sp. 1	9	3	1	0	4	0	2	0
Glenognatha sp. 1	1	0	0	0	0	0	0	0
Leucauge sp.	0	0	0	0	0	1	0	1
Leucauge sp. 1	0	1	1	0	0	2	0	5
Leucauge sp. 2	0	0	1	0	0	0	5	0
Tetragnatha sp.	0	2	0	0	0	0	0	0
Theridiidae								
Theridiidae sp. 1	0	0	0	0	0	0	0	1
Achaearanea sp. 1	0	0	0	0	0	1	0	0
Achaearanea sp. 18	0	0	0	1	0	0	0	0
Achaearanea tingo Levi, 1963	0	1	1	0	0	1	0	0
Ameridion unanimum (Keyserling, 1891)	0	0	0	0	4	0	0	0
Anelosimus ethicus (Keyserling, 1884)	0	0	0	0	1	0	0	0
Anelosimus nigrescens (Keyserling, 1884)	1	0	0	0	0	0	0	0
Argyrodes elevatus Taczanowski, 1873	0	0	0	1	0	0	0	0
Argyrodes sp. 1	0	0	0	0	0	1	0	1
Ariamnes attenuatus (O. P.-Cambridge, 1881)	0	0	2	1	0	0	1	2
Ariamnes longissimus Keyserling, 1891	1	1	0	0	1	1	0	0
Ariamnes sp. 2	0	0	0	0	0	0	1	0
Chrosiothes niteroi Levi, 1964	0	0	0	3	13	4	7	9
Chrosiothes perfidus Marques & Buckup, 1997	0	1	1	3	2	3	0	5
Chrosiothes sp. 1	0	0	0	2	0	0	0	0
Chrysso gounellei Levi, 1962	1	13	0	0	0	1	0	0
Chrysso nigrosterna Keyserling, 1891	0	0	0	0	0	3	3	0
Chrysso rubrovittata (Keyserling, 1884)	0	0	0	0	1	0	0	0
Chrysso sp. 3	1	2	0	1	0	0	0	6

Chrysso sp. 32	0	0	0	0	0	0	0	1
Coleosoma sp. 1	0	0	0	0	2	0	0	0
Cryptachaea altiventer (Keyserling, 1884)	2	1	0	0	1	0	0	0
Cryptachaea digitus (Buckup & Marques, 2006)	0	0	0	0	0	0	0	3
Cryptachaea cinnabarina (Levi, 1963)	0	0	0	0	0	0	1	2
Cryptachaea hirta (Taczanowski, 1873)	0	0	0	0	8	0	0	0
Cryptachaea isana (Levi, 1963)	3	0	0	0	0	0	0	0
Cryptachaea jequirituba (Levi, 1963)	0	0	0	0	0	2	0	0
Cryptachaea migrans (Keyserling, 1884)	0	0	0	3	0	0	0	0
Cryptachaea passiva (Keyserling, 1891)	2	2	3	6	2	5	2	7
Cryptachaea rioensis (Levi, 1963)	0	0	0	0	0	0	1	0
Cryptachaea sicki (Levi, 1963)	0	0	0	0	0	0	0	1
Cryptachaea sp. 1	0	0	0	0	0	0	1	0
Cryptachaea taim (Buckup & Marques, 2006)	1	0	1	1	0	2	4	3
Cryptachaea triguttata (Keyserling, 1891)	0	4	3	2	1	3	3	0
Dipoena atlantica Chickering, 1943	0	0	0	0	1	1	0	1
Dipoena bryantae Chickering, 1943	0	0	0	0	0	1	0	0
Dipoena cordiformis Keyserling, 1886	0	0	1	0	0	0	0	0
Dipoena duodecimpunctata Chickering, 1943	0	0	0	1	0	0	0	0
Dipoena ira Levi, 1963	4	0	0	1	1	0	1	1
Dipoena keyserlingi Levi, 1963	1	0	0	0	0	0	2	0
Dipoena pumicata (Keyserling, 1886)	1	4	3	2	3	0	1	1
Dipoena pusilla (Keyserling, 1886)	0	0	4	5	0	2	0	1
Dipoena santacatarinae Levi, 1963	5	1	4	0	0	0	0	0
Dipoena sp.	1	0	0	0	0	0	1	2
Dipoena sp. 2	8	10	11	3	1	20	42	4
Dipoena sp. 3	0	0	0	0	0	0	1	0
Dipoena sp. 6	0	0	0	0	0	3	0	0
Dipoena sp. 8	1	0	0	0	3	0	0	0
Dipoena sp. 12	5	9	5	12	3	4	11	9
Dipoena sp. 21	0	1	0	0	0	0	0	0
Dipoena sp. 22	0	0	0	0	0	0	1	1

