

**The diversity and ecology of the spider communities
of European beech canopy**



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In the vegetable as well as in the animal kingdom,
the causes of the distribution of species are among the number of mysteries,
which natural philosophy cannot reach...

—Alexander von Humboldt

Table of Contents

I. General Introduction.....	1
II. Effects of tree age on diversity and community structure of arboreal spider: implications for old-growth forest conservation.....	11
III. Underestimated spider diversity in a temperate beech forest.....	33
IV. Seasonal dynamics of arboreal spider diversity in a temperate forest.....	51
V. Neutral and niche theory jointly explain spider diversity within temperate forest canopies.....	69
VI. Biodiversity prediction by applying Verhulst Grey Model (GM 1,1).....	85
VII. Summary and Outlook.....	93
VIII. Zusammenfassung und Ausblick.....	99
IX. Acknowledgements.....	105
X. Curriculum Vitae and Appendix.....	107
XI. Ehrenwörtliche Erklärung.....	114

Declaration

This dissertation is the result of my own work and includes nothing that is the outcome of work done in collaboration.

Chapter I

General Introduction

Canopy research and temperate forests

Forests, coral reefs and soil contain the majority of the world's known biodiversity (Connell 1978; Ozanne et al. 2003; Floren and Schmidl 2008), and as much as half of all the macroscopic life forms are believed to dwell in forest canopies, where they remain insufficiently investigated, or undiscovered entirely (Floren and Schmidl 2008). The study of canopy arthropod communities is a relatively young subfield of ecology, and it can be traced back to the study of the extremely diverse flora and fauna of tropical tree canopies in the late 1970s (Perry 1978; Erwin and Scott 1980; Stork and Hammond 1997). These investigations of tropical lowland rain forests revealed that canopies harbor extremely rich assemblages of arthropods restricted and specialized to this stratum (Erwin 1982; Stork 1991; Floren and Linsenmair 1997). The canopy layer is also important for the establishment and maintenance of arthropod diversity in temperate zones too (Floren and Schmidl 2008); here, as in tropical forests, it provides a wide range of resources and structurally heterogeneous habitats for arboreal arthropods which in turn influences their occurrence and abundance. Without taking this important faunal component into consideration, the dynamics of forest ecosystems cannot be fully understood (Southwood et al. 1982).

In contrast to the many studies targeted at the tremendously rich biodiversity and complex structure and dynamics of arboreal arthropod communities dwelling in lowland tropical rainforest canopies, little research has been concentrated on temperate forest canopies (Martin 1966; Gagne and Martin 1968; Southwood et al. 1982; Scharff et al. 2003; Southwood et al. 2005; Müller and Goßner 2007; Floren et al. 2008; Gossner et al. 2008; Sobek et al. 2009). These studies were aimed at assessing the biodiversity patterns in temperate canopies mainly in quantitative terms. These early investigations showed that temperate forest canopies also can harbor many rare, endangered and species new to science (Kitching et al. 1993; Russell-Smith and Stork 1994). However, no study has yet attempted to investigate the upper stratum of old-growth forests in Central Europe — perhaps because these forests were rarely preserved after the industrial revolution. In Europe, century-old management practices to maintain a sustainable wood supply, and extensive and repeated clear-felling have fundamentally changed temperate forest structure and composition (Harris 1984; Schroter et al. 2005; Puettmann and Coates 2009).

Unfortunately, comprehensive data on arthropod communities from undisturbed natural European forests is currently lacking: one key consequence is that we do not know what species were possibly lost during many centuries of ever-increasing human disturbance, which poses a grave threat to the conservation of this ecosystem. This was the impetus for the present study on temperate arthropod assemblages living in temperate tree crowns in Central Europe.

Research location and European beech

European beech (*Fagus sylvatica* L.) is a dominant deciduous tree species widely distributed in the temperate region from Sicily to Sweden, and Galicia to the Caucasus (Hewitt 1999). Würzburg University Forest in northern Bavaria, Germany (50°01' N, 10°30' E) is a rare representative of temperate forest in Central Europe. Here, in this 2,664 ha forest, European beech is the most dominant tree species (21% of the occupied forest area), followed by oak (*Quercus robur*, 19%) and spruce (*Picea abies*, 12%). It is among the few forests considered to represent a still 'near-natural' state of a mixed central European forest. The mean annual temperature and precipitation are 7.5 °C and 675 mm, respectively. This forest is currently managed for the timber industry and firewood, and was certified by the Forest Stewardship Council in 2001. However, the biodiversity and community structure of the canopy fauna in this forest, like elsewhere in Central Europe, are only superficially known. Therefore, my study provides new information for a temperate ecosystem which is strongly influenced by silvicultural management. A management plan for the conservation of its natural resources can only be developed and implemented on the basis of sound inventories (Whitmore et al. 2002). Without such basic knowledge it is near impossible to recognize and monitor the effects of environmental change due to human activities and to resort to countermeasures in time before the changes become irreversible.

Neutral verses niche theory

The distribution of species is governed by resource allocation, which can be partitioned to include food, microclimate affected by spatial (both horizontal and vertical) and temporal (both seasonal and daily or diurnal) environmental gradients (Davis 1999). This leads to the conclusion that co-existing arthropods must share similar ecological requirements. Neutral and niche theory, as structuring principles of communities, are still mired in controversy about which force better explains how the co-existence of ecologically similar species is maintained. The classical niche-based

theory asserts that differing life-history tradeoffs between species for competition, colonizative and adaptations to environmental heterogeneity can stabilize coexistence by preventing competitive exclusion (Vandermeer 1972; Tilman 1994; Chesson 2000; Tilman 2004; Kraft et al. 2008). It assumes that each species occupies a defined position in the multi-dimensional niche space of its environment, in which it is superior to all potential competitors (Sugihara 1980; Giller 1984). Here interspecific competition is the main structuring mechanism resulting in a state of species saturation and similar communities with a climax equilibrium state in different habitats (Giller 1984; Gotelli and Graves 1996). Thus habitat-specific repeatable patterns in communities suggest that the structure and dynamics are deterministic and predictable (Giller 1984; Wiens 1984; Begon et al. 1996). In contrast, the neutral theory assumes that individuals are demographically identical, and equivalent functionally, regardless of the species, and that stochastic processes alone are sufficient for maintaining species diversity (Hubbell 1997; Bell 2001; Hubbell 2001, 2005). It follows that under neutral theory the communities are unpredictable in space and time and no permanent equilibrium in species composition exists. This condition can be characterized by high variability in species richness, high species turnover, unpredictable appearance and disappearance, and lack of successional stages or climax equilibrium (Wiens 1984; Floren and Linsenmair 1997, 1998b). The neutral theory can provide a reasonable explanation not only for the co-existence of greater numbers of species at the same resource in tropical rainforests (Chesson and Case 1986; Floren and Linsenmair 1998a), but also for the unsaturated species richness found in some temperate communities (Boecklen and Price 1991; Cornell 1993).

In temperate forests, there are large seasonal variations in temperature and it is essential to carry out biodiversity sampling over an extended period comprising all seasons to clarify the basics of variable temporal diversity patterns (Floren and Schmidl 2008). Furthermore, tree crowns in the temperate zone offer an excellent opportunity to investigate inter-annual variations because the fauna is presumably displaced by each winter, thus allowing one to observe and measure the re-structuring of the local community. Thus arboreal arthropod communities can serve as a model system to investigate the key environmental factors regulating community structure and to compare two prominent theories that have been proposed to explain community assembly and maintenance.

The significance of spiders

The future of our planet's biological reserves is intimately linked to arthropod

abundance and diversity. Spiders are among the most speciose and abundant arthropods (Coddington and Levi 1991; Nyffeler 2000), comprising the second most speciose taxon after insects with 42,055 described species to date, and a total estimated at 60,000–170,000 species (Coddington and Levi 1991; Platnick 1999, 2010), and as such they contribute significantly to the dynamics of terrestrial ecosystems (Floren and Sprick 2007). They are well known for their competitive interrelationships with other spider species as most of them belong to the same trophic level. Although all spiders are predators, individual guilds and species differ strongly in their resource requirements and hunting strategies (web weavers or cursorial hunters) and in their effects on co-occurring spiders.

Many studies have already shown that the distribution and abundance of herbivorous insects is related to tree species in general and to leaf nutrients, leaf age, light conditions and defense parameters of their host-plants in particular (Basset 1991). However, as predators, one would expect spiders to be less influenced by such factors than herbivores (Stork 1987; Basset 1992). Spiders may be more influenced by microclimate, prey availability (Gagne and Martin 1968), suitable sites for web construction (Hurd and Fagan 1992), and/or enemy-free space (Halaj et al. 2000). Based on the extraordinarily high diversity of spiders, components of life histories that affect their distribution are also very diverse so as to cope with biotic and abiotic environmental conditions. Selection of web site and mobility are two crucial parameters determining the local distribution of spiders and can therefore be considered key-elements of community structure.

In addition to contributing to our understanding of arthropod community structure in the tree crowns of temperate forests, spiders are very valuable surrogates for assessing overall arthropod diversity and for studying general patterns of spatial and temporal biodiversity (Marc et al. 1999; Cardoso et al. 2004). This spatio-temporal distribution mirrors important aspects of their ecology dealing with utilization of habitat heterogeneities and their foraging strategies. From an applied point of view, spiders are also the most important arthropod predators, catching incredible quantities of insects as prey (Nyffeler and Benz 1987; Nyffeler 2000). Moreover, the use of spiders is not limited to their roles as biological regulators against pests in woodlands (Pekar and Kocourek 2004; Zrubecz et al. 2008); they also function as precise bio-indicators in terrestrial ecosystems for monitoring habitat changes (Robinson 1981; Hsieh et al. 2003; Perner and Malt 2003; Buchholz 2010). Since spiders are crucial for ecosystem organization and provide predation services in the food web of arthropods, knowledge about the density of arboreal spiders and ecosystem processes within the temperate canopies should be systematically investigated.

Research objectives

My dissertation focuses on local-scale processes essentially shaping the coexistence within a potentially competitive community of arboreal spiders in a temperate system. The results, however, can also be considered in a broader context and serve to establish regional-scale studies investigating the influence of large-scale factors; for example, comparisons of spider communities of the same habitat-entities in different European countries to study the effects of different forestry policies.

By studying arboreal arthropods in temperate forest canopies, we can begin to examine spatio-temporal dynamics of species richness and their partitioned contribution to overall biodiversity, and test whether temperate arboreal arthropod communities exhibit deterministic or stochastic patterns of community composition. The spider communities associated with the canopies of European beech were sampled effectively using fogging techniques, and the use of conspecific trees meant that the results are more robust and comparable than if heterospecific trees were included. In my dissertation, my specific objectives were to (1) describe the spider communities within the beech canopies of old-growth, mature and young trees and compare them to test the hypothesis that old-growth and younger European beeches can be regarded as similar habitats; (2) investigate the importance of the old-growth beech trees for arboreal spiders; (3) test whether or not young beeches can be used in a sampling protocol for rapid biodiversity assessment; (4) investigate canopy re-colonization among seasons; and (5) examine whether neutral or niche theory, or both, can explain the co-existence of species and spider diversity within temperate forest canopies.

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Chapter II

Effects of tree age on diversity and community structure of arboreal spiders: Implications for old-growth forest conservation

Abstract

To date, many studies have shown that the composition of arboreal arthropod assemblages is influenced by not only the tree species, but also by their phenology, morphology and chemistry. However, studies explicitly using tree age as a further decisive factor are noticeably rare. Here, we compare assemblages and diversity of arboreal spiders in European beeches (*Fagus sylvatica* L.), using canopy fogging in the Würzburg University Forest, Germany. Our findings clearly demonstrate that communities of predators occurring in the canopies of three silvicultural forest patches of different age (old-growth patch: >150 years old; mature: 50–60 years old and young: 20–25 years old) may spatially exist in very close proximity to one another, but are nevertheless shaped by tree age. We report the novel and unique result that alpha diversity and evenness of spiders was higher in old-growth beech trees. Mature and young beech trees were not distinguishable in species and guild composition, yet both of them differed from those of old-growth beeches. The results of this study challenge the classic view that conspecific trees provide similar habitats and are inhabited by similar arthropod assemblages in an ecosystem. Therefore, the biodiversity of forest canopies needs to be accurately revisited by explicitly considering tree age. These results also imply that old-growth forests are of special conservation value for predators, and therefore should always be part of near natural forests for maintaining ecosystem function.

Highlights

1. Tree age governs the community composition and diversity of arboreal spiders.
2. Old-growth beech trees had highest alpha diversity and evenness of arboreal spiders.
3. Mature and young beeches were not distinguishable in species and guild composition.
4. Old-growth beeches are of special conservation value for spiders.

Keywords

Araneae; canopy fogging; European beech; forest biodiversity; old-growth forest; tree age

Introduction

The study of canopy arthropod communities is a relatively young field of ecology. It can be traced back to the study of the extremely diverse flora and fauna of tropical tree canopies in the late 1970s (Perry, 1978; Erwin and Scott, 1980; Stork and Hammond, 1997). These investigations of tropical lowland rain forests have shown that canopies harbor extremely rich assemblages of arthropods restricted and specialized to this stratum. Without taking this important faunal component into consideration the dynamics of forest ecosystems cannot be understood fully (Southwood et al., 1982). Canopies form the interface between the atmosphere and the biosphere, and thus represent the layer where abiotic and biotic processes interact most closely, affecting many ecosystem functions (Erwin, 1982; Floren and Linsenmair, 1998). These include, among others: energy flow, important biogeochemical cycles, and processes influencing climate dynamics from local to global scales (Shukla et al., 1990).

In contrast to the many studies targeted at the tremendously rich biodiversity and complex structure and dynamics of arboreal arthropod communities dwelling in lowland tropical rainforest canopies, only little research has been concentrated on temperate forest canopies (Martin, 1966; Gagne and Martin, 1968; Southwood et al., 1982; Scharff et al., 2003; Southwood et al., 2005; Müller and Goßner, 2007; Floren et al., 2008; Gossner et al., 2008; Sobek et al., 2009). These studies aimed at assessing the biodiversity patterns in temperate canopies mainly in quantitative terms. These early investigations showed that temperate forest canopies also harbor many rare, endangered and species new to science (Kitching et al., 1993; Russell-Smith and Stork, 1994). This prompted us to perform this study on temperate arthropod assemblages living in European beeches in Central Europe.

The composition of arboreal arthropod assemblages can be influenced by tree phenology, morphology and chemistry (Basset, 1991; Staudt et al., 2001; Stork et al., 2001; Basset et al., 2003). However, studies explicitly taking tree age (and its structural correlates) into account as a further decisive factor are noticeably rare (Basset, 2001; Bar-Ness et al., 2006; Moning and Müller, 2009). Nevertheless, much basic research still needs to be done to better understand the processes responsible for the spatially complex patterns and the temporal dynamics we observe in the canopy.

In this study, we used spiders as indicators to investigate the effect of different developmental stages of beech canopies on arboreal arthropod diversity. Spiders are, for several reasons, very valuable surrogates for assessing overall arthropod diversity and for studying general spatial and temporal biodiversity patterns (Marc et al., 1999; Cardoso et al., 2004). Arachnida is the second most species-rich taxon after Insecta; they are also the most important arthropod predators, catching incredible quantities of insects as prey (Nyffeler and Benz, 1987; Nyffeler, 2000). Therefore, the use of spiders is not limited to biological control against pests in woodlands (Pekar and Kocourek, 2004; Zrubecz et al., 2008), because they can also function as precise bio-indicators in terrestrial ecosystems for monitoring habitat changes (Robinson, 1981; Hsieh et al., 2003; Perner and Malt, 2003; Buchholz, 2010).

While the diversity of arboreal spiders has already been investigated in the tropics (Russell-Smith and Stork, 1994; Pinto-Leite et al., 2008), no previous research has investigated the effects of tree age on diversity and community composition of the spider fauna in temperate silvicultural forest. In this study, we have investigated the structure of spider assemblages of the representative and most common tree species in Europe (the European beech, *Fagus sylvatica*), considering their assemblage structure on three forest patches in terms of tree age classes: old-growth (tree age >150 years), mature (50–60 years) and young (20–25 years) beech patches. Our specific objectives were (1) to analyze the alpha diversity and evenness of arboreal spiders in each beech patch (2) to compare the three assemblages for among-patch similarity; (3) to identify the importance of tree age as a factor structuring the community composition of arboreal spider assemblages.

Methods

Study area

We carried out the field work in Würzburg University Forest, northern Bavaria, Germany (50°01' N, 10°30' E) (Fig. 1). It lies adjacent to the future Steigerwald National Park, located between the Schweinfurter Basin and Haßberge in the eastern part of the Franconian tectonic plate. Here, annual precipitation averages 650–700 mm, mean annual temperature is 7.5 °C (weather station Köslau in Hassberge, 1990–2010), and the region is covered by snow 35 days per year, on average. The altitude of this hilly forest ranges from 225 m to 400 m. Its total area comprises 2664 ha, of which 494 ha are classified as “High Conservation Value Forest” by the Forest Stewardship Council.

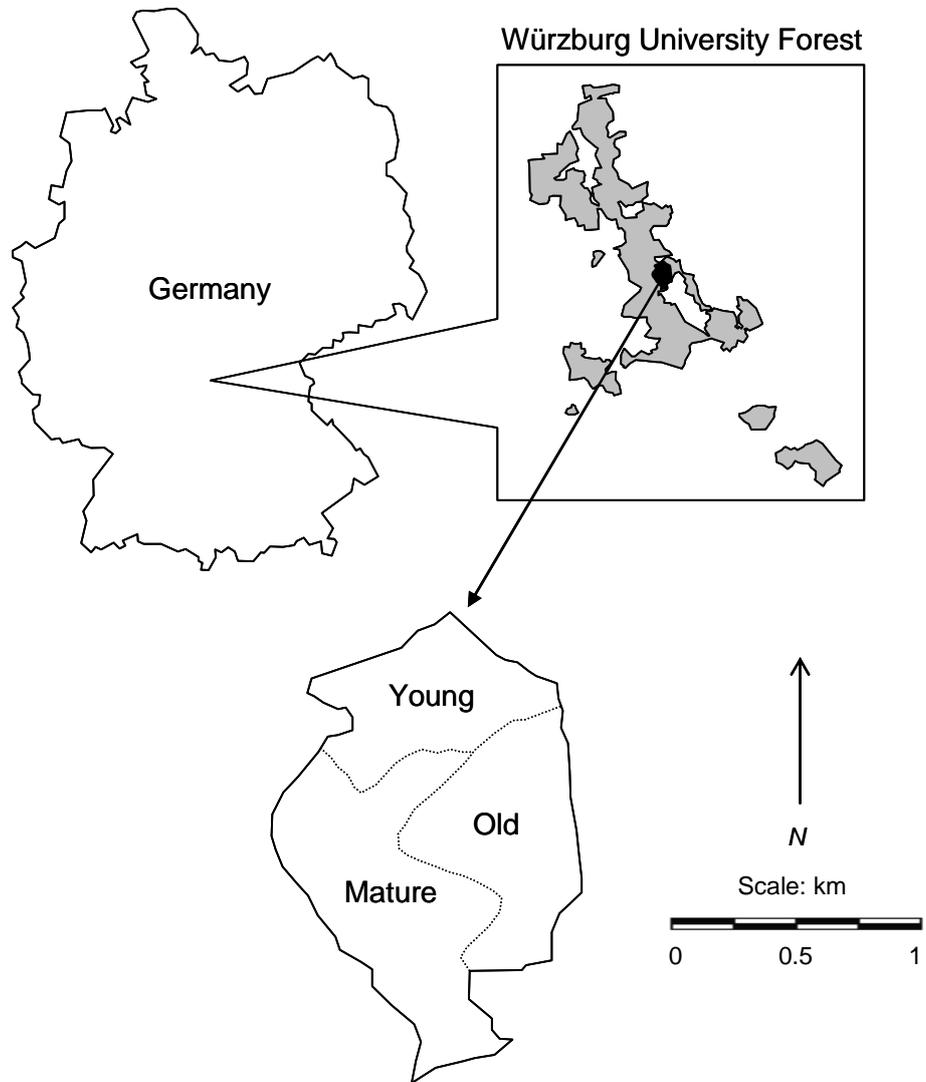


Figure 1. Map of the study site in Würzburg University Forest, Germany

Sampling sites

Würzburg University Forest represents the type of a near-primary mixed temperate forest in Central Europe. Twenty-four percent of the forest area in northern Bavaria (lower Franconia) is covered by European beech (*Fagus sylvatica*), which is also the dominant deciduous tree species distributed in the temperate region between southern Europe and the British Isles. European beech is an interesting study object, not only because it is the most representative and naturally most abundant tree species in Germany and elsewhere in Europe (Ellenberg, 1986), but also because it is an extensively utilized species; therefore, it is intensively managed. We selected silvicultural beech patches in very close proximity to one another and categorized them according to age and height of the trees: old-growth beech patch contained trees with a height of 20–26 m (>150 years old); mature beech patch (13–19m tall and 50–60 years old) and young beech patch (5–6 m tall and 20–25 years old).