Dipoena sp. 58	0	0	0	0	0	2	0	0
Dipoena variabilis (Keyserling, 1886)	0	1	0	1	0	0	0	1
Emertonella taczanowskii (Keyserling, 1886)	0	0	0	1	1	1	0	0
Episinus sp.	0	0	0	0	0	1	0	0
Episinus sp. 1	3	2	6	4	9	6	17	5
Episinus sp. 2	0	0	0	0	21	0	0	0
Episinus teresopolis Levi, 1964	1	0	0	0	2	0	0	0
Euryopis sp.	1	0	0	0	0	0	0	0
Euryopis sp. 1	2	0	0	0	2	1	0	0
Exalbidion sp. 1	6	1	0	3	1	1	0	0
Exalbidion sp. 2	0	1	0	0	0	0	0	0
Faiditus acuminatus (Keyserling, 1891)	0	0	0	0	0	2	0	0
Faiditus sp. 1	0	0	1	1	0	0	0	0
Faiditus sp. 2	0	1	0	1	0	0	1	1
Faiditus sp. 3	0	0	0	3	0	0	1	0
gen. 2 sp. 2	0	0	0	0	0	0	1	0
Guaraniella mahnerti Baert, 1984	0	0	0	0	4	15	31	5
Guaraniella sp.	0	0	0	0	0	0	1	0
Guaraniella sp. 1	3	0	0	5	0	0	0	0
Hadrotarsinae sp. 1	0	0	0	0	0	0	1	0
Hadrotarsinae sp. 2	0	0	0	0	3	0	0	0
Hadrotarsinae sp. 3	0	0	0	3	0	0	0	0
Helvibis sp. 1	2	3	0	0	0	0	1	0
Hetschkia gracilis Keyserling, 1886	14	5	2	0	4	0	1	0
Janula bicorniger (Simon, 1894)	0	1	13	6	0	2	21	32
Neopisinus cognatus (O. P.-Cambridge, 1893)	0	1	0	0	0	0	0	0
Phycosoma altum (Keyserling, 1886)	4	6	2	0	13	2	0	0
Rhomphaea sp. 1	1	0	1	1	0	0	0	0
Rhomphaea sp. 2	0	0	1	0	0	0	0	1
Spintharus gracilis Keyserling, 1886	2	10	8	25	1	10	74	30
Stemmops sp. 2	1	0	0	0	0	0	0	0
Styposis selis Levi, 1964	0	0	0	0	1	1	0	1