Canopy sampling

Arthropods in the canopy are usually sampled by broad-spectrum techniques such as branch beating, light-trapping, flight-interception traps and insecticide knockdown (Stork and Hammond, 1997; Adis et al., 1998). Although each method has its distinct biases (Basset et al., 1997; Jimenez-Valverde and Lobo, 2005), insecticide fogging is the only ground-based technique for quantitatively capturing almost all of the free living arthropods in the entire tree crown. Furthermore, it is the most effective method for the evaluation of qualitative aspects of taxonomy, life history and additional aspects of the arboreal arthropod community (Paarmann and Stork, 1987). The first investigation of forest canopy fauna using this type of ‘insecticide knockdown’ was by Martin (1966) in Canada. Erwin and Scott (1980) standardized this technique for studying the arboreal fauna of a lowland forest tree (*Luehea seemanii*) in Panama.

Since it was our goal to study the diversity patterns and abundance of spiders, we needed reliable quantitative data, which is provided best by insecticidal fogging. We used pyrethrum diluted in pure diesel, applied with a special fogging machine (SwingfogTM SN-50). The substance was blown into the respective tree crown for ten minutes. We used only natural pyrethrum as an insecticide, since it is highly specific to arthropods, non-toxic for vertebrates, and completely biodegraded within a few hours. Effective tree crown-selective fogging can only be carried out during good weather conditions, namely at daybreak when there is no wind (Sorensen, 2004). Only then is it guaranteed that the warm mist can rise from the ground to all parts of the

tree crown without drifting to neighboring trees (McKamey, 1999). No fogging ever took place after rain or during windy or misty conditions.

For collecting the knocked down arthropods, 90% of the fogged tree's crown projection on the ground (old-growth and mature: 46 m²; young: 6 m²) was covered with plastic sheets fixed above the ground (to prevent ground-dwelling arthropods, such as food-searching ants, from crawling onto the sheet). Within the first two hours after the fogging, all spiders killed or anesthetized that dropped onto plastic sheets were collected and transferred directly to storage bottles containing 70% ethanol. Using a fixed dropping time of two hours was a compromise between maximizing the number of arthropods sampled and reducing the number of specimens escaping due to recovery from the anesthetizing effect of the insecticide (Erwin, 1989). To analyze the dynamics of the arthropod communities, six trees from each of the patches were randomly chosen in pure beech stands and each was fogged three times in each summer from 2005 to 2007 (162 trees were fogged in this way over the 3-year period).

In the laboratory, collected spider specimens were first sorted according to their developmental stage and sex. Spiders were identified to species level using species-specific attributes of the palpal organ or epigynum, employing the keys provided by Heimer and Nentwig (1991), and Roberts (1996); nomenclature followed Platnick (2010). Most immature specimens were identified to family, and were also used in the guild diversity analysis. Voucher specimens were deposited in the zoological collection of the Department of Animal Ecology and Tropical Biology, University of Würzburg, Germany.

Spider guild diversity

We categorized spiders into different guilds based on their hunting strategies (web weaver or cursorial hunter) (Hatley and Macmahon, 1980) and according to how they use environmental resources (Root, 1967; Uetz et al., 1999). Because spider guilds vary with spatial heterogeneity (Brown, 2003), landscape heterogeneity (Romero-Alcaraz and Avila, 2000), habitat and microhabitat complexity (Downes et al., 1998; Gunnarsson et al., 2004; Buchholz, 2010), a comparison of guild composition can reveal differences regarding the habitat structure and the utilization of resource. For each patch, the relative abundance of spiders belonging to each guild was pair-wise tested applying Chi-square tests of homogeneity.

Statistical analyses

First, spider densities were calculated based on the size of the collecting sheets for comparison of canopy habitats. Fisher's alpha diversity and Evenness index were used to measure spider diversity per tree and to characterize spider assemblages for each patch on PAST software (Hammer et al., 2001). Samples consisting only of immature specimens were excluded from the analyses. Differences in species composition and diversity measures of different-aged beech patches were tested using one-way Analyses of Variance (ANOVA) and post-hoc pair-wise tests (Tukey's Honestly Significant Difference (HSD) test). Jarque-Bera tests were used to ensure that data met the assumptions of homogeneity of variances and normality (Jarque and Bera, 1987). Twenty-seven sets of beeches were used to analyze canopy preferences of the nine most abundant spiders, with each set consisting of six spider communities collected from the same patch in the same month.

In addition to traditional diversity indices, we also measured quantitative relationships between different spider species to examine the similarity of spider communities among the sampling patches. The Bray-Curtis method was used for visualizing Non-Metric Multidimensional Scaling (NMDS) with the minimal spanning tree (MST). MST based on greedy theory is the best-known graph-theoretic divisive clustering algorithm (Zahn, 1971), providing a better reduction (Kwon and Cook, 1998) and stronger visual cues for multidimensional data (Kim et al., 2000). Twenty-seven sets of beeches were also used here for plotting NMDS, and Analysis of Similarities (ANOSIM) with 10000 permutations was performed between each pair of beech patches and between each pair of years to determine whether the correlation was statistically significant.

Results

Comparison of community structure between European beech patches

A total of 16,899 individuals were collected from 162 samples covering 5,292 m² of projected canopy area from 2005 to 2007, with the identified specimens (n = 6,356) belonging to 74 species from 16 families (Appendix). The specimen number per square meter varied clearly between the three beech patches, with young beeches having, on average, the highest density of spider individuals (Table 1). Fisher's alpha values showed that spider diversity was significantly highest in old-growth beech trees. Additionally, the evenness index revealed that evenness in old-growth canopies was higher than in mature and young beeches.

Table 1. Mean (SE in parentheses) of spider densities, Fisher's alpha diversity and evenness index of different-aged patches of beech trees (*Fagus sylvatica*) in Würzburg University Forest, Germany (Tukey's HSD tests show significant differences ($P < 0.05$) across different beech patches.).

	Patch			<i>F</i>	<i>P</i>	Tukey's HSD test
	Old-growth	Mature	Young			
Density (m ²)	0.83 (0.08)	3.70 (0.30)	19.01(1.43)	131	<0.001	Y > M > O
Fisher's alpha diversity	5.32 (0.50)	3.75 (0.24)	3.35 (0.29)	8.6	<0.001	O > M = Y
Evenness index	0.88 (0.02)	0.55 (0.02)	0.63 (0.02)	65.06	<0.001	O > Y > M

Table 2. Results of ANOVA tests examining tree canopy preference of nine most abundant spiders.

Species	Relative abundance (%)	Mean (SE) of abundance / beech set			<i>F</i>	<i>P</i>	Tukey's HSD test
		Old-growth	Mature	Young			
<i>Anyphaena accentuata</i>	33.84	1.67 (0.74)	132.78 (33.3)	104.56 (26.87)	7.8	< 0.01	M = Y > O
<i>Metellina menzei</i>	13.40	9 (5.33)	102.29 (40.01)	10.43 (2.52)	5.24	< 0.05	M > O = Y
<i>Mangora acalypha</i>	8.78	27 (8.23)	54.2 (19.27)	30.4 (7.94)	1.312	0.305	O = M = Y
<i>Neriene peltata</i>	7.06	2 (1.51)	17.71 (8.22)	44.43 (17.81)	3.568	< 0.05	M = Y > O = M
<i>Diaea dorsata</i>	6.42	1.86 (0.74)	50 (17.59)	6.43 (3.24)	6.61	< 0.01	M > O = Y
<i>Cyclosa conica</i>	5.02	8.17 (2.55)	26.33 (9.51)	16.67 (3.69)	2.258	0.139	O = M = Y
<i>Tetragnatha pinicola</i>	4.88	7.8 (2.73)	40 (6.63)	14.2 (5.46)	10.72	< 0.01	M > O = Y
<i>Araneus sturmi</i>	3.89	7.17 (2.61)	16 (5.17)	18 (5.4)	1.59	0.236	O = M = Y
<i>Ballus chalybeius</i>	3.49	9.5 (2.96)	2.63 (1.39)	15.63 (7.69)	1.818	0.187	O = M = Y

Theridiidae made up the largest portion of all collected spiders (20.45%), followed by Araneidae (20.42%) and Anyphaenidae (15.15%). The frequency of spiders at the species level differed among the three beech patches (Table 2). *Anyphaena accentuata* was a dominant species in both mature and young beeches. *Metellina menzei*, *Diaea dorsata* and *Tetragnatha pinicola* also dominated in mature beeches, whereas *Mangora acalypha*, *Cyclosa conica*, *Araneus sturmi* and *Ballus chalybeius* were common in all beech patches.

Comparison of guild composition between the three beech patches

The following primary foraging modes are found in central European spiders: (1) orb-web weavers including families Araneidae, Tetragnathidae and Uloboridae; (2) space-web weavers: Dictynidae, Linyphiidae and Theridiidae; (web weavers) (3) foliage runners: Anyphaenidae, Clubionidae and Sparassidae; (4) ambushers and stalkers: Philodromidae, Pisauridae, Salticidae and Thomisidae (cursorial hunters) (modified from Uetz et al. 1999). Agelenidae, Lycosidae and Segestriidae (four species in total) were excluded for the guild analysis due to their low abundances. For each beech patch, the abundance of each spider guild was evaluated and Chi-square tests of homogeneity were performed on each pair of forest canopy types. Eighty percent of caught adult spiders (56 of 70 species) belonged to the ecological guild of web weavers and 20% of the catch (14 of 70 species) to the guild of cursorial hunters. The guild composition of canopy spiders is illustrated in Fig. 2. Pair-wise comparisons of spider guilds using Chi-square tests of homogeneity indicated that the contribution of guilds to the entire spider assemblage was highly variable between old-growth and mature beeches (Chi-square = 526.09, d.f. = 4, $P < 0.001$); between old-growth and young beeches (Chi-square = 268.47, d.f. = 4, $P < 0.001$). However, a similar pattern was observed between the spider guild compositions of mature and young beeches (Chi-square = 6.32, d.f. = 4, $P = 0.18$). The old-growth beech assemblages were dominated by a higher percentage of orb-web weavers (50.8 %) together with fewer foliage runners (2.2 %) In contrast, mature beeches had fewer orb-web weavers (34.0 %) and more foliage runners (24.1 %). Furthermore, the community collected from the young beeches also consisted of a higher percentage of foliage runners (31.9 %), space-web weavers (34.8 %), but fewer orb-web weavers (24.6 %) and ambushers and stalkers (8.68 %).

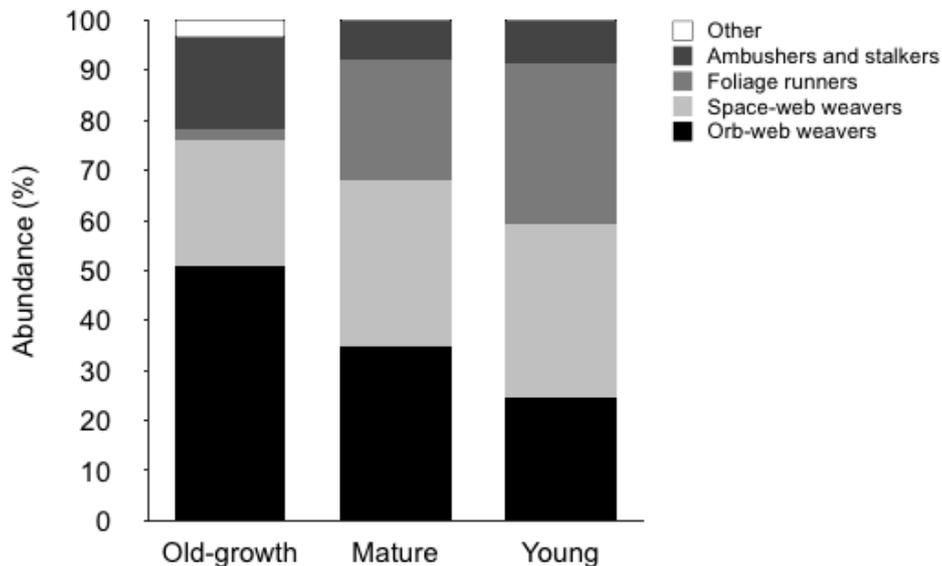


Figure 2. Arboreal spider guild composition in old-growth, mature and young European beech trees (*Fagus sylvatica*).

Similarity of species composition between sampled forest patches and years

Comparison of samples obtained from 2005 to 2007 using ANOSIM tests indicated a stable composition of spider assemblages on beeches stable over the years ($R = -0.001$, $P = 0.45$, Table 3). Species composition patterns were affected by the successional stage of the beeches ($R = 0.32$, $P < 0.001$), however, no significant difference between mature and young beech patches was detected in the spider composition ($R = 0.01$, $P = 0.32$). In order to perform pair-wise comparison of spider species communities between the twenty-seven beech sets, we used the relative abundance of different spider species in three patches to generate MDS via MST for visualizing the plot. The clustering pattern also supported a noticeable influence of tree age on assemblage composition (Fig. 3): distinct spider assemblages in old-growth beeches were clearly separated from those in mature and young beeches whereas assemblages in mature beeches were not significantly separated from those in young beeches and had a high degree of constancy (Stress = 0.13).

Table 3. Results of pair-wise ANOSIM tests comparing spider species between different beech patches and years

Comparison	Species composition	
	<i>R</i>	<i>P</i>
Among canopies		
Global R	0.32	<0.001
Old-growth vs. Mature	0.47	<0.001
Old-growth vs. Young	0.45	<0.001
Mature vs. Young	0.01	0.32
Among years		
Global R	-0.001	0.45
2005 vs. 2006	0.02	0.31
2005 vs. 2007	0.04	0.21
2006 vs. 2007	-0.06	0.92

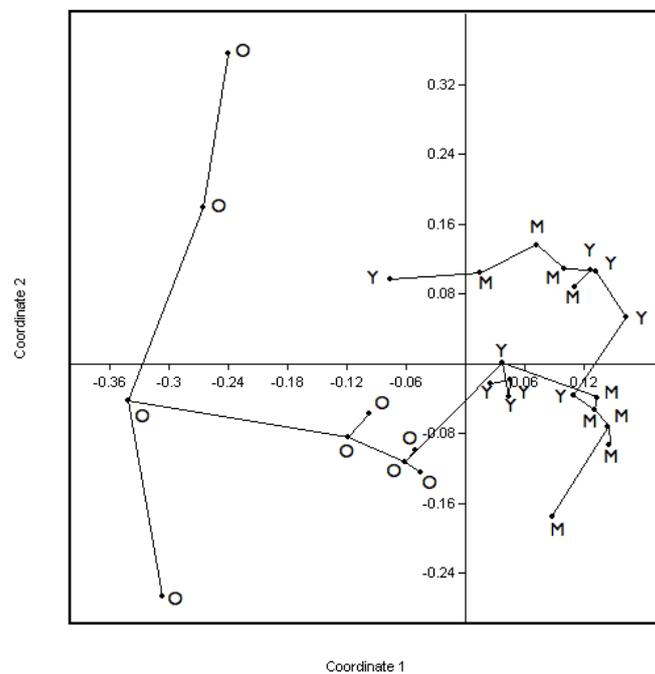


Figure 3. Result of non-metric multidimensional scaling analysis comparing species composition of different-aged stands of European beech (*Fagus sylvatica*) (O: old-growth, M: mature and Y: young beeches).

Discussion

In order to understand the influence of tree age, results were analyzed with respect to the hypothesis that conspecific trees provide similar habitats and are inhabited by similar arthropod assemblages (Southwood and Kennedy, 1983). After examining systematically the community structure and diversity of arboreal spiders dwelling in European beeches for three consecutive summers, we could show that the species composition of spider assemblages varied with the successional stage of the trees. Alpha diversity measures obtained for spider assemblages in old-growth beeches were significantly higher than those of mature and young beeches. With this result, the hypothesis that old-growth and younger European beeches can be regarded as similar habitats should be rejected. Many studies have already shown that the distribution and abundance of herbivorous insects is related to tree species in general and to leaf nutrients, leaf age, light conditions and defense parameters of their host-plants in particular (Basset, 1991). However, as predators, one would expect spiders to be less influenced by such factors than herbivores (Stork, 1987; Basset, 1992). They may be more influenced by microclimate, prey availability (Gagne and Martin, 1968), suitable sites for web construction (Hurd and Fagan, 1992) or enemy-free space (Halaj et al., 2000). This study shows that the influence of these parameters varied between old-growth and younger beeches.

High evenness in old-growth beeches revealed that this canopy community was less influenced by single dominant species than in the other communities. In this managed forest, each studied forest patch is homogeneous in terms of tree species and tree age. Old-growth European beeches lose their branches at the low part of the stem due to self-shading and shade stress from neighbors. Thus, old-growth beeches develop the character of an island standing high up the tree stem, and possessing a low spider density. In our study, we used NMDS combined with MST to visualize the spider species composition more clearly. This method is constructed upon a similarity matrix to provide a low-dimensional visual clustering pattern of points that keep their relative positions in higher dimensions. It showed that arboreal spider communities collected from old-growth beeches had a discrete species composition. The composition likely varies due to the different physical properties of the European beeches and probably also the microclimates of the beech forests. For example, old-growth tree bark is rather smooth (Nicolai, 1986), without leaved branches offering protection against predators. Thus only few spiders use this pathway to move between the lower and the higher strata in the canopy (e.g. only a small proportion of cursorial hunters were collected at the high stratum). Guild diversity showed that stratum specific spider distribution can be explained in terms of their lifestyle (Basset

et al., 2003). For example, old-growth beeches harbor a large proportion of web weavers, and many members of this guild are ballooning species (Larrivee and Buddle, 2011) able to drift into high canopy stratum while dispersing. They are more sensitive to overcrowding and can only build large webs in less dense communities, and thus there is little need for them to leave this stratum. In contrast, many cursorial hunters stayed in the lower strata and appeared to be closely linked to mature and young beeches. Unlike old-growth beeches, mature and young beeches had branching from the ground to the top of the tree, which likely explains why they harbored higher spider densities. They are also both dominated by foliage runners (e.g., *Anyphaena accentuata*), suggesting a similar suite of vegetation structures and microclimates.

Although the composition of spider guilds was similar between mature and young beech canopies, canopy preference of some spiders differed slightly between these two stages. Mature beeches had the lowest evenness and harbored more *Metellina mengei* and *Tetragnatha pinicola* (orb-web weavers) than young beeches. One reason likely to elucidate the differences between these two stages is the fact that mature beeches provide more open space between branches for building these species' orb webs. Because these particular species are significantly affected by tree age between mature and young beech trees, it makes them suitable as indicator species to evaluate changes in tree growth and forms in beech stands in Central Europe. In comparison with old-growth beeches, young trees comprised more *Neriene peltata*, a member of the Linyphiidae, which usually inhabits the lower branches of deciduous trees or grassy areas (Heimer and Nentwig, 1991). Some species of this family are restricted to the canopy strata as adults but need to migrate from trees to the leaf litter and soil for mating or laying eggs. For this reason, they tend to live in the lower stratum (i.e. in young beeches).

Conclusion

Most theoretical ideas about forest ecology were developed in the temperate regions. In contrast, most research to date on forest canopies and their dwellers has been carried out in the tropics, showing a unique richness. Nevertheless, an increasing number of studies have proven that temperate forest canopies harbor a very diverse spectrum of arboreal fauna that cannot be ignored. This study challenges our current understanding of the distribution and diversity of arboreal spiders in temperate zones, and perhaps even in tropical rainforests. In particular, our results indicate that tree age plays a more important role in governing spider diversities of European beeches than was previously thought. Currently, old-growth beeches are rarely preserved in managed forests in Europe due to their economic value. From a conservation

perspective, in order to maintain the unique spider composition and higher diversity in higher strata of beech canopies, old beeches should not be over-logged and should always be included in near natural forest.

Two further types of investigation are required to establish the broader significance of these findings. First, the question must be asked whether the variation of arboreal spider diversity at different successional stages is a widespread phenomenon or not: by testing in other forests dominated by beech as well as other tree species. Do species richness and community structure of spiders in other tree species, in both temperate and tropical regions, vary significantly between different successional stages? We propose that the most effective and efficient way to answer these questions is to build a standard protocol in a temperate forest and fog the canopies of other tree species. This standardized approach, if successful, could then be applied in tropical rainforest where possible. Since the Würzburg University Forest is qualified as a high conservation value forest and the European beech is also a representative species in Europe, we hope this study can serve as a model for the use of spider diversity to monitor the effects of forest patch management.

Secondly, do other forestry policies also affect arboreal spider diversity? Which successional stage of beech timber can be logged in which season, and how might this affect the diversity of arthropods? These questions can only be addressed with continued, long-term sampling, and by conducting experiments within the canopy itself using some form of canopy access (via lift, crane or scaffolding). Certainly there are concentrations of spiders which have been overlooked in current studies and need to be taken into account in regard to different tree ages as well as different tree species, climate zones and areas of human impact. As further field studies of invertebrates are carried out at different successional stages, estimates of biodiversity will likely increase and the relative importance of tree age may need to be revised. Towards this end, the present work is the first study comparing spider diversity and community composition at different successional stages of European beech canopies. It clearly shows that changes in tree age can shape the spider diversity found in forest canopies.

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Appendix: Arboreal spider species list on European beeches in Würzburg University Forest (O: old-growth, M: mature and Y: young).

Taxon	2005			2006			2007			Total
	O	M	Y	O	M	Y	O	M	Y	
Agelenidae										
<i>Coelotes terrestris</i>	.	.	.	1	1
Anyphaenidae										
<i>Anyphaena accentuata</i>	1	156	263	5	503	321	9	536	357	2151
Araneidae										
<i>Araneus diadematus</i>	2	.	.	1	2	.	2	.	1	8
<i>Araneus sturmi</i>	4	2	14	27	50	61	12	44	33	247
<i>Araneus triguttatus</i>	1	1
<i>Araniella cucurbitina</i>	.	.	2	1	1	4
<i>Cyclosa conica</i>	15	23	16	25	102	52	9	33	44	319
<i>Gibbaranea bituberculata</i>	.	1	.	2	6	.	1	6	.	16
<i>Mangora acalypha</i>	23	10	8	54	135	60	58	126	84	558
<i>Zilla diodia</i>	1	1
Clubionidae										
<i>Clubiona coerulescens</i>	1	.	1
<i>Clubiona comta</i>	.	4	.	.	3	1	.	2	3	13
<i>Clubiona terrestris</i>	2	.	.	2	4
Dictynidae										
<i>Nigma flavescens</i>	4	4
Linyphiidae										
<i>Araeoncus humilis</i>	1	.	.	1
<i>Bathyphantes gracilis</i>	.	1	.	.	1	.	1	.	.	3
<i>Centromerus sylvaticus</i>	2	.	2
<i>Cnephalcotes obscurus</i>	1	1
<i>Collinsia inerrans</i>	1	.	.	1
<i>Dicymbium nigrum</i>	1	1
<i>Diplocephalus picinus</i>	2	2
<i>Drapetisca socialis</i>	6	2	6	1	18	5	.	3	4	45
<i>Entelecara acuminata</i>	.	.	4	.	.	1	1	.	11	17
<i>Eperigone trilobata</i>	1	.	.	1	2	4
<i>Erigone atra</i>	2	.	1	.	.	3
<i>Erigone dentipalpis</i>	3	.	.	3
<i>Labulla thoracica</i>	.	.	.	1	1

Taxon	2005			2006			2007			Total
	O	M	Y	O	M	Y	O	M	Y	
<i>Lepthyphantes flavipes</i>	1	.	.	2	2	5
<i>Lepthyphantes minutus</i>	.	2	.	.	1	.	.	1	.	4
<i>Lepthyphantes tenebricola</i>	2	.	2
<i>Linyphia hortensis</i>	1	1
<i>Linyphia triangularis</i>	4	12	2	2	5	2	.	.	1	28
<i>Maso sundevalli</i>	3	3
<i>Meioneta rurestris</i>	1	5	2	2	.	10
<i>Mermessus trilobatus</i>	1	1	2	4
<i>Microneta viaria</i>	.	1	1
<i>Moebelia penicillata</i>	4	4
<i>Neriere emphana</i>	1	10	4	.	.	1	.	.	1	17
<i>Neriere peltata</i>	11	32	91	2	85	173	1	7	47	449
<i>Oedothorax retusus</i>	1	.	.	1
<i>Porrhomma microphthalmum</i>	1	.	.	.	1	.	1	3	.	6
<i>Tenuiphantes alacris</i>	.	1	1
<i>Tenuiphantes flavipes</i>	.	2	2
<i>Tenuiphantes tenuis</i>	.	1	.	1	1	.	1	2	.	6
Lycosidae										
<i>Pardosa lugubris</i>	1	1
<i>Pardosa saltans</i>	1	1
Philodromidae										
<i>Philodromus aureolus</i>	1	2	3	.	.	6
<i>Philodromus collinus</i>	.	1	1	.	.	2
Pisauridae										
<i>Pisaura mirabilis</i>	1	1
Salticidae										
<i>Ballus chalybeius</i>	14	.	10	28	6	20	34	15	95	222
<i>Evarcha falcata</i>	1	.	.	.	1
<i>Heliophanus cupreus</i>	.	.	.	1	.	.	.	1	.	2
Segestriidae										
<i>Segestria senoculata</i>	.	1	1
Sparassidae										
<i>Micrommata virescens</i>	1	1	.	.	1	3
Tetragnathidae										
<i>Metellina mengei</i>	39	230	22	19	429	23	5	57	28	852
<i>Metellina segmentata</i>	7	13	.	1	3	2	1	1	1	29

Taxon	2005			2006			2007			Total
	O	M	Y	O	M	Y	O	M	Y	
<i>Pachygnatha degeeri</i>	2	2
<i>Tetragnatha obtusa</i>	1	5	2	.	8
<i>Tetragnatha pinicola</i>	8	33	34	7	77	26	24	90	11	310
Theridiidae										
<i>Achaearanea lunata</i>	.	1	1	2
<i>Achaearanea simulans</i>	.	3	.	.	1	1	.	4	2	11
<i>Anelosimus vittatus</i>	1	1
<i>Dipoena melanogaster</i>	.	.	2	2
<i>Enoplognatha ovata</i>	.	8	12	.	1	2	.	3	41	67
<i>Keijia tinctoria</i>	4	18	3	5	101	19	.	22	7	179
<i>Neottiura bimaculata</i>	1	1	.	.	2
<i>Paidiscura pallens</i>	2	37	3	.	20	6	1	13	14	96
<i>Theridion mystaceum</i>	3	8	1	1	35	8	3	14	4	77
<i>Theridion pinastri</i>	1	.	.	3	8	2	1	2	.	17
<i>Theridion varians</i>	.	.	11	1	7	19
Thomisidae										
<i>Diaea dorsata</i>	1	1	3	3	140	7	9	209	35	408
<i>Xysticus VS45</i>	1	.	1
<i>Xysticus lanio</i>	1	1
Uloboridae										
<i>Hyptiotes paradoxus</i>	.	25	1	.	43	2	.	5	.	76

Chapter III

Underestimated spider diversity in a temperate beech forest

Abstract

We used canopy fogging to study the high (20–26 m), intermediate (13–19 m) and low (5–6 m) strata in three European beech patches (*Fagus sylvatica* L.) in nine months (2005-2007) and estimate species richness and diversity of arboreal spiders. Eight species (10%) were previously unseen in European beech trees, and one of these is likely a new species. Moreover, two species are on the Bavarian Red List. Our results revealed that the high stratum of the old-growth trees provided unique resources and possessed the greatest diversity and evenness, whereas intermediate and low strata had high similarity in respect to diversity, dominance, species, and family composition. Since the majority of beech forests consists of mature and young trees in Central Europe, and old-growth forests are rarely preserved, we recommend young beech be used in a sampling protocol for rapid biodiversity assessment. However, adding samples from the two higher strata to the lowest stratum (55 species), almost doubled the estimated species richness (102 species). This suggests that the lower stratum alone does not represent a true image of the total canopy fauna inventory in this, and likely other, beech stands. To complete this comprehensive inventory in European beeches, the Chao1 predicted that additional sampling would be needed in the highest stratum, where there is a high probability to find previously undetected species in a next survey. Our study clearly shows that neglecting the crowns of the largest, tallest trees risks underestimating the overall spider diversity in Central European forests.

Keywords

Araneae; Canopy fogging; European beech; Forest biodiversity; Species richness estimation; True diversity

Introduction

The canopy stratum forms the habitat for many arboreal mammals, reptiles, birds, bats and countless invertebrates. Among the invertebrates, arthropods are particularly diverse in any terrestrial environment (May 1978); they are the main component in terms of numbers of individuals and species. Arthropods can greatly influence canopy structure and processes (Mattson and Addy 1975; Ohmart et al. 1983; Schowalter et al. 1986; Schowalter 1994, 1995; Linsenmair et al. 2001; Basset et al. 2003). For examples, in the crown of a single tropical tree, an equivalent or an even larger number of ant species can be found than is contained in the entire British fauna (Wilson 1987; Floren and Linsenmair 2001). Arboreal arthropods also represent the most important links in the food web of forest ecosystems because they are highly abundant and effective herbivores in the broadest sense (this includes wood-feeding, fungus-feeding, etc.) (Clinton et al. 1993; Lewis 1997), prominent invertebrate predators and important pollinators, and may even serve as food resource for insectivorous vertebrate communities (Perrins 1991). For these reasons, canopy arthropods play a fundamental role that needs to be well understood for understanding the dynamics of forest ecosystems. Furthermore, such knowledge could insight into how vital services of forests are produced and how biodiversity may be affected by anthropogenic impact.

Spiders are among the most species-rich animal orders (Coddington and Levi 1991; Nyffeler 2000), including about 42,055 described species with an estimated total of about 60,000–170,000 species (Coddington and Levi 1991; Platnick 1999, 2010), thus they contribute significantly to terrestrial arthropod abundance and diversity (Floren and Sprick 2007). The Araneae make up the majority of generalist predators in many terrestrial communities, and have an important collective impact on invertebrate herbivore populations (Riechert and Bishop 1990; Nyffeler 2000). This group is both ubiquitous and sensitive to habitat changes, and can be rather easily sampled; in this way spider communities represent a potentially useful indicator for comparing biodiversity patterns across environments (Uetz 1991; Raizer and Amaral 2001; Hsieh et al. 2003; Buchholz 2010). Although a few field studies have started to investigate the arboreal spider fauna of tree crowns in the temperate zones (Barbaro et al. 2005; Gossner and Ammer 2006; Blick 2008; Floren et al. 2008; Larrivee and Buddle 2009; Blick 2011), no study has yet attempted to investigate pure old-growth forest in Central Europe — perhaps because these forests were rarely preserved after the industrial revolution. Exploring the spider fauna in the canopy strata of old-growth trees offers an exciting and novel research exercise.

The natural landscape of Central Europe has been dramatically altered by

anthropogenic activities (Whitehead 1997). Unfortunately, comprehensive data on arthropod communities from undisturbed natural European forests is lacking: we cannot know what species were possibly lost during many centuries of ever-increasing human disturbance. The Würzburg University Forest in northern Bavaria, Germany, is a rare representative temperate forest in Central Europe, one among the few forests that are considered to represent a still near-natural state of mixed European forest. Here European beech (*Fagus sylvatica* L.) is the most dominant tree species (21%), followed by oak (*Quercus robur*, 19%) and spruce (*Picea abies*, 12%). This forest is currently managed for the timber industry and firewood, and was certified by the Forest Stewardship Council in 2001. However, the biodiversity and community structure of the canopy fauna in this forest, like elsewhere in Central Europe, are only superficially known. A management plan for the conservation of its natural resources can only be developed and implemented on the basis of sound, basic inventories (Whitmore et al. 2002). Without this knowledge, we argue, it is very difficult to monitor environmental changes due to human activities. Therefore, an understanding of biodiversity patterns in this area is urgently needed for its sustainable management.

The forest canopy is a complex and heterogeneous environment. In this study, we sampled arboreal spiders via fogging of European beeches in three canopy strata. The importance of the single stratum for the preservation of biodiversity depends upon the extent to which this canopy stratum shares its fauna with the other strata. If the community in the low stratum is similar to that in the intermediate or even high stratum, the young beech could be used in sampling protocols such as rapid biodiversity assessments. If one stratum, however, contains a distinct spider fauna, the preservation of these reservoirs of diversity could be of high importance for both the conservation of the entire arboreal community and for studying the latter's dynamics. In the present study, our specific objectives were to (1) systematically examine the community structure of the arboreal spider fauna in European beeches in Central Europe; (2) estimate and compare species richness and diversity of spiders between three canopy strata; (3) examine whether or not young beeches could be used in sampling protocols for rapid biodiversity assessment.

Methods

Study area

We conducted the study in the Würzburg University Forest, in northern Bavaria, Germany. This area (50°01' N, 10°30' E) comprises 2,664 ha of Haßfurt, District of Lower Franconia, where the dominant deciduous tree species is European beech

(*Fagus sylvatica*). Beech canopies were categorized according to three major strata based on their heights and ages of trees: high (20–26 m tall, age over 150 years), intermediate (13–19 m, 50–60 years old) and low stratum (5–6 m, 20–25 years old). The mean annual temperature and precipitation are 7.5 °C and 675 mm, respectively.

Canopy sampling

Toti et al. (2000) suggested that late spring and early fall are the two best times to inventory spiders in temperate communities in order to estimate their species richness. On this basis, spiders were collected by insecticidal knockdown (canopy fogging) in late spring (June), summer (August) and early fall (October) from 2005 to 2007 (total nine months over the 3-yr period). This enabled both a qualitative and quantitative comparison of spider communities among canopy strata to gain a robust view of local biodiversity patterns. We used a natural pyrethrum insecticide, not toxic to terrestrial vertebrates, in a Swingfog (SN-50) machine to fog the six beeches in each stratum monthly (total 162 beeches). To collect falling spiders from trees, we used plastic sheets (46 m² for old-growth and mature beeches; 6 m² for young beeches for covering 90% of the fogged tree's crown vertical projection area on the ground). Fogging began at daybreak and lasted approximately 10 minutes; after waiting for two hours samples were collected from the plastic sheets. The samples were stored in bags with 70% alcohol for transport to laboratory. We identified spider specimens to species level by using species-specific attributes of the palpal organ or epigynum employing the keys provided of Heimer and Nentwig (1991) and Roberts (1996). The nomenclature follows Platnick (2010). Voucher specimens were deposited in the zoological collection of the Department of Animal Ecology and Tropical Biology, University of Würzburg, Germany.

Data analysis

Statistical sampling-based approaches included parametric and nonparametric methods, which are both reliable methods for studying biodiversity useful for informing conservation and management decisions (Colwell and Coddington 1994). The former method uses a parametric distribution to fit the observed frequency counts, i.e. the geometric series (Motomura 1932), log-series (Fisher et al. 1943), log-normal curve (Preston 1962) or broken-stick model (MacArthur 1957) for species abundance and examined by the Chi-square goodness-of-fit tests. These tests were performed on PAST software (Hammer et al. 2001).

Non-parametric methods were also applied to estimate species richness and

diversity using SPADE software (Chao and Shen 2003). Jost (2006, 2007) reviews the background and concept for the true (estimated) diversities. The true diversity of order zero is completely insensitive to species frequencies and is better known as species richness; true diversity of order one follows Whittaker's (1972) multiplicative law, as represented by the exponential Shannon entropy. Furthermore, the true diversity of order two is sensitive to common species, as per the inverse Simpson index. In our study, to characterize spider assemblages several diversity indices were calculated: species richness (Toti et al. 2000) was estimated by abundance-based Chao1 estimator (Chao 1984), since it is highly precise (Hortal et al. 2006); the exponential Shannon entropy was estimated by Jackknife (Zahl 1977); inverse Simpson indices by minimum variance unbiased estimator (MVUE) (Magurran 1988). A 95% confidence interval (CI) was constructed using 200 bootstrap replications to define the sampling variation (Chao 1987; Chao et al. 2006).

We also used SPADE to measure the degree of similarity between canopy strata using the multiple-sample abundance data. The abundance-based method treats all individuals equally (Chao et al. 2006). The similarity of species compositions between the three strata were quantified by the abundance-based Morisita index. We used a calculation based on Chao1 (Chao et al. 2009) to predict sufficient sampling for reaching the estimations and the probability that the next sampled individual represents a previously undetected species in a further survey for future sampling planning.

Results

The structure of canopy spider communities in European beech

A total of 15,181 individuals were collected from 162 canopies covering 5,292 m² of the ground-projected tree crown in June, August and October from 2005 to 2007. The identified specimens (n = 6,309) belonging to 80 species from 16 families (Appendix). Among these, 8 species (10%) were newly recorded arboreal spiders in beeches in Europe (cf. Toft 1976, 1978; Szinetár and Horvtáh 2005; Blick 2008, 2011), and *Xysticus* VS45 is probably a new species. Two species are on the Bavarian Red List (Blick and Scheidler 2003) of endangered spiders: *Araneus triguttatus* and *Gibbaranea bituberculata*.

Linyphiidae had the greatest number of species (33), followed by Theridiidae (11) and Araneidae and (9). The most abundant species was *Anyphaena accentuata*; totaling 1,869 individuals (29.6%). The second most abundant species was *Metellina menzei* (n = 886, 14%), followed by *Mangora acalypha* (n = 559, 8.9%), *Neriene*

peltata (n = 476, 7.5%), *Diaea dorsata* (n = 411, 6.5%). Approximately 58.4% of the collected specimens were immature: Theridiidae had the greatest number of juveniles (n = 1699), followed by Linyphiidae (n = 788), Araneidae (n = 704), Clubionidae (n = 407).

Twenty-two species (27.5%) of arboreal spiders were well distributed in all three canopy strata, whereas 36 species (45%) were found in one single stratum. Three families (Amaurobiidae, Lycosidae and Pisauridae) appeared unique to the high stratum, while Segestriidae was found only in the intermediate stratum and Dictynidae in the low stratum (Table 1). Despite the large number of spiders collected, the final percentage of rare species — those with one or two individuals (23 singletons and 12 doubletons) — was high at 43.8% (35 of 80 species). Furthermore, the species-abundance distributions showed that only the spider assemblages from high and intermediate canopy strata fitted into log-normal model (Table 2).

Table 1. Number of families, unique families, species, unique species, rare species (singletons and doubletons) and abundances of arboreal spiders in three canopy strata of beech trees (*Fagus sylvatica*).

Site	High	Intermediate	Low	Overall
Families	13	11	12	16
Unique families	3	1	1	5
Species	44	58	44	80
Unique species	11	15	10	36
Singletons	16	19	13	23
Doubletons	3	8	8	12
% Rare species	43.2	46.6	47.7	43.8
Abundances	582	3638	2089	6309

Table 2. Tests of species-abundance models at three canopy strata of beech trees (*Fagus sylvatica*).

Model	High		Intermediate		Low	
	Chi-square	<i>P</i>	Chi-square	<i>P</i>	Chi-square	<i>P</i>
Geometric	384.2	<0.001	9755	<0.001	2727	<0.001
Log series	56.88	<0.01	935.4	<0.001	383.3	<0.001
Broken stick	284.3	<0.001	5032	<0.001	2153	<0.001
Log-normal	2.454	0.653	2.59	0.76	16.2	<0.01

Canopy strata preference

Theridiidae made up the largest portion of individual spiders collected (20.9%), followed by Araneidae (20.7%), Anyphaenidae (15%), Tetragnathidae (12%), Linyphiidae (11.8%), Clubionidae (9.3%), Thomisidae (5.6%). The family composition of arboreal spiders shows a clear association for certain beech canopy strata (Figure 1). Pair-wise comparisons between canopy strata using Chi-square tests of homogeneity indicated that family composition in the high stratum was significantly different from intermediate and low strata (high-intermediate: Chi-square = 39.60, d.f. = 8, $P < 0.001$; high-low: Chi-square = 41.61, d.f. = 8, $P < 0.001$): it consisted of many Araneidae, but few Clubionidae and Anyphaenidae. The family compositions between intermediate and low strata were similar, however (Chi-square = 14.13, d.f. = 8, $P = 0.08$). Although fewer Araneidae were in the intermediate and low strata, more Clubionidae and Anyphaenidae were collected there.

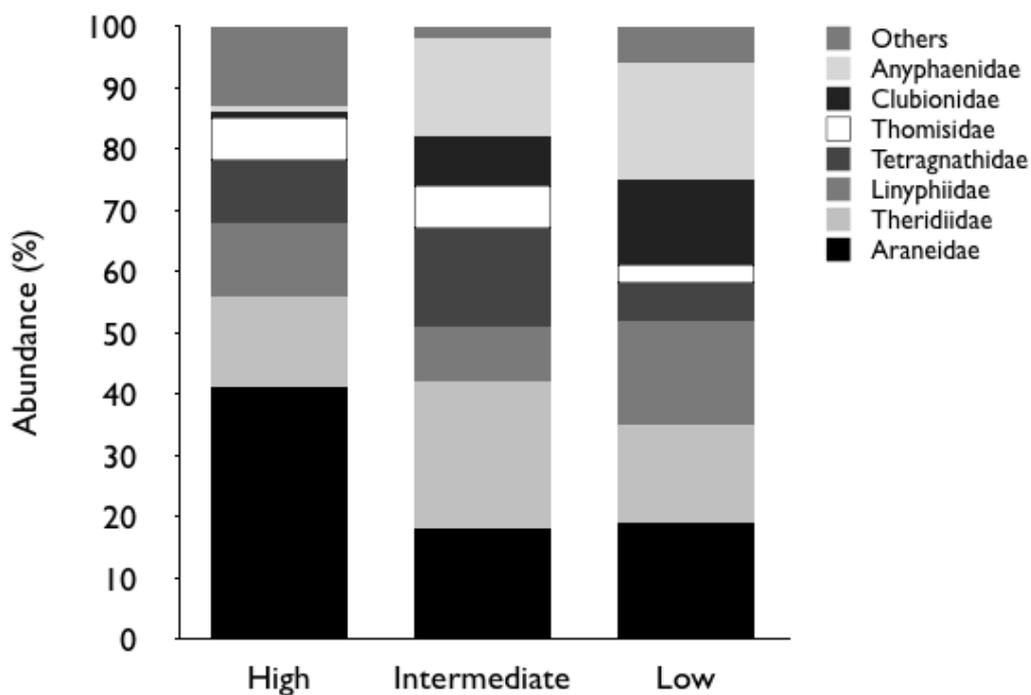


Figure 1. Contributions of various families to the arboreal spider composition in the high, intermediate, low canopy strata of European beech forest patches.

Estimates for canopy spider diversity and similarity

The Chao1 estimated that at least 55 more species are expected in the low canopy stratum; at least 102 species were expected at species saturation of the whole beech forest; and the percentage of inventory completion reached about 78.4% (Table 3). The calculator based on Chao1 also predicted with high probability that, in a further survey, the next sampled individual in the high stratum would represent a previously undetected species (0.027). Overall, additional 34,425 spiders would need to be collected and identified to reach the 100% of estimation of local species richness.