Tekellina crica Marques & Buckup, 1993	1	0	0	0	0	0	2	0
Tekellina sp. 3	0	0	0	1	0	0	0	0
Tekellina sp. 4	0	0	0	0	0	0	0	1
Theridion biezankoi Levi, 1963	1	0	0	0	0	0	1	0
Theridion minutissimum Keyserling, 1884	0	1	0	0	0	0	0	0
Theridion opolon Levi, 1963	0	0	1	0	0	0	0	0
Theridion plaumanni Levi, 1963	11	2	0	0	43	0	0	1
Theridion quadripartitum Keyserling, 1891	0	0	1	3	0	0	0	0
Theridion sp. 1	1	0	0	0	1	0	0	0
Theridion sp. 2	0	0	0	1	0	0	0	0
Theridion sp. 11	0	0	0	0	0	1	0	0
Theridion sp. 28	0	0	0	0	0	0	0	1
Theridion sp. 32	1	12	1	23	0	0	0	8
Theridion sp. 36	0	0	0	1	0	0	0	0
Theridion sp. 40	0	1	0	0	0	0	0	0
Theridion sp. 47	0	0	1	1	0	0	0	0
Theridion sp. 63	0	0	0	1	0	0	0	0
Theridion sp. 68	0	0	0	1	1	0	0	0
Theridion teresae Levi, 1963	1	0	0	0	1	0	0	1
Theridula gonygaster (Simon, 1873)	0	0	0	0	1	0	0	0
Thwaitesia affinis O. P.-Cambridge, 1882	7	9	7	1	2	7	12	41
Thwaitesia sp. 1	0	0	1	1	0	0	0	0
Thymoites anicus Levi, 1964	8	2	0	0	4	0	0	0
Thymoites melloleitaoni (Bristowe, 1938)	0	0	0	1	0	15	1	1
Thymoites sp.	1	0	0	0	0	1	0	0
Thymoites sp. ?	0	0	0	0	0	2	0	0
Thymoites sp. 1	4	1	2	4	1	0	1	0
Thymoites sp. 2	5	0	1	3	0	0	0	0
Thymoites sp. 4	1	0	0	0	0	0	1	2
Thymoites sp. 5	0	0	1	0	0	0	0	0
Thymoites sp. 7	0	0	2	3	0	7	1	0
Thymoites sp. 12	1	0	0	0	0	0	0	0

Wamba crispulus (Simon, 1895)	4	1	0	0	0	0	0	0
Wirada sp. 1	0	0	0	0	0	0	1	0
Theridiosomatidae								
gen. indet. 1	0	1	0	0	1	0	0	0
gen. indet. 3	1	0	1	5	0	0	0	0
gen. indet. 4	0	0	0	1	0	0	0	1
gen. sp. 1	0	0	1	0	0	0	0	1
Chthonos sp.	1	0	0	0	0	0	0	0
Chthonos sp.1	0	0	0	0	0	1	3	0
Chthonos sp.2	0	0	0	0	0	0	1	0
Naatlo sp.	0	0	2	0	0	2	0	1
Naatlo sp. 1	0	0	0	0	0	0	1	0
Plato sp. 1	0	0	0	0	0	0	0	1
Theridiosoma sp. 1	5	0	0	1	0	0	0	0
Theridiosoma sp. 3	0	0	0	2	0	0	0	0
Theridiosoma sp. 4	0	0	0	1	0	0	0	1
Thomisidae								
Acentroscelus sp. 1	0	2	1	0	0	0	1	1
Aphantochilus taurifrons (O. P.-Cambridge, 1881)	0	0	1	1	0	1	0	0
Deltoclita sp. 1	1	0	1	1	2	1	2	0
Epicadinus sp. 1	0	1	0	2	0	0	2	1
Misumenops sp. 1	1	0	0	0	0	0	0	0
Onocolus sp. 1	0	0	7	1	0	0	0	1
Titidius sp. 1	8	10	1	0	2	5	0	0
Tmarus sp. 1	3	12	4	3	9	3	9	5
Tmarus sp. 2	4	7	2	0	2	2	2	1
Tmarus sp. 3	0	0	1	1	0	0	0	0
Tmarus sp. 4	0	0	0	1	0	0	0	0
Tmarus sp. 5	0	1	0	0	0	0	0	0
Titanoecidae								
Goeldia sp. 1	0	0	0	0	7	0	0	0
Trechaleidae								