The exponential Shannon entropy showed that the upper canopy stratum had the highest diversity (15.67 with a 95% CI of [13.94, 17.4]), whereas the intermediate (10.5 [10.04, 10.97]) and low strata (10.35 [9.75, 10.95]) possessed a similar diversity. The inverse Simpson index showed that the spider assemblages were more influenced by dominant species in the two lower strata (the values were 6.26 [5.73, 6.78] and 5.80 [5.27, 6.33] respectively). The abundance-based Morisita similarity indices also showed that the highest similarities were between the intermediate and low strata (82.7% with a confidence interval of [80.3, 85.1]). However, the lower similarities were between the high and intermediate strata (41.6% [36.8, 46.4]) and between high and low strata (35.3% [31.2, 39.5]).

Table 3. Estimation of species richness, diversity and evenness (with a 95% confidence interval) at three canopy strata of beech trees (*Fagus sylvatica*).

	High	Intermediate	Low	Overall
Estimated species richness				
Chao1	87	81	55	102
% inventory completion	50.6	71.6	80	78.4
<i>P</i>	0.027	0.005	0.006	0.004
<i>N</i>	9860	24562	8243	34425
Exponential Shannon entropy				
Jackknife	15.67 (13.94, 17.4)	10.50 (10.04, 10.97)	10.35 (9.75, 10.95)	12.67 (12.25, 13.1)
Inverse Simpson index				
MVUE	9.34 (8.88, 9.8)	6.26 (5.73, 6.78)	5.80 (5.27, 6.33)	7.38 (6.83, 7.93)

P: The probability that the next sampled individual represents a previously unseen species. *N*: The number of additional individuals needs to reach estimated richness

Discussion

Community structures and estimation of spider diversity

To the best of our knowledge, this is the first study to investigate true diversity of spider assemblages in canopies of European beeches in Central Europe. Although old-growth beech trees are rarely preserved in Europe, their high canopy stratum harbored the most discrete spider community with most families and highest diversity — hence the entire community cannot be adequately assessed by only sampling lower canopy strata. This emphasizes the importance of old-growth trees as reservoirs of arthropod biodiversity. In contrast, the intermediate and low strata of beech canopies had similar spider community structures and family compositions. Although more taxa were collected from the intermediate stratum, the spiders fogged from the low stratum represented an epitome of European beech forest. Those two strata had also similar diversity and dominance (true diversity of order one and two). Based on these results, we propose that low stratum (young beech) should be included in sampling protocols for the rapid biodiversity assessment of arboreal spider diversity in European beech forest in Central Europe. This is because the majority of beech forests consist of mature and young trees. In particular, young beeches are only 5–6 meters tall and thus the inventory can be made easily and cost-effectively. This approach might represent a substantial breakthrough for a wide range of biodiversity studies in this and other forest ecosystems.

Forest tree canopies provide the spiders dwelling there with shelter, sites for foraging, ovipositioning, sun-basking, sexual display and overwintering, all of which require properties related to habitat architecture (Lawton 1983). Our study showed that the spider assemblages dwelling in the three beech canopy strata differed in their family composition. The high canopy stratum on the one hand, and two lower strata, on the other hand likely provided heterogeneous ecological conditions affecting the distribution of spiders: the old-growth beeches have broad canopy coverage, offering more open spaces meeting the requirements of Araneidae to build large orb-webs by a small number of individuals (Hurd and Fagan 1992). And conversely, the mature and young beeches have a quite dense tree crown, especially suitable for cursorial hunters running between foliages (e.g. Anyphaenidae and Clubionidae).

The families of Theridiidae, Araneidae and Anyphaenidae dominated the beech forest patches in our study in terms of individual abundance. A comparison with the fogging samples from Poland by Floren *et al.* (2008) of our working group (using the same fogging methods but in heterospecific trees) showed that Theridiidae, Linyphiidae and Tetragnathidae were the three most dominant families in the canopies

of *Quercus robur*, *Picea abies* and *Carpinus betulus*. The much larger proportion of Araneidae and Anyphaenidae dwelling in the beeches compared to the three above-mentioned tree species pointed to considerable differences in the family composition of arboreal spiders according to tree species. These differences may be due to the beech tree form and smooth bark which lacks bark structures, and offers microclimate only for certain arboreal spiders.

In the parametric species abundance model, the communities in the high and intermediate canopy strata fitted a log-normal distribution. However, we found that no particular distribution was able to fit data in the low strata for interpreting the assemblages. Thus non-parametric methods can play an important role in estimating diversity of the respective community based on observed data (Chao et al. 2006). In particular, the Chao1 estimator showed that the estimated number of species in the low stratum were unrepresentative of the arboreal spider richness. When the samples from two higher strata were combined, the estimated species richness was almost doubled — the lower stratum is not a substitute for whole tree community inventory. The comparison between empirical and estimated species richness showed that our inventory of arboreal spider assemblages was still incomplete: approximately 21.6% of the species were missed. This indicates that great sampling effort is needed to survey the remaining species, particularly in the high stratum (i.e. old-growth beech trees) where only 50.6% had been sampled.

Collecting method and rare species

The insecticide knockdown is one of the most widely used canopy sampling techniques, which is a model collecting method for studying the biodiversity pattern on the tree in terms of species richness and abundance (Stork and Brendell 1990; Basset 2001). Particularly, it increased the species richness and diversity by collecting many cryptic, unique and rare species, which only dwell in canopies and are not easily collected by hand or with other methods. After three canopy strata of beeches were fogged using insecticide knockdown, 10% were found as newly recorded species for the arboreal spider community of beeches in Europe. This finding increases the number of documented Araneae species in European beech habitats. Using the fogging technique, we found some undetected (rare) species dwelling only in tree crowns, e.g. *Troxochrus nasutus* (Heimer and Nentwig 1991). Without canopy fogging the results of our study would have been much less detailed and possibly biased. Since each canopy stratum had many rare species, disturbance of any canopy stratum will presumably result in loss of a number of these species (Hsieh et al. 2003). Moreover, rare species are of great ecological importance, and should therefore not be

excluded from community studies. Rather, they should be targeted as interesting biological phenomena (e.g. speciation, ecological drift), which is able to regulate biodiversity patterns (Hubbell 2001).

In our study, the abundance of rare species was utilized by the nonparametric approach to estimate the number of unseen species, because only rare species carry the information for estimating the number of unseen species. Since rare species play an important role in generating these estimates, we suggest: (1) Enhancing spatial replication with other methods. Because some arboreal spiders might be strongly vertically stratified, or migrate between the canopy to the ground, we should also use different sampling methods (e.g. pitfall trapping) to avoid artifactual rarity (Longino et al. 2002). (2) Adding seasonal replication. Assessing species richness is always affected by the intensity and time span of the survey (Colwell and Coddington 1994), so that while some species may be temporally rare, they might be abundant or common in cold seasons. It is crucial to have year-round sampling to better understand annual life cycles in general and for analyzing their temporal dynamics in communities of arboreal spiders in late fall, winter and early spring. For these reasons, we urge the forest ecologist to revisit the temperate forest, particularly the high canopy stratum and in cold seasons, to search for these hidden species. Only this can hope to yield a more robust inventory that presents a truer picture of actual forest biodiversity.

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Appendix. A list of arboreal spider species on European beech in Würzburg University Forest.

On Bavaria Red List. * New record arboreal species in European beech.

Taxon	High	Intermediate	Low	Total
Amaurobiidae				
<i>Coelotes terrestris</i> (Wider, 1834)	1	.	.	1
Anyphaenidae				
<i>Anyphaena accentuata</i> (Walckenaer, 1802)	14	1109	746	1869
Araneidae				
<i>Araneus diadematus</i> Clerck, 1757	4	2	1	7
<i>Araneus sturmi</i> (Hahn, 1831)	45	100	111	256
<i>Araneus triguttatus</i> (Fabricius, 1775) #*	.	.	1	1
<i>Araniella cucurbitina</i> (Clerck, 1757)	.	1	3	4
<i>Araniella opisthographa</i> (Kulczyński, 1905)	.	1	1	2
<i>Cyclosa conica</i> (Pallas, 1772)	51	160	114	325
<i>Gibbaranea bituberculata</i> (Walckenaer, 1802) #*	3	14	.	17
<i>Mangora acalypha</i> (Walckenaer, 1802)*	136	271	152	559
<i>Zilla diodia</i> (Walckenaer, 1802)*	.	.	2	2
Clubionidae				
<i>Clubiona caerulescens</i> L. Koch, 1867	.	1	.	1
<i>Clubiona comta</i> C. L. Koch, 1839	.	16	5	21
<i>Clubiona terrestris</i> Westring, 1851	4	.	.	4
Dictynidae				
<i>Nigma flavescens</i> (Walckenaer, 1830)	.	.	11	11
Linyphiidae				
<i>Araeoncus humilis</i> (Blackwall, 1841)	1	.	.	1
<i>Bathypantes gracilis</i> (Blackwall, 1841)	1	2	.	3
<i>Centromerus sylvaticus</i> (Blackwall, 1841)	.	2	.	2
<i>Cnephalocotes obscurus</i> (Blackwall, 1834)	.	.	1	1
<i>Collinsia inerrans</i> (O. P.-Cambridge, 1885)	1	.	.	1
<i>Dicymbium nigrum</i> (Blackwall, 1834)	.	1	.	1
<i>Diplocephalus picinus</i> (Blackwall, 1841)	2	1	.	3
<i>Drapetisca socialis</i> (Sundenall, 1833)	6	18	12	36
<i>Entelecara acuminata</i> (Wider, 1834)*	1	1	26	28
<i>Entelecara erythropus</i> (Westring, 1851)	.	.	1	1
<i>Erigone atra</i> Blackwall, 1833	1	1	.	2
<i>Erigone dentipalpis</i> (Wider, 1834)	3	.	.	3

Taxon	High	Intermediate	Low	Total
<i>Erigonella hiemalis</i> (Blackwall, 1841)	.	1	.	1
<i>Leptyphantes flavipes</i> (Blackwall, 1854)	.	3	2	5
<i>Leptyphantes minutus</i> (Blackwall, 1833)	.	4	.	4
<i>Linyphia hortensis</i> Sundevall, 1830	1	.	.	1
<i>Linyphia triangularis</i> (Clerck, 1757)	6	17	5	28
<i>Maso sundevalli</i> (Westring, 1851)	.	1	3	4
<i>Meioneta rurestris</i> (C. L. Koch, 1836)	3	8	2	13
<i>Mermessus trilobatus</i> (Emerton, 1882)	3	5	2	10
<i>Microneta viaria</i> (Blackwall, 1841)	.	1	.	1
<i>Moebelia penicillata</i> (Westring, 1851)	.	2	.	2
<i>Neriere emphana</i> (Walckenaer, 1842)	1	10	6	17
<i>Neriere peltata</i> (Wider, 1834)	16	133	327	476
<i>Obscuriphantes obscurus</i> (Blackwall, 1841)	.	.	1	1
<i>Oedothorax retusus</i> (Westring, 1851)	1	.	.	1
<i>Porrhomma microphthalmum</i> (O. P.-Cambridge, 1871)	4	6	.	10
<i>Porrhomma oblitum</i> (O. P.-Cambridge, 1871)	.	1	1	2
<i>Tenuiphantes alacris</i> (Blackwall, 1853)	.	1	.	1
<i>Tenuiphantes flavipes</i> (Blackwall, 1854)	.	2	.	2
<i>Tenuiphantes tenebricola</i> (Wider, 1834)	.	5	.	5
<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	2	4	.	6
<i>Troxochrus nasutus</i> Schenkel, 1925	.	1	.	1
Lycosidae				
<i>Pardosa lugubris</i> (Walckenaer, 1802)	1	.	.	1
<i>Pardosa saltans</i> Töpfer-Hofmann 2000	1	.	.	1
Philodromidae				
<i>Philodromus albidus</i> Kulczyński, 1911	.	2	1	3
<i>Philodromus aureolus</i> (Clerck, 1757)	4	2	.	6
<i>Philodromus collinus</i> C. L. Koch, 1835	1	1	.	2
Pisauridae				
<i>Pisaura mirabilis</i> (Clerck, 1757)	1	.	.	1
Salticidae				
<i>Ballus chalybeius</i> (Walckenaer, 1802)	77	21	127	225
<i>Evarcha falcata</i> Clerck, 1757	.	.	1	1
<i>Heliophanus cupreus</i> (Walckenaer, 1802)	1	1	.	2
Segestriidae				
<i>Segestria senoculata</i> (Linnaeus, 1758)	.	1	.	1

Taxon	High	Intermediate	Low	Total
Sparassidae				
<i>Micrommata virescens</i> (Clerck, 1757)	1	.	2	3
Tetragnathidae				
<i>Metellina mengei</i> (Blackwall, 1870)	65	749	72	886
<i>Metellina segmentata</i> (Clerck, 1757)	8	16	2	26
<i>Pachygnatha degeeri</i> Sundevall, 1830	.	2	.	2
<i>Tetragnatha obtusa</i> C. L. Koch, 1837	1	7	.	8
<i>Tetragnatha pinicola</i> L. Koch, 1870*	39	200	71	310
Theridiidae				
<i>Achaearanea lunata</i> (Clerck, 1757)	.	1	2	3
<i>Anelosimus vittatus</i> (C. L. Koch, 1836)*	.	3	.	3
<i>Dipoena melanogaster</i> (C. L. Koch, 1837)	.	.	2	2
<i>Enoplognatha ovata</i> (Clerck, 1757)	3	16	80	99
<i>Neottiura bimaculata</i> (Linnaeus, 1767)	2	.	.	2
<i>Paidiscura pallens</i> (Blackwall, 1834)	30	84	70	184
<i>Parasteatoda simulans</i> (Thorell, 1875)	.	8	3	11
<i>Platnickina tinctoria</i> (Walckenaer, 1802)	11	146	34	191
<i>Theridion mystaceum</i> (L. Koch, 1870)	7	58	13	78
<i>Theridion pinastri</i> L. Koch, 1872	5	10	1	16
<i>Theridion varians</i> Hahn, 1833	.	1	24	25
Thomisidae				
<i>Diaea dorsata</i> (Fabricius, 1777)	13	353	45	411
<i>Synaema globosum</i> (Fabricius, 1775)	.	.	1	1
<i>Xysticus</i> VS45*	.	1	.	1
<i>Xysticus lanio</i> C. L. Koch, 1835	.	.	1	1
Uloboridae				
<i>Hyptiotes paradoxus</i> (C. L. Koch, 1834)	.	49	1	50

Chapter IV

Seasonal dynamics of arboreal spider diversity in a temperate forest

Abstract

Measuring and estimating biodiversity patterns is a fundamental task of the scientist working to support conservation and inform management decisions. Most biodiversity studies in temperate regions were often carried out over a very short period of time (e.g. a single season) and it is often — at least tacitly — assumed that these short term findings are representative of long term general patterns. However, should the studied biodiversity pattern in fact contain significant temporal dynamics, perhaps leading to contradictory conclusions. Here we studied the seasonal diversity dynamics of arboreal spider communities dwelling in 216 European beeches (*Fagus sylvatica*) to assess the spider community composition in the following seasons: two cold seasons (I [November 2005-January 2006]; II [February-April]) and two warm seasons (III [May-July]; IV [August-October]). We show that the usually measured diversity of the warm season community (IV) alone did not deliver a reliable image of the overall diversity present in these trees, and therefore we recommend it should not be used for sampling protocols aimed at providing a full picture of a forest's biodiversity in the temperate zones. In particular, when the additional samplings of other seasons (I, II, III) were included, the estimated species richness nearly doubled. Community I possessed the lowest diversity and evenness due to the harsh winter conditions: this community was comprised of one dominant species together with several species low in abundance. Similarity was lowest (38.6%) between seasonal communities I and III, indicating a significant species turnover due to re-colonization, so that community III had the highest diversity. Finally, using nonparametric estimators, we found that further sampling in colder months (November to April) is needed to complete our inventory. Our study clearly demonstrates that seasonal dynamics of communities should be taken into account when studying biodiversity patterns of spiders, and probably forest arthropods in general.

Keywords

Araneae, canopy fogging, European beech, re-colonization, species richness estimation, true diversity

Introduction

The increased destruction of natural habitats has strengthened the need to understand biodiversity patterns and their spatial and temporal variation for the purpose of supporting conservation and management decisions. Currently, most biodiversity studies, especially rapid assessments, rely on intensive sampling over only short time periods. These studies however, while certainly informative, often — at least implicitly — assume that such short term results can be generalized and taken as representative of long-term patterns (Hughes et al. 2002, Shahabuddin et al. 2005). However, those studies paying attention to seasonal variation have revealed that it may play a very important role in species turnover, and thus its contribution to overall biodiversity may be underappreciated (Thomas and Thomas 1994, Leps et al. 1998, Summerville and Crist 2003). This critically challenges our understanding of biodiversity patterns and requires analyses along temporal scales (Tylianakis et al. 2005): if species' distributions are aggregated in time due to strong seasonality, the time frame of sampling could lead to serious under- or overestimation of diversity and might result in contradictory or misleading inferences and conclusions.

In temperate forests there are large seasonal variations in temperature. For this reason it is essential to carry out biodiversity sampling over an extended period comprising all seasons — in given a year at least — to clarify the basics pattern of temporally variable diversity (Floren and Schmidl 2008). Tree crowns in the temperate zone offer an excellent opportunity to investigate temporal variations, because the fauna is cleared annually by winter's onset and we can measure the appearance and disappearance of spiders across changing seasons. This cycle of colonization and re-colonization could be described by the theory of island biogeography (MacArthur and Wilson 1963, 1967), which might describe in a basic way the seasonal community dynamics of arboreal arthropods in canopies of temperate and higher latitude forests. The theory predicts that the number of species on a true island or habitat island, such as tree crowns in this case (Müller and Goßner 2007), results from the dynamic relationship between local immigrations and extinctions. Thus, by studying arboreal arthropods in these temperate forest canopies, we may examine temporal dynamics of species richness and their seasonal contribution to overall biodiversity.

Among arthropods, spiders are a valuable surrogate for assessing overall arthropod diversity and for studying general spatial and temporal biodiversity patterns (Marc et al. 1999; Platnick 1999; Cardoso et al. 2004). This is because spiders are among the most species-rich animal orders (Coddington and Levi 1991; Nyffeler 2000), including about 42,055 described species with an estimated total of about

60,000 - 170,000 species (Coddington and Levi 1991; Platnick 1999, Platnick 2010), and they contribute significantly to abundance and diversity of terrestrial arthropods (Floren and Sprick 2007). Their study has implications not only for biodiversity and conservation issues but also for the timing and availability of ecosystem services facilitated by arboreal spiders: namely, catching great quantities of insects as prey in temperate regions (Nyffeler and Benz 1987, Nyffeler 2000). Furthermore, shifts in spiders' guild composition can also be used to monitor the habitat change (Brown 2003), to assess microclimate complexity (Downes et al. 1998, Gunnarsson et al. 2004), and perhaps lead to an effective niche separation (Cerda et al. 1998).

The systematic study reported here examined the species richness, diversity, evenness and similarity (or species turnover) of arboreal spider communities at different temporal (seasonal) scales over a one year period. We independently aggregated abundance data from the Würzburg University Forest, Germany at different temporal focal scales. We asked the following questions: (1) Does species richness, diversity and guild composition of communities in different seasons show strong temporal variation? (2) Which families and guilds characterize the process of re-colonization in the warm seasons? (3) Based on nonparametric estimators, how many additional individuals would be needed to complete comprehensive inventories of spider diversity at our forest site?

Material and methods

Study area

We conducted our study in the Würzburg University Forest, northern Bavaria, Germany (50°01' N, 10°30' E), where the mean yearly temperature and precipitation is 7.5 °C and 675 mm. This temperate forest is dominated by European beech (*Fagus sylvatica*, 21% of forest area), followed by oak (*Quercus robur*, 19%) and spruce (*Picea abies*, 12%). We studied three of managed beech patches. Six replicates (individual beeches) were sampled per patch in this study on a monthly basis from November 2005 to October 2006 (i.e., 18 new beeches per month), and the spider communities of these 216 beeches (unrepeated samples) served as basis for studying seasonal variation in tree canopies.

Canopy sampling

Beech canopies were fogged with pyrethrum at daybreak using a fogging machine (SwingfogTM SN-50). The fogging lasted approximately 10 minutes followed

by a two-hour dropping time. Dropping arboreal arthropods were subsequently collected on plastic sheets previously positioned on the ground (588 m² for 18 trees per month). Spiders were sorted for identification to species level by using species-specific attributes of the palpal organ and/or epigynum using the keys provided by Heimer and Nentwig (1991) and Roberts (1996); nomenclature follows Platnick (2010).

Data analyses

Collecting biodiversity data is labor intensive and time consuming (Longino and Colwell 1997, Lawton et al. 1998). A substantial fraction of a community is often represented by many rare species, often singletons, which remain undetected by most biodiversity surveys (Chao et al. 2009). Since rare species usually contain information about incomplete sampling (Preston 1962, 1962), we used nonparametric estimators (Colwell and Coddington 1994). These are based on frequency count and information on the rare species in the collection to estimate “true diversity” (Jost 2006,2007): (1) Estimates of total species richness (the true diversity of order zero) was estimated by the Chao1 estimator (Chao 1984, Shen et al. 2003, Chao et al. 2006), which uses the numbers of singletons and doubletons to estimate the missing species’ numbers because information on missing species is mainly derived from rare species. (2) Exponential Shannon index (the true diversity of order one) was measured by the Jackknife method (Zahl 1977); (3) Inverse Simpson index (the true diversity of order two) were calculated using a Minimum Variance Unbiased Estimator (MVUE, Magurran 1988). The abundance-based data were analyzed with SPADE (Chao and Shen 2003). While incidence-based methods treat all species equally, the abundance-based method treats all individuals equally, thus the two approaches are conceptually different (Chao et al. 2006). We also give the 95% confidence intervals (CI) to define the sampling variation, constructed using 200 bootstrap replications (Chao 1987, Chao et al. 2006).

SPADE was also used to estimate the similarity (species turnover) of spider communities between seasons. The abundance-based Morisita index can investigate the degree of association in the distribution and re-colonization of spiders between seasons. In order to predict the additional amount of sampling needed to reach 100% of the asymptotically increasing species richness, we generated subsamples from the fogging data using Chao1 estimator. We also predicted the probability that the next sampled individual represents a previously undetected species in a further survey for future sampling planning. In addition, the distribution of a particular guild among different seasons can be used to assess seasonal environmental change and to point to

which guild might drive re-colonization. Chi-square goodness-of-fit tests were used to examine whether or not certain guilds were more pronounced in a particular season.

Results

Structure and seasonal pattern of arboreal spider communities

In total 10675 individuals were collected from 216 fogged beeches. Of these 4305 spiders were able to be identified to 78 species belonging to 14 families (Table 1, Appendix). Anyphaenidae made up the largest portion of individual spiders collected (34.3%), followed by Tetragnathidae (15.6%), Araneidae (15.4%), Linyphiidae (14.1%), Theridiidae (12.3%), Thomisidae (3.9%). Linyphiidae had the greatest number of species (33), followed by Theridiidae (10), Araneidae (10), Tetragnathidae (6), Clubionidae, Salticidae and Thomisidae (3). The most abundant species was *Anyphaena accentuata*; a total of 1478 individuals were found (34.3 %). The second most abundant species was *Metellina mengei* (n = 544, 12.6%), followed by *Neriene peltata* (n = 362, 8.4%), *Paidiscura pallens* and *Mangora acalypha* (n = 251, 5.8%), *Cyclosa conica* (n = 243, 5.6%).

Table 1. Number of families, species richness, unique species, rare species (singletons and doubletons) and abundances of arboreal spiders in beech trees (*Fagus sylvatica*) in four seasonal communities in Germany.

Site	I	II	III	IV	Overall
Families	6	9	12	11	14
Species	12	27	52	41	78
Unique species	0	7	23	14	44
Singletons	5	11	16	13	22
Doubletons	1	1	8	5	8
% Rare species	50	44.4	46.2	43.9	38.5
Abundances	438	291	796	2780	4305

In order to analyze temporal dynamics we categorized the four seasonal patterns of spider communities: two cold seasons (community I [November to January]; II [February to April]) and two warm seasons (III [May to July]; IV [August to October]). Community IV possessed higher abundance of arboreal spiders (308.89 ± 103.06 [mean \pm SE, $n = 9$ sets]) whereas communities I (48.67 ± 18.55), II (32.33 ± 7.52) and III (88.44 ± 17.62) had fewer individuals (one-way ANOVA: $F_{3,32}=5.818$, $P < 0.01$, Tukey's comparisons: $IV > I = II = III$). Only six species were constantly active in all four seasons (*Anyphaena accentuata*, *Metellina mengei*, *Paidiscura pallens*, *Diaea dorsata*, *Hyptiotes paradoxus* and *Erigone atra*), whereas 44 species (56.4%) were only collected in one seasonal community and showed clear seasonal preferences. Table 1 shows that up to 60 species were possibly seasonally rare, i.e. comprising one or two individuals only were found during one season (45 singletons and 15 doubletons). However, when pooling all four seasonal communities, the number of rare species is divided by two thus reaching only 30 species (22 singletons and 8 doubletons). Thirty-six sets of beeches were used to analyze seasonal preferences of spiders, with each set consisting of six spider communities (i.e. six beech trees) collected from the same patch in the same month.

Estimates of arboreal spider diversity and seasonal similarity

Table 2 shows that at least 108 species were expected by the individual-based Chao1 estimator at species saturation whereas only 58 species were expected in community IV (samples of the months from August to October). In the cold seasons, 25 species were expected in community I, but 88 species in community II. The calculation based on Chao1 also predicted the additional sample size needed to detect 100% of the estimated species richness: it varied from 4225 individuals (community III) to 19257 individuals (IV) in different seasons. Overall, an additional 35,578 individuals would need to be collected and identified to reach the full set of local species. Moreover, it was predicted with higher probability (4%) that in a next survey the next sampled individual in community II would represent a previously undetected species.

The exponential Shannon entropy estimate showed that seasonal communities II and III had the greatest diversity (II: 11.14 with a 95% of [9.46, 12.83]; III: 13.91 [12.42, 15.39]), followed by community IV (10.29 [9.84, 10.74]) and community I (1.56 [1.37, 1.76]). The inverse Simpson index showed that the spider assemblage in community I (November-January) was most influenced by dominant species (1.17 [-0.43, 2.77]). The abundance-based Morisita indices showed that the similarity between the four seasons was 52.3% with a 95% CI of (48.4, 56.2); furthermore,

similarity was significantly lower (38.6% [33.1, 44.0]) between communities I and III (Table 3).

Table 2. Estimation of species richness, diversity and evenness (95% confidence interval) in four seasonal communities on forest beech trees in Germany

	I	II	III	IV	Overall
Estimated species richness					
Chao1	25	88	68	58	108
% inventory completion	48	30	76.5	70.7	72.2
<i>P</i>	0.01	0.04	0.02	<0.01	0.01
<i>N</i>	5347	10770	4225	19257	35578
Exponential Shannon entropy					
Jackknife	1.56 (1.37, 1.76)	11.14 (9.46, 12.83)	13.91 (12.42, 15.39)	10.29 (9.84, 10.74)	12.61 (12.04, 13.17)
Inverse Simpson index					
MVUE	1.17 (-0.43, 2.77)	6.88 (6.38, 7.37)	7.28 (6.84, 7.72)	6.74 (6.2, 7.28)	6.4 (5.85, 6.94)

P: The probability that the next sampled individual represents a previously unseen species. *N*: The number of additional individuals needs to reach estimated richness.

Table 3. Pairwise similarity (%) with a 95% confidence interval among four seasonal communities studied on 216 beech forest trees in Germany

	I	II	III	IV
I	100			
II	52.9 (44.5, 61.3)	100		
III	38.6 (33.1, 44.0)	55.5 (48.4, 62.5)	100	
IV	55.4 (52.6, 58.2)	72.0 (65.8, 78.2)	63.7 (57.8, 69.5)	100

Seasonal preference of arboreal spider guild

Four spider guilds were analyzed: space-web weavers (Dictynidae, Linyphiidae and Theridiidae, 19.6%); orb-web weavers (Araneidae, Tetragnathidae and Uloboridae, 37.3%); foliage runners (Anyphaenidae, Clubionidae and Sparassidae, 21.6%); ambushers and stalkers (Philodromidae, Salticidae and Thomisidae, 7.4%) (modified from Uetz et al. 1999). Amaurobiidae were excluded for this analysis due to their low abundances. Chi-square tests demonstrated two seasonal patterns in guild composition (Table 4): community II and III consisted of a large proportion of space-web weavers and a small proportion of foliage runners (Figure 1). In contrast, communities I and IV consisted of relatively more foliage runners and fewer space-web weavers.

Table 4. Arboreal spider guild composition between each seasonal community examined by values (lower-left triangle) and significance levels (upper-right triangle) of Chi-square tests of homogeneity.

	I	II	III	IV
I		<0.05	<0.01	0.33
II	11.11		0.26	<0.01
III	17.02	5.24		<0.01
IV	4.58	13.98	14.83	

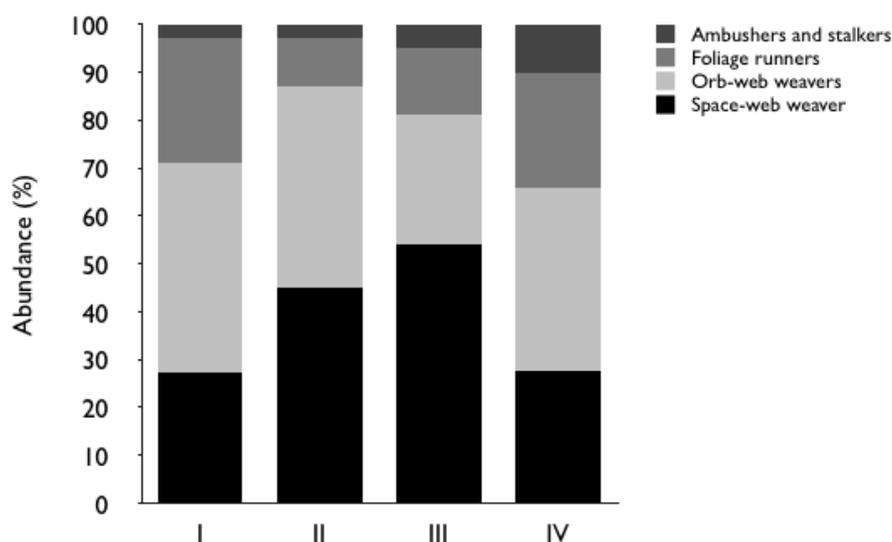


Figure 1. Arboreal spider guild composition of four seasonal communities on 216 beech (*Fagus sylvatica*) forest trees in Germany based on pooled monthly samples

taken over a one-year period.

Discussion

Our study is among the first to study arboreal spider diversity at the canopy strata on a year-round temporal scale. The 216 European beeches were fogged over twelve consecutive months in order to study the biodiversity dynamics of arboreal spiders; as suspected, the results revealed that the community structure and diversity of arboreal spiders changed with seasons. Since no prior study has attempted to determine whether spiders can survive the harsh conditions of the canopy in winter, the study contains novel data from the canopies of deciduous trees in the temperate zone. Using individual tree canopies as experimental units, we can analyze the effects of re-colonization and disappearance on local biodiversity assemblages.

Seasonal community structure and diversity of arboreal spiders

Some insect communities in temperate forests also contain species that are aggregated due to host plant phenology (Summerville and Crist 2003, 2005, Veech et al. 2003). However, the distribution of spiders is mostly governed by microclimate, vegetation architecture, prey availability, as well as oviposition site availability (Halaj et al. 2000). Low diversity and abundance in community I pointed to the obvious fact that the harshest winter conditions for arboreal spiders were from November to January, such that only two species (*Anyphaena accentuata* [55 individuals] and *Hyptiotes paradoxus* [1]) were found on 18 beech trees in January. The low value of the inverse Simpson index suggests that community I (November to January) was dominated by the former species (92%, 405 of 438 individuals), and this relatively high abundance of *Anyphaena accentuata* in community I is surprising. Indeed, this species is known to require specific habitats to hide from predation pressure, given that tree crowns usually start to lose their leaves in November. Most broad-leaved woody plants in the temperate zones shed their leaves in late autumn and go through the entire winter leafless. However, many European beeches exhibit marcescence, that is, they retain their dry leaves through winter and shed them only the following spring (Otto and Nilsson 1981). This phenomenon might have a significant effect on microclimate during harsh wintertimes and seems to provide a very important refuge for winter-active spiders. The distribution of spiders exhibits associations with the marcescence phenomenon, thus *Anyphaena accentuata* became a consistent and ubiquitous colonizer and its high abundance in these winter trees can prevent its local extinction (i.e. rescue effect, Brown and Kodric-Brown 1977, Pulliam 1988). This phonological trait of European beeches might attract winter-active spiders that

become sedentary, with the effect of controlling herbivorous insects, especially in the winter and following spring under milder climate allowing spider activity. Our finding indicates that beech marcescence is important for winter-active arthropods and points to its conservation value.

From February onward, however, the spider communities were no longer dominated by *Anyphaena accentuata* (as suggested by the higher inverse Simpson index value). The families that characterized the process of re-colonization and contributed to forming the community II were mainly Amaurobiidae, Araneidae, Salticidae and some members of Linyphiidae, which did not occur in community I. These families were important in structuring the following warm seasonal communities because being so abundant there was little ‘extinction’ risk (in the island sense) in the warm seasons. Conversely, the small populations of Dictynidae and Philodromidae found in community III stand the greatest chance of becoming locally ‘extinct’ in the canopy ‘island’. But owing to the transient families, community III was well mixed and thus had the highest diversity. After re-colonization communities II and III had significantly different guild compositions compared to community I, and the least similarity between communities III and I further confirmed they were heterogeneous due to higher species turnover.

Although there were no significant differences in the diversity and dominance between communities II and IV, higher species richness was estimated for community II (February to April). This is due to the fact that many space-web weavers started to immigrate into sparse canopies in April (early spring) before the tree crowns were fully covered by fresh leaves. This increased proportion of space-web weavers suggests they are important in spider re-colonization in spring months: most of their members (e.g. Linyphiidae and Theridiidae) are quite small and disperse easily in warm seasons (e.g. by ballooning, Bonte et al. 2008), thus they exerted a quick and strong effect on the re-structuring of the communities. And while communities II and III both contained a large proportion of space-web weavers, many of these species disappeared locally from the canopies in community IV (August to October) and many likely went ‘extinct’. A further reason for the latter’s disappearance might be that some species left the tree, below to the ground in order to search for mating opportunities or suitable oviposition sites (Draney 1997). In parallel some species which had returned to tree canopies since August (e.g. *Drapetisca socialis* and *Metellina segmentata*) were found as late as December, but not from January to July. After six months, the similar species and guild compositions between communities IV and I shows that community IV had re-established itself and become identical to the original community I (last winter composition). This return confirms that communities in the temperate zone were not stable but in a state of flux. This is likely

a characteristic of the beech forest canopy communities and may be essential for maintaining ecosystem function (as prey and predator), particularly during winter.

True diversity estimates and sufficient sampling

Using the Chao1 nonparametric estimator, we made point estimates and direct comparisons between seasons even if the seasonal communities contained different numbers of spiders. The estimator predicted that there are in total 108 arboreal spiders in beech forests within the Würzburg University Forest. The Chao1 estimator showed different estimates of species richness (25–88 species) among seasons, indicating that bias can be generated when only sampling in one single season in a given year, because phenology causes many species to be rare at most time periods (Summerville and Crist 2003, 2005). Since Chao1 only uses the numbers of rare species to estimate the number of missing species (Chao et al. 2006), our study, which takes seasonal variability into account, and thus brings the number of rare species to half its seasonal value (seasonal: 60 rare species; overall: only 30), better avoids the overestimation and represents the true diversity of arboreal spiders in the European beech forest.

Sufficient sampling is important in order to study biodiversity and make proper conservation decisions. The estimation of species richness according to the Chao1 estimator predicted that over 70% of the available taxa had been sampled in communities III and IV, however, 52% and 70% of the available taxa had not been sampled in communities I and II respectively. This shows that substantial sampling is still needed to survey the remaining species during the cold season months (November to April). In short, it is probably impossible to detect all expected species without taking the cold season into explicit account. Further, there is a higher probability of finding an undetected species from February to April (II). Thus the cold season, which harbors a significant amount of undetected rare species and offers the relevant information for estimating true diversity, requires additional focus. We anticipate that such investigations will prompt us to revise species richness and the results of biodiversity studies in the temperate forest ecosystems.

Months from August to October are most suitable for many spiders compared to other months, as shown by higher abundance of spiders in this season (community IV). However, the diversity estimate obtained from data of those months alone is an underestimate: it failed to yield a reliable picture of the beech forest canopies' diversity. If the sampling had been restricted to this season only we would have considerably underestimated the species richness (58 species), to just over half (54%) of the actual estimated species richness over a year's sampling. Based on our results, we can claim that the composition and diversity of arboreal spider communities in

temperate forests is strongly influenced by seasonal variables. We should not only focus on the partitioning of spatial components of community structure (Gering and Crist 2002, Gaston 2004), but also take into consideration temporal factors when studying biodiversity. In this way, current estimates of the number of arthropod species may increase, or even double as shown here, thus enabling us to gain a more accurate image of canopy diversity in forest trees.

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Appendix. Monthly abundance of the 78 spider species observed in European beeches in Germany over a one-year period of sampling on 216 trees.

Taxon	2005		2006									
	N	D	J	F	M	A	M	J	J	A	S	O
Amaurobiidae												
<i>Amaurobius fenestralis</i>	1
<i>Coelotes terrestris</i>	1	.	.
Anyphaenidae												
<i>Anyphaena accentuata</i>	191	159	55	11	2	70	47	25	89	211	307	311
Araneidae												
<i>Araneus diadematus</i>	1	1	1
<i>Araneus sturmi</i>	9	.	54	.	84
<i>Araneus triguttatus</i>	3	.	1	.	.	.
<i>Araniella cucurbitina</i>	1	.	.	.
<i>Araniella opisthographa</i>	2
<i>Cyclosa conica</i>	.	.	.	30	15	.	13	6	.	110	.	69
<i>Gibbaranea bituberculata</i>	1	.	4	.	4
<i>Gibbaranea gibbosa</i>	.	.	.	2	1
<i>Mangora acalypha</i>	1	.	207	.	42
<i>Zilla diodia</i>	1	1
Clubionidae												
<i>Clubiona caerulescens</i>	1
<i>Clubiona comta</i>	8	.	2	.	2
<i>Clubiona terrestris</i>	2	.	.
Dictynidae												
<i>Lathys humilis</i>	1
<i>Nigma flavescens</i>	16	7	1	.	.	.
Linyphiidae												
<i>Araeoncus humilis</i>	1	2
<i>Bathypantes gracilis</i>	1	1	.	.	.	1	.	.
<i>Cnephalocotes obscurus</i>	1
<i>Dicymbium nigrum</i>	1
<i>Diplocephalus picinus</i>	1
<i>Drapetisca socialis</i>	4	2	12	9	3
<i>Entelecara acuminata</i>	1	11	.	1	.	.
<i>Entelecara erythropus</i>	1	.	1
<i>Erigone atra</i>	1	3	.	.	.	19	1	.	5	.	1	1
<i>Erigone dentipalpis</i>	.	1	.	.	.	5
<i>Erigonella hiemalis</i>	3	.	1
<i>Labulla thoracica</i>	1	.
<i>Lepthyphantes flavipes</i>	1	.	.
<i>Lepthyphantes minutus</i>	1	.	.
<i>Linyphia hortensis</i>	2
<i>Linyphia triangularis</i>	9	.	.
<i>Maso sundevalli</i>	1	1
<i>Meioneta rurestris</i>	2	9	.	3	3	.	.	.
<i>Mermessus trilobatus</i>	12	1	2	.	1	.	2
<i>Moebelia penicillata</i>	2	2	.
<i>Neriene emphana</i>	2	1	.	.
<i>Neriene peltata</i>	.	.	.	9	16	.	48	27	2	180	.	80
<i>Obscuriphantes obscurus</i>	1
<i>Oedothorax apicatus</i>	4	.	.	.

Taxon	2005		2006									
	N	D	J	F	M	A	M	J	J	A	S	O
<i>Porrhomma microphthalmum</i>	9	1	4	1	.	.	1
<i>Porrhomma oblitum</i>	2
<i>Porrhomma pygmaeum</i>	1	.	.	.
<i>Saaristoa firma</i>	1
<i>Sintula corniger</i>	1
<i>Tenuiphantes tenebricola</i>	3
<i>Tenuiphantes tenuis</i>	2	.	.
<i>Thyreosthenius parasiticus</i>	3
<i>Troxochrus nasutus</i>	47	8	1
Lycosidae												
<i>Pardosa saltans</i>	2	.	1	.	.	.
Philodromidae												
<i>Philodromus albidus</i>	3
<i>Philodromus collinus</i>	1	.	.	.
Salticidae												
<i>Ballus chalybeius</i>	.	.	.	1	.	.	.	5	2	19	2	33
<i>Evarcha falcata</i>	1	.	.
<i>Heliophanus cupreus</i>	1	.	.
Sparassidae												
<i>Micrommata virescens</i>	1
Tetragnathidae												
<i>Metellina mengei</i>	4	2	3	55	9	242	21	208
<i>Metellina segmentata</i>	.	1	1	3	2
<i>Pachygnatha degeeri</i>	1	2
<i>Tetragnatha montana</i>	.	.	.	2	2
<i>Tetragnatha obtusa</i>	4	.	.	.
<i>Tetragnatha pinicola</i>	50	.	60
Theridiidae												
<i>Achaearanea lunata</i>	1
<i>Achaearanea simulans</i>	4	2	.	.
<i>Anelosimus vittatus</i>	2	.	1	.	.
<i>Enoplognatha ovata</i>	1	.	.	33	17	1	1	1
<i>Keijia tincta</i>	2	13	8	97	1	27
<i>Paidiscura pallens</i>	2	3	.	1	2	2	94	94	27	17	6	3
<i>Robertus arundineti</i>	1
<i>Theridion mystaceum</i>	1	1	.	17	.	27
<i>Theridion pinastri</i>	1	12	1	.
<i>Theridion varians</i>	6	1	.	.	.
Thomisidae												
<i>Diaea dorsata</i>	1	.	.	2	4	.	3	4	1	81	1	68
<i>Synaema globosum</i>	1
<i>Xysticus lanio</i>	1	.	2	.	.	.
Uloboridae												
<i>Hyptiotes paradoxus</i>	1	5	1	.	.	1	1	.	18	11	26	8

Chapter V

Neutral and niche theory jointly explain spider diversity within temperate forest canopies

Abstract

There has been debate for more than two decades regarding whether niche and neutral model play a major role in structuring communities and determining local and regional biodiversity (Whitfield 2002; Wootton 2005; Dornelas et al. 2006; Harpole and Tilman 2006; McGill et al. 2006). The classical niche-based theory asserts that differing life-history tradeoffs between species for competition, colonization and adaptations to environmental heterogeneity can stabilize coexistence (Vandermeer 1972; Tilman 1994; Chesson 2000; Tilman 2004; Kraft et al. 2008), whereas the neutral theory assumes that individuals are demographically identical regardless of the species and that stochastic processes are sufficient in maintaining species diversity (Hubbell 1997; Bell 2001; Hubbell 2001, 2005). However, we lack a process-based knowledge of how community dynamics operate in different spatio-temporal dimensions and whether only one ecological dynamic consistently governs biodiversity patterns at the local level. Here we show that both the neutral and the niche-based models operate side by side and are both needed to explain the dynamics of arboreal spider assemblages among different canopy strata. Although stochasticity (ecological drift) shapes the spider community in old-growth canopies (150+ years old), the assemblages in monoculturally mature (60 years old) and young forest stands (20 years old) are structured by deterministic processes (biotic interaction). Due to silviculture systems (Harris 1984; Puettmann and Coates 2009), which have brought major changes to natural forest ecosystems, old-growth tree crowns in even-aged plantation forests constitute isolated, rare and small islands containing discrete and non-equilibrium spider communities with greater diversity. The study of how this century-old forestry regime influences ecological processes and biodiversity patterns of the canopy fauna in temperate forests merits far more attention. To give broader significance to our findings, investigation of biodiversity mechanisms in highly isolated environments (e.g., soil communities in landscape mosaics within long-term intensively managed agricultural systems) would be necessary.