Neoctenus comosus Simon, 1897	0	0	0	0	1	0	0	0
Uloboridae								
Conifaber sp. 1	0	1	0	0	0	0	0	0
Miagrammopes sp. 1	0	1	8	6	0	2	2	3
Miagrammopes sp. 2	4	0	8	8	0	3	9	9
Uloborus sp.	0	0	0	0	0	0	0	1
Uloborus sp. 1	0	0	0	1	0	0	1	3
Zodariidae								
Zodariidae sp.	0	0	0	0	0	0	1	0
Zoridae								
gen. 1 sp. 14	8	0	0	0	0	0	0	0
gen. 1 sp. A	30	74	88	103	21	110	107	64
gen. 1 sp. B	0	2	1	0	0	5	1	1
gen. 1 sp. C	20	28	2	21	16	50	31	20
gen. 1 sp. D	14	0	20	12	0	0	0	0
gen. 1 sp. E	1	0	0	0	0	0	0	0
gen. 1 sp. F	0	1	0	0	0	0	0	0
gen. 1 sp. G	0	3	0	1	0	2	1	2

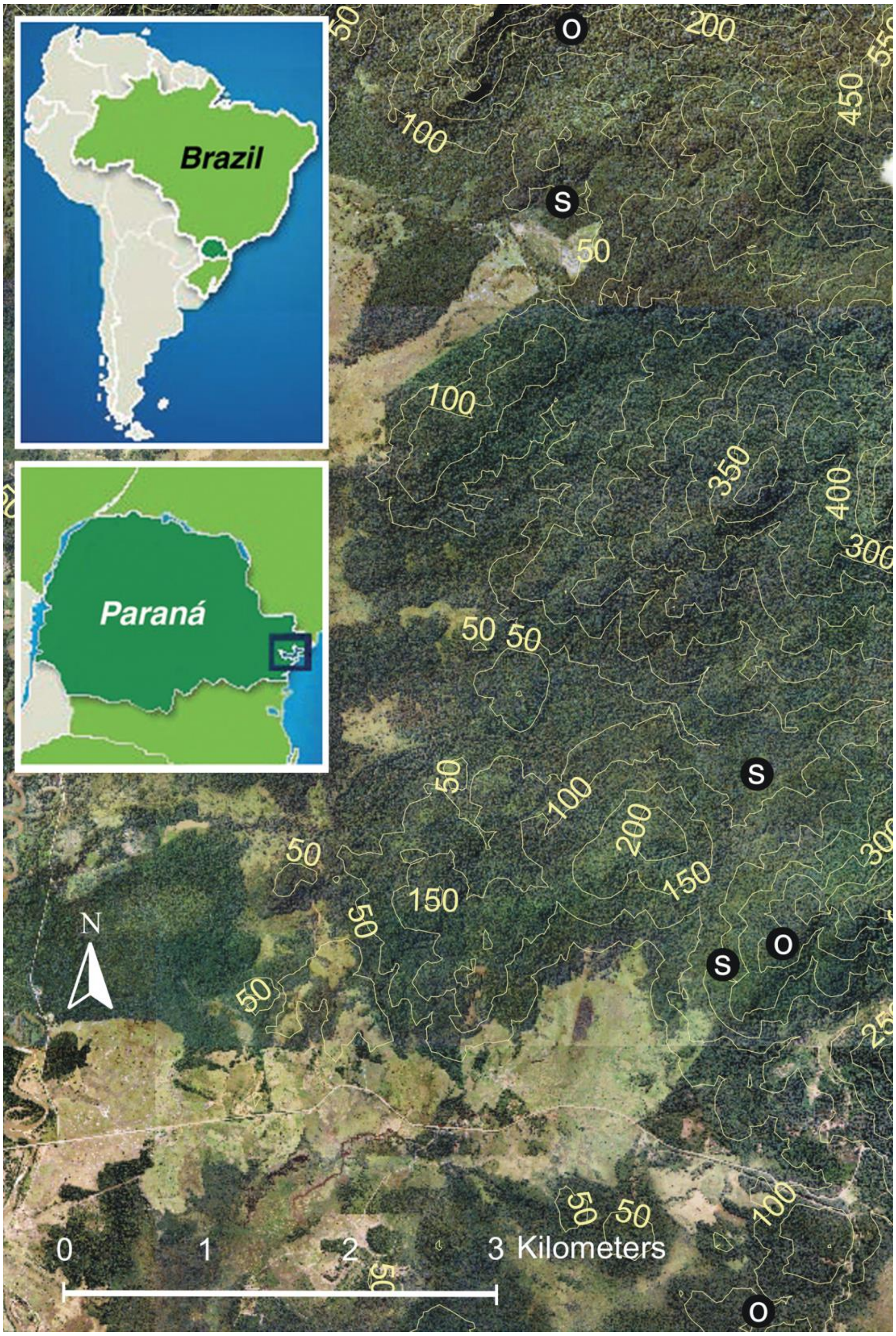
* Nomenclature (order) of the morphospecies originates from the system of the experts/hosting institutions: IBSP - Instituto Butantan, São Paulo; FZB: Fundação Zoobotânica, Porto Alegre.

Supporting Materials Chapter 3

Appendix Chapter 3 – Table 1. Location of the study sites of the SOLOBIOMA project – decimal coordinates (WGS 84)

site number	site code	latitude	Longitude
1	**Ca-H-1**	-25,25375	-48,67635
2	**Ca-H-2**	-25,30634	-48,68340
3	**Ca-H-3**	-25,31717	-48,67106
4	**Ca-A-1**	-25,25620	-48,67055
5	**Ca-A-2**	-25,29103	-48,65582
6	**Ca-A-3**	-25,30374	-48,65969
7	**Ca-M-1**	-25,25314	-48,67277
8	**Ca-M-2**	-25,30072	-48,67142
9	**Ca-M-3**	-25,32819	-48,67675
10	**Ca-F-1**	-25,24398	-48,66944
11	**Ca-F-2**	-25,30215	-48,65403
12	**Ca-F-3**	-25,32434	-48,65530
13	**It-H-1**	-25,31375	-48,45289
14	**It-H-2**	-25,24667	-48,52417
15	**It-H-3**	-25,23790	-48,49781
16	**It-A-1**	-25,31886	-48,46256
17	**It-A-2**	-25,25086	-48,52092
18	**It-A-3**	-25,26217	-48,48744
19	**It-M-1**	-25,30883	-48,45064
20	**It-M-2**	-25,24592	-48,50539
21	**It-M-3**	-25,24753	-48,49206
22	**It-F-1**	-25,30883	-48,46511
23	**It-F-2**	-25,25908	-48,50886
24	**It-F-3**	-25,27325	-48,48714

Supporting Materials Chapter 4



Appendix Chapter 4 – Figure 1. Maps showing the location of the study area as well as the location of the sites with secondary (S) and old-growth forests (O).

Appendix Chapter 4 – Table 1. Sum of (per method) sampled individuals of groups across sites with secondary or old-growth forests for which a significant effect for at least one of the treatments was found (chapter 4, table 1). A full data set is available on request.

soil samples	Treatment	Acari	Coleoptera	Collembola	Formicidae	Hemiptera	Insect larvae	Opiliones	Symphyla	Predators	Decomposers	all arthropods
secondary forest	Control	196	20	228	348	10	16	1	10	13	452	861
	Food	394	34	791	462	18	41	0	31	7	1234	1803
	Food/Space	318	33	542	381	36	26	1	35	18	925	1421
	Space	391	21	152	242	21	9	1	34	15	611	946
old-growth forest	Control	330	36	114	301	21	37	0	25	35	491	921
	Food	427	43	577	372	19	75	0	24	36	1050	1616
	Food/Space	468	50	384	282	50	55	2	13	53	895	1389
	Space	249	31	117	143	18	27	0	13	42	417	682
	sum	**2773**	**268**	**2905**	**2531**	**193**	**286**	**5**	**185**	**219**	**6075**	**9639**