Forests, coral reefs and soil contain the majority of the world's known biodiversity (Connell 1978; Ozanne et al. 2003; Floren and Schmidl 2008), and as much as half of all the macroscopic life forms are assumed to dwell in forest canopies (Floren and Schmidl 2008). However, century-old management practices aiming to maintain a sustainable wood supply and extensive repeated clear-felling have fundamentally changed temperate forests in Europe (Schroter et al. 2005; Puettmann and Coates 2009). It is therefore necessary to understand how different forest treatments shape the diversity and population dynamics of canopy dwellers.

Neutral and niche theory, as structuring principles of communities, are still controversial and hotly debated what force is sufficient in maintaining species diversity. However, we lack a thorough understanding of how the organization of most communities changes with differing spatio-temporal dimensions. In our study, the European beech (*Fagus sylvatica*) was selected as a model tree species to investigate the dynamics of an arboreal community (spiders), because it is the most dominant and abundant deciduous tree in Europe. Among Metazoa, Arachnida is the most species-rich taxon second to Insecta. Spiders are of great ecological importance as major generalist arthropod predators, particularly in trees (Prinzing 2003; Floren and Schmidl 2008); thus, they play an important role in controlling herbivore pest in forestry. They are also suitable as bio-indicators to monitor habitat heterogeneities (Hsieh et al. 2003), including those caused by climate change (Kaufmann 2002). Moreover, spiders belong primarily to a single trophic level and therefore interspecies interactions should occur within community. In addition to herbivorous insects (Floren and Schmidl 2008) and decomposers (Ellwood et al. 2009), canopy-dwelling spiders provide an ideal model to study assembling forces within predatory arthropod communities.

We investigated the spider assemblages of 324 European beech crowns from three different age classes in southern Germany, the center of the European beech distribution. Because of their economic value, forest patches greater than 150 years old are rarely preserved in European forests. Regrettably, comprehensive data on arthropod communities in undisturbed natural forests are lacking and it is critical to examine how differing management policies influence the arboreal communities and determine whether old-growth trees are of special value in preserving maximum arthropod biodiversity. Using canopy fogging (see Methods), we selectively sampled arthropod communities to obtain reliable and quantitative data for all forest types studied. A total of 21,054 spiders were collected, representing 94 species from 19 families, during the 18-month sampling period, which included three warm seasons and one cold season. The winter fogging showed that the tree crowns supported very little arachnid life, such that the empty canopies must be repopulated by spiders

immigrating from the metacommunity. Low mean similarity (high annual species turnover) of spider communities between warm seasons in the old-growth tree crowns (0.22 ± 0.01) indicates that community composition is changing annually (Fig. 1). However, the spider communities in mature (0.57 ± 0.01) and young (0.56 ± 0.01) forest patches are more constant and predictable ($F_{2,14} = 567.7$, $P < 0.001$, Fisher's LSD: M, Y > O). Spatially, each patch is completely homogeneous across the metacommunity landscape in terms of tree species composition (monospecific stands) and age-class, which is an advantage when designing sampling methods. This avoids noise, as would otherwise be expected from studying mixed forests with different tree species harboring different spider communities (Floren and Schmidl 2008). When European beeches grow up, the lower strata suffer from shade stress by the thick leaf layer of the tree crowns, which leads to the loss of (leaved) branches on the lower part of the tree. As only a limited set of generalists use the stem's bark as an avenue into the crown (Prinzing 2003), the old-growth tree crowns sitting on long bare stems act as isolated islands in the forest canopy and harbor discrete spider communities. This results in lower degrees of similarity between old-growth and young patches (0.28) and between old-growth and mature patches (0.28), and greater similarity between mature and young beech patches (0.53) ($F_{2,31} = 1290$, $P < 0.001$, LSD: MY > OY, OM). These results reveal that local community compositions are strongly affected by dispersal and recruitment limitations from their metacommunity (Hubbell 1997).

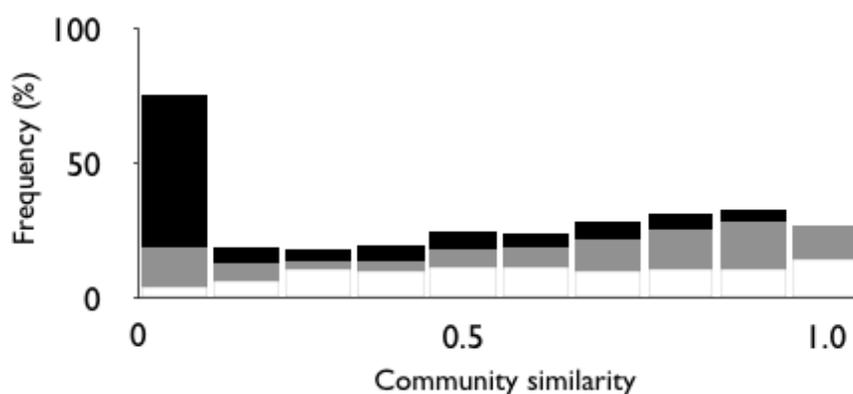


Figure 1 | Frequency distribution of Morisita-Horn abundance-based similarities among three warm seasons. Distributions of arboreal spider communities on old-growth (black), mature (gray) and young (white) forest patches, respectively. The heights of the bars sum up to 100% for each age class. Low mean similarity (high species turnover) among years in old-growth beech canopies reveals that the spider communities in old-growth canopies are unpredictable from year to year. Mature and young forest patches have similar patterns and high mean similarity.

The composition of arboreal spiders reflects different ecological processes in this deciduous forest (Fig. 2). When controlling for strata, we were able to reveal that the communities were unpredictable in the highest stratum (old-growth tree crowns). The two lower strata (mature and young forest patches) showed competitive structuring, consistent with the niche model. During seasonal changes in temperate zones, most broad-leaved woody plants shed all their leaves in late autumn and go through the entire wintertime leafless. However, some European beeches exhibit marcescence, retaining dry leaves through winter and shedding them the following spring (Berkley 1931) (Fig. 3). This trait is most commonly seen in young beeches, but some lower branches of mature trees also retain leaves up to a height of about 3 meters (3.38 ± 0.33 m, $n = 25$). During sampling, 90% of spiders ($n = 1199$, 12 families) caught during wintertime were collected with a beating tray from marcescent beech branches (paired $t = 13.59$, $P < 0.001$, $n = 200$ trees) (see Methods). Those marcescent branches provide refuge for perennially active spiders during the winter months (e.g., *Anyphaena accentuata*). Many of these spiders are good competitors (and thus common species), and become the dominant spiders in the newly composed communities during the warm months. This results in more predictable and deterministic communities with lower annual temporal species turnover in mature (0.57 ± 0.19) and young (0.55 ± 0.20) beech patches compared to old-growth tree crowns (0.79 ± 0.21) ($F_{2,16} = 21.308$, $P < 0.001$, LSD: O > M, Y) during the next warm season. Identical results were independently obtained during the three warm seasons, strongly indicating that deterministic mechanisms play an important role in structuring communities in the lower strata during the warm season. Contrastingly, stochasticity is more important in shaping arboreal spider assemblages in the highest old-growth tree crowns because communities are only accessed by the new community members and are not dominated by common species.

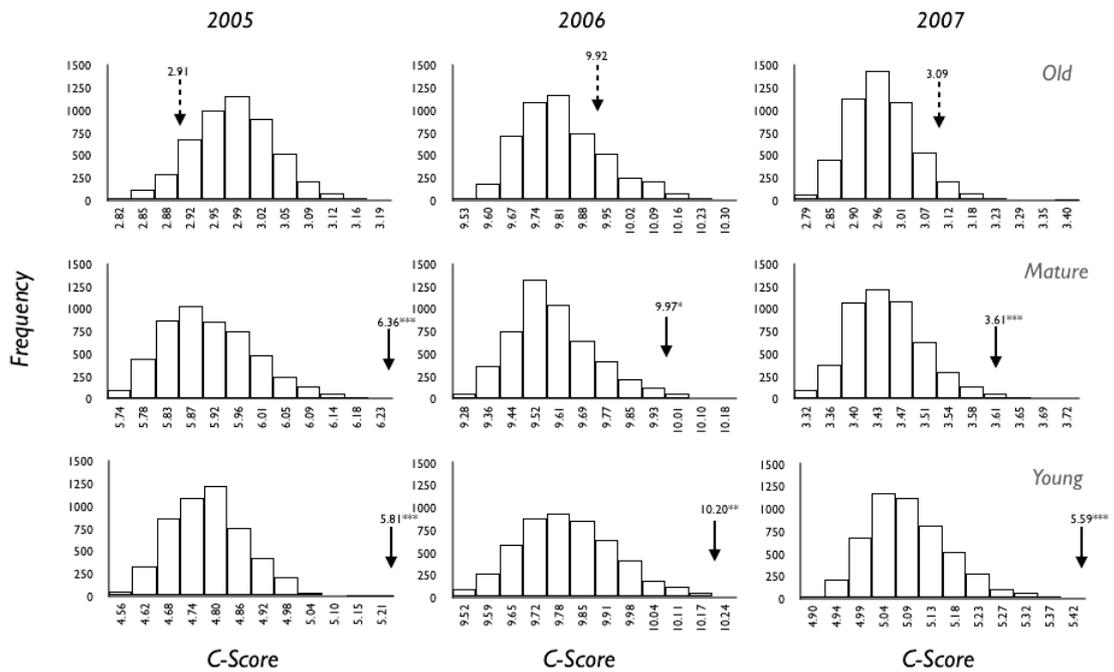


Figure 2 | Frequency distribution of C-scores from 5000 simulated random communities based on the co-occurrence of arboreal spider species in canopies. Observed C-scores shown as arrows; solid arrows: observed indices significantly greater than simulated indices (interspecific competition based on niche-assembly model) indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; * $P < 0.001$); dotted arrows: no statistical significance, indicating stochastically assembled communities.** Two different ecological processes govern the spider compositions at different strata. The communities from three warm seasons were used, and identical patterns show the robustness: stochasticity structures spider communities in old-growth beech canopies, whereas the assemblages in mature and young beech stands are structured deterministically.



Figure 3. Marcescent beeches retain dry leaves and provide refuge for winter-active spiders only at lower strata.

Since dispersal connects all local communities unequally within the metacommunity (Hubbell 2001), estimated parameters of fundamental biodiversity (θ) and migration probability (m) (see Methods) for old-growth, mature and young forest patches were averaged: $\theta = 6.7, 3.83$ and 3.83 and $m = 0.77, 1$ and 0.98 , respectively. This confirms that old-growth tree crowns have a strong dispersal and recruitment limitation. Thus, this living space is occupied by rare (competitively inferior) species because the best competitors for the mature and young patches are missing in isolated crowns of old-growth trees (Hubbell 2005). Therefore, the migration limitation from the lower strata and dispersal stochasticity in the uppermost stratum raise Hubbell's θ -diversity significantly. Figure 4 shows comparisons of spider species abundance and distribution between empirical and neutral communities simulated based on θ and m . Standard goodness-of-fit analysis shows that spider communities in old-growth beech canopies fit the neutral model (McGill 2003) (χ^2 Preston \log_2 bins = 63, $df = 56$, $P = 0.24$), which maintains high spider diversity in this isolated forest patch. The spider assemblages are deterministically structured in mature (χ^2 Preston \log_2 bins = 72, $df = 48$, $P < 0.01$) and in young forest patches (χ^2 Preston \log_2 bins = 96, $df = 64$, $P < 0.005$). Their higher probabilities of migration and recruitment are assumed to bring common species into contact with rare species, causing competition which in turn leads to local extinction of rare species, thus changing biodiversity patterns (Connell 1978; Wootton 2005).

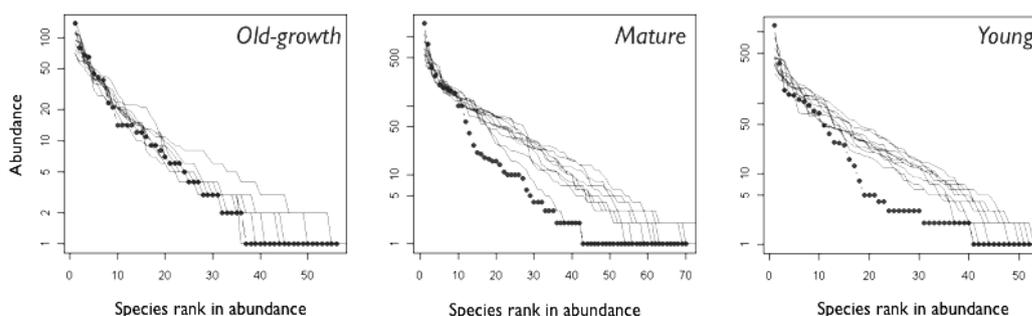


Figure 4. Relative abundance distributions of spider species in temperate European beech forest patches. Comparisons of spider species relative abundance distributions between empirical (black) and simulated neutral communities (gray) in three beech age classes indicated that spider communities in old-growth beech canopies fit the neutral model based on a zero-sum distribution. When reaching the tree crowns at high canopy levels, we discovered that a totally different mechanism shapes spider communities and diversity.

Based on intensive collections, no spatio-temporal rarity (singletons and doubletons) could be found, and thus sixty-one spider species were reliably estimated by the non-parametric Chao-1 estimator (Magurran et al. 2010) for this community from young beeches. When adding additional samplings from the high strata, estimated species richness more than doubled in the results (130). This is important for forest conservation, showing that the lower stratum alone does not deliver a reliable image of the forest canopies' biodiversity and therefore cannot be used for sampling protocols aimed at delivering an approximately full picture of a forest's biodiversity. Furthermore, the multinomial model (Shen et al. 2003) predicts that most of the additional species expected in further surveys are to be found in the highest stratum (2.6%) and considerably less so in the other two strata (M:0.6%; Y:0.5%). This also matches the estimated speciation probabilities proposed by the neutral theory (O:0.21, M:0.01, Y:0.01). Most rare species only exist and survive in a heterogeneous landscape (Hsieh et al. 2003), and they can functionally maintain the ecosystem (Lyons and Schwartz 2001); however, most of them are also vulnerable to environmental shifts, climate change (Magurran and Henderson 2003) and competitive pressure from common species. We therefore call on ecologists to pay closer attention to canopy communities in temperate forests because they harbor rich communities with far more rarity persisting with little-understood ecological dynamics in the canopy strata.

Most recent ideas and paradigms on forest ecology were historically developed in the temperate zone (Floren and Schmidl 2008) but most work on forest canopies has been performed in the tropics (Connell 1978; Ozanne et al. 2003; Floren and Schmidl 2008). After 30 years of canopy research in the tropics, we have now begun to discover the long-neglected faunal richness of temperate tree canopies (Floren and Schmidl 2008). Our results indicate that stochastic and deterministic processes determine the spider composition, but that their effects differ by strata. This is a result of the reduction in immigration rates of common and competitively superior species due to patch isolation and reshuffling of composition due to harsh winter conditions (with many species leaving, dying or getting caught by predators). To our knowledge, this is not only the first systematic study of temperate zone canopy communities investigating the mechanisms governing community assembly, but the first to show that communities might exist in very close proximity to one another and nevertheless be shaped by mechanisms that fit both neutral and niche theories.

Methods summary

European beech patches were selected according to three different age classes (old-growth, mature and young) within the 2,664-ha Würzburg University Forest. Using insecticidal knockdown fogging, we sampled arboreal spider communities from 324 beeches during 18 months spread over three years (see Methods). The tree crowns are covered with leaves during the warm season (May-October) and are without leaves during the cold season (November-April). To measure compositional similarity (species turnover) between communities, the Morisita-Horn index was used to reflect neutral variation in species abundance (Magurran et al. 2010).

Niche-based model

In the spatial (high and low strata), intra-annual temporal (warm and cold seasons) and inter-annual (three warm seasons) sets of beech canopy fogging, we tested for significant differences between the observed data and the statistical randomizations of the null model to examine whether species among the observed arboreal spider communities were distributed randomly. The null hypothesis is that the presence of a given spider species has no influence on the occurrence of any other species. The patterns of species co-occurrence among arboreal spider communities were compared for their possible fit to niche models with statistical randomization of the species occurrence data. These were suited for evaluation of the influence of interspecies interactions (see Methods). In a competitively structured deterministic community, the *C*-score should be significantly higher than expected by chance.

Neutral model

Whereas Fisher's log-series distribution is the expected steady-state distribution at the speciation-extinction equilibrium in an infinite community, Hubbell's unified neutral theory predicts that the relative distribution of species abundances of a finite community should follow zero-sum dynamics. It is parameterized by the function of the fundamental biodiversity number (θ), the migration probability (m) and the speciation probability (Hubbell 1997, 2001) (see Methods). Using these parameters, we simulated and visualized 10 neutral communities with ecological drift and examined whether the empirical data fit the neutral model.

Methods

Area

The natural experiment (Diamond 1983) was carried out in the Würzburg University Forest, Haßfurt-Sailershausen, southern Germany (50°01' N, 10°30' E). This University Forest, Germany's largest, is situated adjacent to the planned Steigerwald National Park in Lower Franconia (Northern Bavaria) (Müller and Goßner 2007). The annual precipitation averages 700 mm, mean annual temperature is 8°C and the region is covered by snow (minimally 0.1 mm) approximately 35 days per year (data based upon the Köslau weather station in Hassberge, 1990-2010). The altitude of this hilly forest varies from 225 m to 400 m. The area comprises 2,664 ha, of which 494 ha are classified as "High-Conservation Value Forest". This forest represents the prototype of temperate forests in central Europe from the Middle Ages until now (Haber et al. 2007), and it has maintained a traditional even-aged clear-felling forestry regime since the industrial revolution. Twenty-four percent of Lower Franconia is covered by European beech (*Fagus sylvatica*), which is the representative and naturally dominant deciduous tree species in Germany and in many parts of Europe (Schulze et al. 2010). Beech forests are an interesting subject of study, not only because this tree species is intensively managed, but also because it is related to the cultural and socio-economic history of Europe (Haber et al. 2007; Schulze et al. 2010) (nominated as a UNESCO world heritage site).

Canopy Fogging

We used refined pyrethrum diluted in diesel that was applied for ten minutes into each tree crown (Adis et al. 1998) using a fogging machine (SwingfogTM SN-50). In contrast to pyrethroids, which are used by most other working groups, our insecticide is highly specific for arthropods, non-toxic to vertebrates and completely biodegradable within a few hours. Effective and tree crown-selective fogging can only be carried out during good weather conditions at daybreak, when it is guaranteed to rise from the ground to all parts of the tree crown without being blown to neighboring trees. Fogging was never carried out after rain, snow, windy or misty conditions. To quantitatively collect the arthropods that were knocked down, 90% of the fogged trees' crown projection area (on average 46 m² for old-growth and mature trees, and 6 m² for young ones) on the ground was covered with plastic sheets fixed above the ground (to prevent ground-dwelling arthropods from crawling onto the sheet). All arthropods killed or anesthetized within the first two hours after fogging were

collected and transferred directly to storage bottles containing 70% ethanol. Using a drop time of two hours was a compromise to maximize the number of arthropods sampled while reducing the number of specimens escaping due to recovery from the toxic effects of the insecticide. To analyze the dynamics of arthropod communities temporally, a total of 324 trees were randomly chosen in three pure beech stands. During each fogging campaign, six never-before fogged trees from old-growth, mature and young forest patches were fogged eighteen times in 18 months from 2005 to 2007. Thus, the annual space and timeframe of sampling avoided the bias generated from significant spatio-temporal heterogeneity.

Beating in winter

From December 2006 to March 2007 we used beating trays to collect spiders monthly from branches with and without marcescent leaves to compare spider assemblages. Beating is a relatively simple and fast technique for sampling arthropods. The beating tray had a large opening ($60 \times 40 \text{ cm}^2$) and a long tray (62 cm) with very steep sides, made of smooth balloon silk (Mody and Linsenmair 2004). A 500-ml polyethylene collection bottle is screwed underneath the tray (Adis et al. 1998). The bottle can be easily replaced to process the next sample. Sampling involved pressing a branch into the tray and shaking them until all the arthropods had fallen into the bottle, with little risk of losing any specimens. We sampled arthropods from 25 branches with marcescent leaves and 25 branches without leaves every month. One branch at a 2-meter height was sampled from each beech tree. We also measured the height of the position where beech trees maintained marcescent leaves.

Interspecific competition

The Null model analysis is suited for evaluating whether co-occurring species overlap significantly in their use of resources and have a competitive relationship (Gotelli and Graves 1996). We used the computer program EcoSim 700 (Gotelli and Entsminger 2008) to generate 5000 Monte Carlo randomizations for each analysis and compared these data statistically within the observed communities. This allowed us to test observed distribution data implying competitive and deterministic processes against the hypothesis of a random distribution. The randomization algorithm maintains fixed sums based on the original matrix (Stone and Roberts 1990) for the rows and columns. The *C*-score co-occurrence index, which is correlated with species co-occurrence and counts the average number of checkerboard units by taking all possible pairs of species into consideration, was calculated for species that occur at

least once in the co-occurrence matrix (Connor and Simberloff 1979; Gotelli 2000). Not only does this algorithm have good Type I properties (low chance of falsely rejecting the null hypothesis), but also it has proven powerful for detecting non-random patterns. As we expect 5% of these combinations to be significant by chance, we tested the observed number of significant deviations against this expectation with a one-tailed binomial test.

Unified neutral theory of biodiversity and biogeography

We used Etienne's sampling formula for neutral biodiversity (Etienne and Olff 2004; Etienne 2005), implemented in the R package, UNTB (Hankin 2007), to estimate (backward maximum likelihood) the probabilities of immigration from the metacommunity (m), the fundamental diversity number (θ) and speciation probabilities.

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Chapter VI

Biodiversity prediction by applying Verhulst Grey Model (GM 1,1)

Abstract

In this paper the Verhulst Grey Model is applied to predict spider diversity dynamics in the Würzburg University Forest, Germany. Here, we use a moving forecasting to predict the following biodiversity values: Margalef Species Richness, Fisher Alpha Index, Simpson Index and Evenness. Among these, the Fisher Alpha Index revealed a decreasing trend in the temporal dynamic across years. Our application of the model for prediction can help lower the cost of studying biodiversity patterns and provide a crucial baseline reference for improving forest management policy.

Keywords

Biodiversity; canopy fogging; European beech; forest management; spider; Verhulst Grey Model

Introduction

Würzburg University Forest represents the type of a near-primary mixed temperate forest in Central Europe, dominated by European beech (*Fagus sylvatica* L.), a deciduous tree species of high economic value. Recently, the European system of environmental forestry monitoring showed that beech crown defoliation in Germany abruptly increased from 13% to 55% in the past 20 years; and that German forest enterprises had a low profitability due to low prices from resulting bad-quality timbers (Moog and Borchert 2001). The reasons for these trends are likely not only directly due to global warming (Gessler et al. 2007), but also indirectly due to rising infestation by herbivorous insects (Schott and Summerer 1983). Hence, a better understanding of the role of the forest canopy for sustaining the diversity and community compositions of arboreal arthropods is urgently needed — this can serve as an important reference to help make forest management more ecologically sustainable.

Yet little basic research has been done towards understanding the key processes responsible for the spatially complex patterns and the temporal dynamics that characterize forest canopy. In this study we used spiders as indicators to investigate the effect of different developmental stages of beech canopies on arboreal arthropod diversity. Spiders are, for several reasons, very valuable surrogates for assessing the overall arthropod diversity and for studying general spatial and temporal biodiversity patterns (Cardoso et al. 2004). Arachnida is the second most species-rich taxon after Insecta, and they are also the most important arthropod predators, catching incredible quantities of insects as prey (Nyffeler 2000). Therefore, the use of spiders is not limited to biological control against pests in woodlands (Pekar and Kocourek 2004), because they can also function as precise bio-indicators in terrestrial ecosystems for monitoring habitat changes (Hsieh et al. 2003).

Method

Sample Method and Biodiversity Indices

To sample the specimens and analyze the temporal dynamics of the spider communities, six beech trees from each of the three developmental stages (old-growth, mature and young patches) were randomly chosen in pure beech stands and fogged with pure natural pyrethrum as insecticide in June, August and October from 2005 to 2007. The well-known biodiversity indices were used: Margalef Species Richness, Fisher Alpha Index, Simpson Index and Evenness.

Prediction Model: A New Grey Relational Analysis Function of HM (Harmonic Mean) Type

Although prediction is important for conservation and environmental management, few studies have focused on the temporal dynamics of biodiversity. In this study, we used the Verhulst Grey Model prediction to forecast spider diversity dynamics in the Würzburg University Forest (Wen and Chang 2005). Among different prediction methods such as time series, regression analysis and neural networks, either a lot of samples is needed or the results are rather difficult to interpret and explain. By contrast, Grey prediction requires little data but can still offer good accuracy. In comparison to the White system with its fully-known parameters, characteristics, and structures, and the Black system with its entirely unknown information, the Grey System contains a mix of both known and unknown properties (Deng 1982). It has been applied in agriculture, economics, meteorology, hydrology, and business management but rarely ever in the fields of biodiversity and conservation.

The Grey System has several parts: (1) system analysis, (2) data processing, development of a system model, (3) grey prediction, (4) grey decision making, and lastly, (5) grey control. The idea of the Grey System is to measure the stability of data change within a time series, to describe the accumulation trend of values and how this influences the system. Grey prediction works by using generating operation to recognize the mathematical connections linking the factors within the system, and then reveal the mathematical characteristics of these factors. In this vein, a Verhulst Grey Model was built up from a set of equations, which may be written as follows:

$$\frac{dx^{(1)}}{dx} + ax^{(1)} = b(x^{(1)})^2 \quad (1)$$

1. The solution of differential equation model is of first-order and has just one variable:

$$x^{(0)}(k) = -az^{(1)}(k) + b(x^{(1)}(k))^2 \quad (2)$$

Parameter a and b by $\hat{a} = (B^T B)^{-1} B^T Y$, where $Y = B\hat{a}$

$$B = \begin{bmatrix} -Z^{(1)}(2) & 1 \\ -Z^{(1)}(3) & 1 \\ \dots & \dots \\ -Z^{(1)}(n) & 1 \end{bmatrix} \quad Y = \begin{bmatrix} x^{(0)}(2) \\ x^{(0)}(3) \\ \dots \\ x^{(0)}(n) \end{bmatrix} \quad \hat{a} = \begin{bmatrix} a \\ b \end{bmatrix}$$

2. Verhulst Grey Model:

$$\hat{x}^{(1)}(k) = \frac{\frac{a}{b}}{1 + \left(\frac{a}{b} \times \frac{1}{x^{(0)}(1)} - 1 \right) e^{a(k-1)}}; k \geq 2 \quad (3)$$

By the definition of Accumulated Generating Operation (AGO):

$$\hat{x}^{(0)}(k) = \frac{(1-e^{-a}) \times \frac{a}{b} \times \left[1 + \left(\frac{a}{b} \times \frac{1}{x^{(0)}(1)} - 1 \right) e^{a(k-1)} \right]}{\left[1 + \left(\frac{a}{b} \times \frac{1}{x^{(0)}(1)} - 1 \right) e^{a(k-1)} \right] \left[1 + \left(\frac{a}{b} \times \frac{1}{x^{(0)}(1)} - 1 \right) e^{a(k-2)} \right]} \quad k \geq 2 \quad (4)$$

3. Accuracy rate definition of GM (1, 1):

$$e(k) = \left| \frac{x^{(0)}(k) - \hat{x}^{(0)}(k)}{x^{(0)}(k)} \right| \times 100\% \quad (5)$$

where $x^{(0)}(k)$ is the true value and $\hat{x}^{(0)}(k)$ is the predictive value. We built the Verhulst Grey Model with the diversity values (i.e. Margelef Species Richness, Fisher Alpha Index, Simpson Index and Evenness values) from June, August and October in 2005 and 2006, and the predicted values in 2007 using a moving forecasting. Then we compared the predicted values with the empirical values collected in 2007 to examine whether the prediction rate was acceptable. After determining whether the results were accurate, we predicted the diversity values for the following two years using a moving forecasting. We put this newly predicted value into the raw data series and deleted the oldest value, then rebuilt the Verhulst Grey Model with new information in order to forecast the next value. Using the empirical values from 2005 to 2007 and the predicted values from 2008 and 2009, we plotted the regression lines of different biodiversity values and examined their dynamical patterns through the years. With these results, the current forestry policy could be checked to see whether or not it affected the spider diversity in the Würzburg University Forest.

Results

Prediction of Spider Diversity Dynamics

A total of 15,181 individuals were collected from 162 beech trees in June, August and October from 2005 to 2007, with the identified specimens ($n = 6,309$) belonging to 80 species from 16 families. We took Margalef Species Richness from June, August and October 2005 and 2006 as an original data series: $x^{(0)} = (1.3, 1.37, 2.29, 2.34, 2.6, 2.27)$ and then generated the AGO series: $x^{(1)} = (1.3, 2.67, 4.96, 7.3, 9.9, 12.17)$. Using the Verhulst Grey Model with moving forecasting we got the predicted values for June, August and October 2007 (1.71, 2.05, 2.19) (Fig. 1). According to the definition of GM (1, 1), the accuracy rate of Margalef Species Richness in 2007 was 87.5 %. Because the indices of Fisher Alpha (78.3 %), Simpson (99.6 %) and Evenness (92.7 %) also had good accuracy rates we applied the Verhulst Grey Model to forecast the diversity indices in 2008 and 2009. All regression lines of biodiversity indices showed no significant changes in the following two years in the forecasted community properties: Margalef Species Richness ($y = -0.02x + 2.12$, $r^2 = 0.06$, $p = 0.36$), Fisher Alpha Index ($y = -0.07x + 4.56$, $r^2 = 0.07$, $p = 0.3$), Simpson Index ($y = 20.82x - 6.38$, $r^2 = 0.26$, $p = 0.05$) and Evenness ($y = 0.001x + 0.77$, $r^2 = 0.01$, $p = 0.71$) (Fig. 1). However, when the values of the Fisher Alpha Index were analyzed separately for each developmental stage, the spider diversity in the mature forest patch was decreasing (Fig. 2): old-growth ($y = -0.01x + 4.16$, $r^2 = 0.002$, $p = 0.85$); mature ($y = -0.18x + 5.39$, $r^2 = 0.291$, $p = 0.03$) and young beech patch ($y = 0.05x + 3.37$, $r^2 = 0.030$, $p = 0.54$).

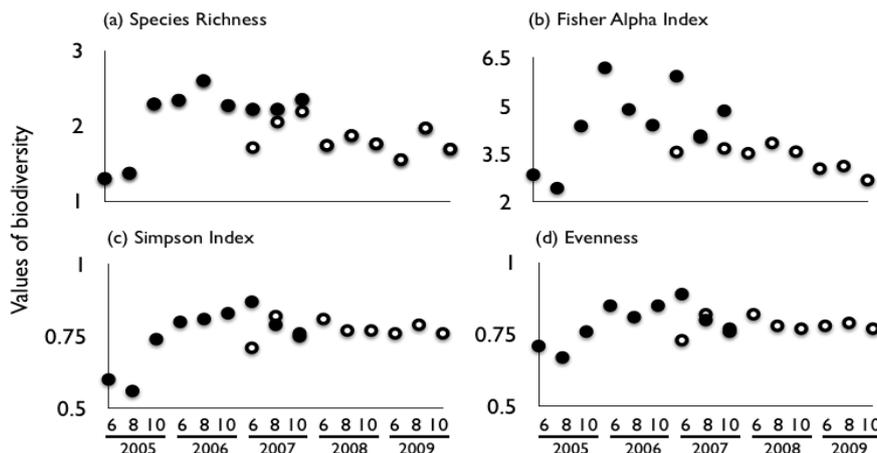


Fig. 1. Forecasting of Grey System for diversity indices in 2008 and 2009 using data collected from 2005 to 2007 (Observed values: black, forecasting values: white).

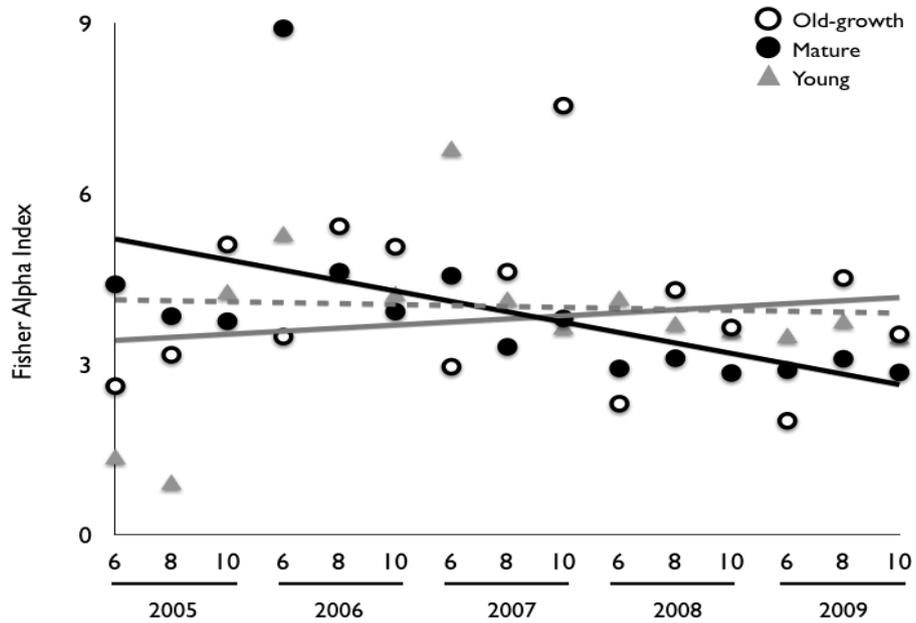


Fig. 2. Changes of Fisher Alpha diversity of arboreal spiders in each beech patch from 2005 to 2009. (2005-2007: observed values; 2008-2009: forecasting values). Lineal regression lines are generated from three beech patches respectively (Old: dotted; mature: black; young: grey).

Conclusions

Arboreal spiders were collected by insecticidal fogging from three developmental stages of European beeches in three consecutive summers. Analyses of biodiversity among various years, demonstrated significant differences between the years. This revealed that diversity changes dynamically from year to year; therefore both long-term monitoring and prediction are needed. In our study, we made predictions based on several diversity indices each for different years and the Grey System helped us elucidate a relationship between changes of several diversity indices in consecutive years, and was able to successfully forecast the values in the next two years.

The Accumulated Generating Operation agreed with the Verhulst Grey Model produced a high level of accuracy in forecasting. In our study, some significant information appeared only when the spider diversity under analysis was considered in light of tree ontogeny. We found that the model failed to show some crucial details when the developmental stages of trees were ignored: namely, decreasing alpha diversity in the mature beech forest patch according to the Fisher Alpha Index.

One possible explanation for this is that in the summer the foresters carried out the preparation for selective logging of some dominant beeches in the mature tree patch. In some cases, these dominant beeches in the mature forest patch suppress neighboring trees. Present forest management policy cuts these dominant beeches selectively in order to release the suppressed beeches to grow straight up and ensure better-quality timber. However, if this policy continues, the prediction model presented here shows that the spider diversity may decrease in the mature forest patch. We therefore suggest that mature beeches not be logged during summer to prevent biodiversity loss of spiders, which are especially important regulators of herbivorous insects in the forests (Nyffeler and Benz 1987). They should be logged later, in winter months instead to minimize possible impacts on the spider diversity. Our results show that a true picture of canopy-dwelling arthropods in forests can only be gained when assessing their temporal dynamics between different years. To the best of our knowledge, this work is the first to assess the different biodiversity dynamics of spider communities in the canopy of European beeches via a predictive Grey Model, and to show that the diversity in canopies is not uniform: it can have different dynamic patterns depending on tree stature.

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Chapter VII

Summary and outlook

A major goal of the main topics of ecology is to answer the question of how species can co-exist and maintain biodiversity. To understand how community dynamics operate in different spatio-temporal dimensions to govern biodiversity patterns requires a process-based knowledge. Thus, this study focused primarily on biodiversity patterns and ecological processes at both spatial and temporal scales. Spatially, the diversity and similarity of spider communities in high, intermediate, and low strata of beech trees represented a set of age-related effects: Old-growth trees provided unique and distinct resources to spiders and in turn possessed discrete spider compositions. Intra-annually, spider communities in different seasons showed a repeated, predictable temporal dynamics. Inter-annually, comparison revealed that neutral and niche models can operate *in tandem*, and that both are needed to fully explain the dynamics of arboreal spider assemblages among different canopy strata in this beech forest.

Spatial Distribution

To date, many studies have shown that the composition of arboreal arthropod assemblages is influenced by not only the tree species identity, but also by the respective tree species' phenology, morphology and chemistry. However, studies explicitly taking tree ages as a further decisive factor into consideration are noticeably scarce. The spatial comparison of spider communities clearly demonstrated that communities of predators occurring in the canopies of three silvicultural forest patches of different age (old-growth patch: >150 years old; mature: 50–60 years old and young: 20–25 years old) may exist in very close neighborhood, but are nevertheless shaped by tree age-specific properties. Spatially, each patch is completely homogeneous across the metacommunity landscape in terms of its tree species composition (monospecific patches) and age-class, which is a powerful advantage when designing sampling methods.

Although mature and young beeches (i.e., the two lower strata) were not distinguishable in diversity, dominance, species, family and guild composition of spider communities, both of these differed from those of old-growth beech trees (i.e., the upper stratum). The results challenge the classic view that conspecific trees provide similar habitats and are inhabited by similar arthropod assemblages in an ecosystem. Therefore, the biodiversity of forest canopies needs to be accurately

revisited by explicitly considering tree age (or size-related ontogenic changes). These results also imply that old-growth forests, which are rarely preserved in Central Europe, are of special conservation value for predators, and should be a part of near natural forests to maintain a full suite of ecosystem functions.

Since the majority of beech forests consist of mature and young trees in Central Europe, I recommend that young beeches be used in a sampling protocol for rapid biodiversity assessments. In particular, because young beeches are only 5-6 meters tall they can be inventoried easily and cost-effectively. However, adding samples from the two higher strata to the lowest stratum (55 species), almost doubled the estimated species richness (102 species). This important source of new predators has been underestimated in the temperate forest because of the difficulties to access the uppermost canopies. Without canopy fogging, it would have been impossible to get reliable and quantitative data: this suggests that the lower stratum alone cannot deliver a true image of the total canopy fauna inventory in this, and likely other, beech stands. To complete this comprehensive inventory of European beech trees, the Chao1 estimator predicted that additional sampling would be needed in the highest stratum, where there is a high probability to find previously undetected species in a next survey. My study clearly shows that neglecting the crowns of the largest, tallest trees risks underestimating the overall spider diversity in Central European forests.

Intra-annual distribution

My dissertation demonstrated not only that tree age should be considered as a very important factor affecting the spatial distribution of different spiders, but also that the intra-annual variability generated predictable, temporal distribution patterns. I analyzed the seasonal diversity dynamics of arboreal spider communities dwelling in 216 European beeches (*Fagus sylvatica*) to assess the spider community composition in the following seasons: two cold seasons (I [November 2005-January 2006]; II [February-April]) and two warm seasons (III [May-July]; IV [August-October]). I found that the usually measured diversity of the warm season community (IV) alone did not deliver a reliable image of the overall diversity present in these trees. For this reason, it should not be used for sampling protocols aimed at providing a full picture of a forest's biodiversity in the temperate zones. In particular, when the additional samplings of other seasons (I, II, III) were included, the estimated species richness nearly doubled. Not surprisingly, community I possessed the lowest diversity and evenness due to the harsh winter conditions: this community was comprised of one dominant species together with several species low in abundance. Similarity was lowest (38.6%) between seasonal communities I and III, indicating a significant

species turnover due to re-colonization, so that community III had the highest diversity. Finally, using nonparametric estimators, I found that further sampling in colder months (November to April) is needed to complete our inventory. My study clearly demonstrated that the seasonal dynamics of communities should be taken into account when studying biodiversity patterns of spiders, and probably applies to forest arthropods in general.

The Chao1 estimator showed different estimates of species richness (25–88 species) among seasons, indicating that bias can be generated when only sampling in one single season in a given year, because phenology causes many species to be rare at most time periods. Since Chao1 only uses the numbers of rare species to estimate the number of missing species, my study, which takes seasonal variability into account, and thus brings the number of rare species to half its seasonal value (seasonal: 60 rare species; overall: only 30), better avoids the overestimation and represents the true diversity of arboreal spiders in the European beech forest.