pitfall traps	Treatment	Acari	Coleoptera	Collembola	Formicidae	Hemiptera	Insect larvae	Opiliones	Symphyla	Predators	Decomposers	all arthropods
secondary forest	Control	113	145	4839	257	48	40	7	0	78	4987	5592
	Food	488	399	12913	326	120	238	7	0	101	13467	14731
	Food/Space	352	287	9777	286	74	332	1	0	107	10216	11365
	Space	123	142	4879	432	25	26	3	0	81	5059	5798
old-growth forest	Control	167	167	5062	146	39	71	1	0	86	5249	5797
	Food	729	330	9237	287	75	507	4	0	92	10041	11369
	Food/Space	1261	232	8187	342	60	448	4	0	90	9472	10673
	Space	182	186	5195	180	37	98	4	0	83	5386	5988
	sum	**3415**	**1888**	**60089**	**2256**	**478**	**1760**	**31**	**0**	**718**	**63877**	**71313**

Appendix Chapter 4 – Table 1. (continued)

sticky traps	Treatment	all arthropods
secondary forest	Control	396
	Food	578
	Food/Space	509
	Space	216
old-growth forest	Control	314
	Food	612
	Food/Space	414
	Space	201
	sum	**3240**

Appendix Chapter 4 – Table 2. Mean number of individuals across all sampled plots for the pitfall trap and soil samples. The groups are sorted from lowest to highest abundance in the pitfall trap samples. Abundances (individuals per sample) measured by the two methods are strongly correlated (*r* = 0.82; with log(x+1)-transformed data).

Taxon/Group	Pitfall traps		Soil sample extraction	
	Sum	Individuals sample^{-1}	Sum	Individuals sample^{-1}
Symphyla	0	0	185	1.54
Isoptera	3	0.025	57	0.475
Pseudoscorpiones	4	0.033	68	0.567
Blattodea	25	0.208	3	0.025
Dermaptera	29	0.242	10	0.083
Chilopoda	30	0.25	75	0.625
Opiliones	31	0.258	5	0.042
Diplopoda	41	0.342	150	1.25
Orthoptera	304	2.53	0	0
Isopoda	307	2.56	59	0.491
Hemiptera	478	3.98	193	1.61
Araneae	653	5.44	71	0.592
Insect larvae	1760	14.7	286	2.38
Coleoptera	1888	15.7	268	2.23
Formicidae	2256	18.8	2531	21.1
Acari	3415	28.5	2773	23.1
Collembola	60089	501	2905	24.2

Appendix Chapter 4 – Table 3. Effects of forest stage, increased nutrient-rich organic material, or increased habitat space using artificial litter of no nutritional value on the abundance of all arthropods and two guilds. Altogether we sampled 120 plots (3 sites in each successional stage; five replicates of each treatment within sites) using three methods. Data were analyzed using generalized mixed models using a Poisson distribution and the canonical link function including a correction for over-dispersion. Sites were modeled as random factors. In contrast to Table 1 in the main text, the sampling methods were analyzed individually. We present the *z*-values (= estimates/standard error) of the coefficients. Significant results indicated in grey.

Method	Group	Stage		Food		Space		Food*Space		Stage*Food		Stage*Space	
		Z	P	z	P	z	P	z	P	z	P	z	P
Pitfall	All arthropods	0.62	0.54	6.13	<0.001	-0.26	0.80	-0.83	0.41	-1.71	0.09	-0.13	0.90
	Decomposers	0.76	0.45	5.89	<0.001	-0.47	0.64	-0.67	0.50	-1.87	0.06	-0.08	0.93
	Predators	0.56	0.57	1.45	0.15	0.22	0.83	0.05	0.96	-0.75	0.46	-0.32	0.75
Berlese	All arthropods	-0.24	0.81	3.05	0.002	-0.95	0.34	-0.06	0.95	-0.05	0.96	0.02	0.98
	Decomposers	0.03	0.97	4.96	<0.001	0.26	0.80	-1.26	0.21	-0.25	0.81	-0.51	0.61
	Predators	2.43	0.02	-1.22	0.22	0.28	0.78	1.29	0.20	1.09	0.27	0.10	0.92
Sticky traps	All arthropods	-1.60	0.11	3.28	0.001	-4.47	<0.001	2.65	0.008	1.63	0.10	0.66	0.51

Curriculum Vitae

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Publications

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