Inter-annual distribution

The highly inter-annual variability (low mean similarity) of spider communities between three warm seasons in the highest canopy stratum (old-growth beech patches) indicates that community composition is changing remarkably between years and is not predictable (at least over a 3-yr period). Instead, the sampling revealed that each tree hosted an individual arthropod community which differed from that of other conspecific trees. Since the spider community had only been sampled once, the significant differences in community structure of other individual trees could have been considered to be the result of a stochastic process. In contrast, the mature and young beech trees hosted inter-annually stable spider communities, inferred from a highly constant and predictable re-establishment and assembly. This stable structure of communities corresponding to very similar sets of particular spider species could not be explained by random assembly — rather spiders were likely attracted by some stable, specific characteristics of the beech trees and their microenvironments. Such species as foliage runners (e.g. Anyphaenidae) showed a stronger habitat specificity linked to the lower strata, and this means that certain beech characteristics were more relevant for their life history. Thus, deterministic rather than random processes lead to the formation of arthropod communities in the two lower strata. Taken together, these results emphasize the existence of habitat heterogeneities in beech tree canopies and provide evidence that spider communities are shaped by both stochastic (ecological drift) and deterministic (interspecific competition) processes operating side by side among different canopy strata. Due to the current silviculture system, which has

brought major changes to the natural forest ecosystem, old-growth tree crowns in even-aged forest patches constitute isolated, rare and small islands containing discrete and non-equilibrium spider communities with remarkably greater diversity, while the two lower strata (formed by mature and young beech trees) possess lower diversity.

The two lower strata were similarly influenced by interspecific competition for the same resources, which led to a high degree of species aggregation. However, the characteristic communities in mature and young beech trees could not be explained by species interaction alone. Aggregation on certain strata means that they are more attractive for the aggregating species than other strata. This aggregated distribution led to the predictable and stable spider composition. Therefore, understanding the factors determining those habitat characteristics that determine aggregated species distribution can be very helpful in explaining the predictable composition of the studied communities. In addition to species interactions, beech characteristics (e.g. marcescence) were considered as potential deterministic factors responsible for persistent spider community composition.

Future research and direction

Although most canopy studies focus on tropical regions, the novel investigation of spider communities in a temperate forest presented here shows that vast numbers of spiders can dwell in tree crowns of European beeches, and that more than 45% of spider species are only restricted to one single canopy stratum. There is still much work to be done using the canopy as an experimental unit to gain novel information of biodiversity and ecology in temperate forests. Canopies provide an excellent opportunity to investigate the effects of competition and exclusion on the development of communities, and can help advance our knowledge of a wide range of biodiversity and ecological processes. Two further types of investigation are required to establish the broader significance of these findings. First, the question must be asked whether or not the variation of arboreal spider diversity at different successional stages is a widespread phenomenon: by testing in other forests dominated by beech as well as other tree species. Do species richness and community structure of spiders in other tree species, in both temperate and tropical regions, vary significantly between different successional stages? I propose that the most effective and efficient way to answer these questions is to develop a standard sampling protocol for temperate forest and fog the canopies of other tree species. This standardized approach, if successful, could then be applied in tropical rainforest where possible. Since the Würzburg University Forest is qualified as a high conservation value forest, and the European beech is also a representative species in Europe, I hope this study can serve as a

model for the use of spider diversity to monitor the effects of forest patch management.

Secondly, do other forestry policies also affect arboreal spider diversity? Which successional stage of beech timber can be logged in which season, and how might this affect the diversity of arthropods? These questions can only be addressed with continued, long-term sampling, and by conducting experiments within the canopy itself using some form of canopy access (via lift, crane or scaffolding). Certainly there are concentrations of spiders which have been overlooked in current studies and need to be taken into account in regard to different tree ages as well as different tree species, climate zones and areas of human impact. As further field studies of invertebrates are carried out at different successional stages, estimates of biodiversity will likely increase, and the relative importance of tree age may need to be revised. Towards this end, the present work is the first study comparing spider diversity and community composition in European beech canopies at different spatiotemporal scales. It clearly shows that spatio-temporal dynamics can shape the spider diversity found in forest canopies.

Chapter VIII

Zusammenfassung und Ausblick

Ein wesentliches Ziel ökologischer Forschung ist es, die Frage zu beantworten, wie Arten koexistieren können und die biologische Vielfalt erhalten bleibt. Um zu verstehen, wie dabei Gemeinschaften in unterschiedlichen räumlich-zeitlichen Dimensionen interagieren, um die biologische Vielfalt zu erhalten, ist ein umfassendes prozessorientiertes Wissen erforderlich. Demzufolge konzentrierte sich meine Studie im Wesentlichen auf die Biodiversität und die sie beeinflussenden raum-zeitlichen ökologischen Prozesse. Vergleicht man die Ähnlich- bzw. Unähnlichkeit der in verschiedenen alten Beständen lebenden Spinnengemeinschaften der Buchen (*Fagus sylvatica* L.), dann zeigt sich, dass die älteste Baumkohorte offensichtlich einzigartige Ressourcen besitzt, welche die Zusammensetzung der Spinnengemeinschaften deutlich prägen. Über das Jahr hin zeigten die Spinnengemeinschaften trotz der jahreszeitlich unterschiedlich ökologischen Randbedingungen eine sich wiederholende, vorhersehbare Dynamik. Der Vergleich über die Jahre ergab, dass das "Neutrale Modell" und das "Nischen-Modell" gleichzeitig funktionieren können. Beide sind notwendig, um die Dynamik der in den Buchenkronen der verschiedenen Altersklassen lebenden Spinnengemeinschaften vollständig erklären zu können.

Räumliche Verteilung

Bis heute haben viele Studien gezeigt, dass die Zusammensetzung der Arthropodengemeinschaften in den Bäumen nicht nur durch die Baumart selbst beeinflusst wird, sondern auch von deren Phänologie, Morphologie und Chemie abhängt. Allerdings berücksichtigten die Studien nur selten das Baumalter als einen weiteren entscheidenden Faktor. Der Vergleich der in unterschiedlich alten Buchenbeständen (alte Bäume: >150 Jahre alt; mittel: 50-60 Jahre alt; jung: 20-25 Jahre alt) lebenden Spinnengemeinschaften hat gezeigt, dass diese auch bei sehr enger Nachbarschaft von Baumalter-spezifischen Eigenschaften geprägt sind. Räumlich ist jedes der beprobten Waldstücke in sich völlig homogen, sowohl im Hinblick auf die Zusammensetzung der Baumarten (es handelt sich um Monokulturen) als auch auf das Alter, was einen großen Vorteil bei der Probenahme darstellte. Mittlere und junge Buchen (d.h. die beiden jüngeren „Ebenen“) waren nicht unterscheidbar in der Vielfalt, Dominanzstruktur, Arten-, Familien- und Gilden-Zusammensetzung ihrer der Spinnengemeinschaften, aber sie unterschieden sich gegenüber den alten Buchen

unterschiedlich (d.h. gegenüber der ältesten „Ebene“). Die Ergebnisse meiner Forschung widersprechen der klassischen Ansicht, dass in einem Ökosystem gleiche Baumarten ähnliche Lebensräume bieten und damit dann auch ähnliche Arthropodengemeinschaften beherbergen sollten. Daher musste die biologische Vielfalt der Baumkronen unter expliziter Berücksichtigung des Baumalters (und größenbedingter ontogenetischer Veränderungen) überprüft werden. Die Ergebnisse implizieren, dass alte Wälder, die nur selten in Mitteleuropa erhalten sind, die aber einen besonderen Schutzraum für Räuber bieten können, stets einen Teil der naturnahen Wälder bilden sollten, um die Gesamtheit der Ökosystemfunktionen aufrecht erhalten zu können.

Da die Mehrzahl der Buchenwälder in Mitteleuropa nur aus mittelalten und jungen Bäumen besteht, empfehle ich, dass die jungen Buchen in einem Probenahmeprotokoll für die schnelle Bewertung der biologischen Vielfalt aufgenommen werden sollen. Insbesondere, weil die jungen Buchen nur 5-6 Meter hoch sind, können sie leicht und kostengünstig in ihrem Arthropodenbestand erfasst werden. Das Hinzufügen der Proben aus den beiden fortgeschritteneren Altersstufen zur jüngsten (mit in meinen Untersuchungen nachgewiesenen 55 Arten) verdoppelt nahezu die geschätzte Artenzahl und hebt sie auf 102 Arten an. Dieser wichtige, spinnenreiche Lebensraum in den Wäldern der gemäßigten Zonen war aufgrund der praktischen Schwierigkeiten, die obersten Baumkronenschichten erreichen und wenigstens einigermaßen quantitativ besammeln zu können, bisher unterschätzt worden. Ohne Baumkronenbenebelung wäre es unmöglich gewesen, an zuverlässige und weitgehend quantitative Daten zu kommen. Die jüngste Altersstufe allein kann kein auch nur annähernd vollständiges Abbild der Fauna der gesamten Kronenüberdachung in diesem Buchenwald liefern. In Ergänzung einer umfassenden Bestandsaufnahme der europäischen Buchen hat der "Chao1-Schätzer" vorhergesagt, dass bei zusätzlichen Probenahmen auf der höchsten Ebene mit hoher Wahrscheinlichkeit bisher unbekannte Arten bei einer neuen Untersuchung gefunden werden würden. Meine Studie zeigt deutlich, dass die Vernachlässigung der Kronen der größten und höchsten Bäume das Risiko birgt, die gesamte Vielfalt der Spinnen in mitteleuropäischen Wäldern erheblich zu unterschätzen und damit dann wichtige Schutzmaßnahmen zu deren Erhaltung nicht so früh wie möglich einzuleiten.

Intra-annuelle Verteilung

Meine Befunde zeigen, dass nicht nur das Baumalter als ein sehr wichtiger Faktor für die räumliche Verteilung verschiedener Spinnengilden in Betracht gezogen werden muss, sondern auch, dass die intra-annuelle Klimavariabilität vorhersehbare

zeitliche Verteilungsmuster generiert. Ich analysierte die saisonale Dynamik der Diversität und Zusammensetzung der Spinnengemeinschaften an 216 Rotbuchen in zwei kalten Jahreszeiten (I: November 2005-Januar 2006; II: Februar-April 2006) und zwei warmen Jahreszeiten (III: Mai-Juli 2006; IV: August-Oktober 2006). Ich fand, dass die bei vergleichbaren Studien in der Regel in der warmen Jahreszeit (IV) gemessene Vielfalt allein kein zuverlässiges Bild der gesamten Vielfalt der Spinnenzönosen in diesen Bäumen liefern konnte. Aus diesem Grund sollten diese Ergebnisse nicht als Vorbild für Probennahmeprotokolle dienen, da diese kein vollständiges Bild der Artenvielfalt in einem Wald der gemäßigten Zonen liefern. Insbesondere, wenn zusätzliche Proben aus anderen Jahreszeiten (I, II, III) enthalten waren, verdoppelte sich die geschätzte Artenanzahl fast. Nicht überraschend war, dass die winterliche Spinnengemeinschaft I die niedrigste Vielfalt und geringste Evenness zeigt: Diese Gemeinschaft bestand aus einer einzigen dominanten und mehreren Arten mit geringerer Abundanz. Die geringste Ähnlichkeit (38,6%) wiesen die saisonalen Gemeinschaften I und III untereinander auf, was den signifikanten Artenturnover durch Re-Kolonialisierung widerspiegelt, so dass Community III die höchste Diversität aufwies. Außerdem zeigten nichtparametrische Schätzer, dass eine weitere Probenahme in kälteren Monaten (November bis April) erforderlich gewesen wäre, um diese Erfassung zu vervollständigen. Meine Studie beweist klar, dass die saisonale Dynamik der Gemeinschaften berücksichtigt werden muss, wenn man die biologische Vielfalt von Spinnen erforscht.

Der Chao1-Schätzer verwendet nur die Anzahl der seltenen Arten, die während der Datenaufnahme gesammelt wurden, um auf die fehlenden Arten zu schließen. Dies führt zu einer Überschätzung der Anzahl seltener Arten, die ich in meiner Studie vermeiden kann, da ich die tatsächliche Diversität von Baumspinnen in europäischen Buchenwäldern zu verschiedenen Jahreszeiten (eines ganzen Jahres) aufgenommen habe. Aufgrund der Berücksichtigung jahreszeitlicher Schwankungen verringert sich nun die geschätzte Anzahl seltener Arten. Der Chao1 Schätzer lieferte sehr unterschiedliche Werte der zu erwartenden Artenzahlen für die verschiedenen Jahreszeiten (25 bis 88 Arten). Dies kann zu fehlerhaften Aussagen führen, wenn man nur in einer einzigen Jahreszeit und in einem bestimmten Jahr sammelt, da viele Arten in den meisten Zeiträumen aufgrund ihrer Phänologie selten sind. Bezogen auf meine Studie könnte man die vermeintlich seltenen Arten (eins bis zwei Individuen) in einer Jahreszeit über das ganze Jahr aufsummieren und käme auf 60 Arten im ganzen Jahr, während es tatsächlich nur 30 seltene Arten sind. Arten, die in einer bestimmten Jahreszeit als selten definiert waren, sind auf ein ganzes Jahr betrachtet nicht mehr als selten einzustufen und reduzieren deshalb die Artenanzahl seltener Spezies um die Hälfte.

Inter-annuelle Verteilung

Die hohe inter-annuelle Variabilität der Spinnengemeinschaften (= geringe Ähnlichkeit), die in drei aufeinanderfolgenden warmen Jahreszeiten auf der höchsten räumlichen Ebene – der der Kronen alter Buchen – nachgewiesen werden konnte, zeigt, dass sich die Zusammensetzung der Spinnengemeinschaften zwischen den Jahren bemerkenswert ändert und nicht vorhersagbar ist (zumindest über einen dreijährigen Zeitraum). Stattdessen zeigten die Probenahmen, dass jeder Baum eine individuelle Arthropodengemeinschaft beherbergte, die sich von der anderer Bäume derselben Art, demselben Bestand und einer gleichen Altersstufe unterschied. Da die Spinnengemeinschaft eines Baumes nur einmal besammelt wurde, könnten die erheblichen Unterschiede in der Gemeinschaftsstruktur zwischen den Bäumen zum einen das Ergebnis eines stochastischen Prozesses sein. Die deutlichen interindividuellen Unterschiede in den Gemeinschaftszusammensetzungen könnten zum anderen aber auch darauf hindeuten, dass sich die Baumindividuen entsprechen stark voneinander unterscheiden und sie deshalb von unterschiedlichen, von Jahr zu Jahr aber in etwa gleichbleibenden Arthropodengemeinschaften besiedelt werden. Im Gegensatz dazu beherbergten die mittleren und jungen Buchen inter-annuell stabile Spinnengemeinschaften, worauf man auf eine sehr konstante und vorhersehbare Re-Kolonialisierung und Zusammensetzung schließen kann. Diese stabilen Strukturen aus vielen ähnlichen Gemeinschaften von besonderen Spinnenarten kann nicht durch zufälliges Rekrutieren erklärt werden – es ist eher wahrscheinlich, dass die Spinnen von spezifischen Eigenschaften der Buchen und ihrem Mikroklima angezogen wurden. Arten wie die Laubläufer (z.B. Anyphaenidae) zeigten eine starke Bindung an die tieferen Vegetationsschichten, welche offensichtlich attraktive Eigenschaften besitzen, die im Kronenraum fehlen. Diese Ergebnisse unterstreichen die Existenz von Lebensraumheterogenitäten in den Buchenkronen und liefern Beweise dafür, dass Spinnengemeinschaften – abhängig von der Vegetationsschicht, die sie bewohnen – entweder von stochastischen (ökologische Drift) oder deterministischen (interspezifische Konkurrenz) Prozessen geprägt werden. Aufgrund des derzeitigen Forstsystems, das große Veränderungen in das natürliche Ökosystem gebracht hat, bilden alte Baumkronen in alten Waldstücken isolierte, seltene und kleine Inseln, die unterschiedliche und sich nicht im Gleichgewicht befindende Spinnengemeinschaften mit bemerkenswert großer Vielfalt beherbergen, während die beiden tieferen Ebenen (gebildet durch mittelalte und junge Buchen) eine geringere Vielfalt besitzen.

Die beiden unteren Ebenen werden in ähnlicher Weise durch interspezifische Konkurrenz um gleiche Lebensräume beeinflusst, was zu einem hohen Grad von

Artenaggregation führte. Allerdings können die typischen Gemeinschaften in mittleren und jungen Buchen nicht allein aus den Beziehungen zwischen Arten erklärt werden. Aggregation auf bestimmten Ebenen bedeutet auch, dass manche Ebenen attraktiver für die aggregierenden Arten sind als andere Ebenen. Um die Zusammensetzung der untersuchten Gemeinschaften zu erklären und die Verteilung von aggregierenden Arten zu verstehen, ist es jedoch notwendig, die Faktoren zu erkennen, die solche Lebensraummerkmale bestimmen. Nur so ist die vorhandene Verteilung und stabile Zusammensetzung der Spinnen vorhersehbar. Zusätzlich zu Interaktionen zwischen den Arten, wurden Merkmale der Buche (z. B. Marcescence) als mögliche deterministische Faktoren, die für eine vorhersehbare Zusammensetzung der Spinnengemeinschaften verantwortlich sein können, in Betracht gezogen.

Künftige Forschung

Die meisten Studien über Baumkronen wurden bislang in tropischen Regionen durchgeführt. Meine Studie über Spinnengemeinschaften im Wald der gemäßigten Breiten liefert somit völlig neue Ergebnisse. Diese zeigen, dass eine große Zahl von Spinnenarten in den Kronen von Rotbuchen wohnt, und dass mehr als 45% der Spinnenarten nur in einer einzigen der drei untersuchten Ebenen der Kronen zu finden sind. Es gibt noch viel an den Baumkronen (als experimentellem Element) zu tun, um neue Informationen für ein besseres Verständnis der Ökologie gemäßigter Wälder im Allgemeinen und ihrer Biodiversität im Speziellen zu gewinnen. Baumkronen bieten ausgezeichnete Möglichkeiten, die Auswirkungen des Konkurrenzausschlusses über die Dynamik der Arthropodengemeinschaften zu untersuchen.

Zwei weitere prinzipielle Untersuchungen sind erforderlich, um eine generellere Bedeutung meiner Befunde zu prüfen:

Erstens muss die Frage gestellt werden, ob die an den Buchen gefundene, vom Alter des Baumbestands (seinem Sukzessionsstadium) abhängige Vielfalt der Spinnenzönosen ein weitverbreitetes Phänomen ist, das man nicht nur in Buchenbeständen, sondern auch bei weiteren Baumarten in anderen Wäldern und deren Sukzessionsstadien findet. Um die verschiedenen Diversitätsmuster vergleichen zu können, schlage ich das wirksamste und effizienteste Standard-Protokoll (Baumkronenbenebelung) für die Probenahme in den Kronen anderer Baumarten der gemäßigten Wälder vor.

Zweitens können Ergebnisse solcher Untersuchungen, wie ich sie durchgeführt habe, Anregungen für die forstliche Praxis liefern, z.B. bei der Wahl der optimalen Zeiträume für den Einschlag, bei dem bisher stets nur Auswirkungen auf Wirbeltiere beachtet wurden. Um diesem Anspruch aber gerecht zu werden, sind weitere

kontinuierliche Langzeitstudien – auch in den obersten Ebenen der Baumkronen – nötig, in welche man sich heutzutage mittels geeigneter Ausrüstung Zugang verschaffen kann (via Kran oder Gerüst). Zeitlich unbegrenztes Monitoring ist außerdem eine Voraussetzung, um globalen Wandel im Allgemeinen und den Klimawandel im Besonderen mit Hilfe eines geeigneten Monitorings zu beobachten. Dadurch eröffnet sich die Möglichkeit, Störungen im System frühzeitig zu erkennen, um u.U. zeitnah entgegen steuern zu können. Sobald weitere Studien an wirbellosen Tieren unterschiedliche Sukzessionsstadien berücksichtigen, werden die nachgewiesenen und geschätzten Werte der Artenvielfalt vermutlich deutlich steigen und es wird sich zeigen, dass die Bedeutung des – vor allem hohen – Baumalters bisher stets unterschätzt worden ist.

Zum jetzigen Zeitpunkt ist die vorliegende Arbeit die erste Studie, die die Spinnendiversität und die Gemeinschaftszusammensetzung in den Baumkronen europäischer Rotbuchen über verschiedene raumzeitliche Skalen vergleicht. Sie zeigt deutlich, dass die raum-zeitliche Dynamik die Artenvielfalt von Spinnen in den Kronen stark beeinflusst.

Chapter IX

Acknowledgements

First of all, I wish to give my deepest thanks to Prof. Dr. Karl Eduard Linsenmair for being an awesome Doktorvater. I really appreciate that he and Dr. Brigitte Fiala helped me to apply and get the scholarships for coming over in this oldest university in Bavaria and carrying out my own biodiversity research as well as experiencing the Bayern-Franken culture. His door was always open to me for mentoring and discussion, and he also gave me a lot of freedom to let me to study what I did really want. This was the best period of my life to enjoy the broad knowledge and research of the natural science. Thank him also for giving me his rifle as a master-apprentice gift. I am grateful to Prof. Dr. Jürgen Tautz for reviewing my dissertation in the committee.

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Chapter IX

Curriculum Vitae and Appendices

Journal Reviewer

European Journal of Forest Research
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- Hsieh, Y.-L. and K. E. Linsenmair. 2006. The arthropod community structure on European beech. 23rd European Colloquium of Arachnology. Barcelona.
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Hsieh, Y.-L. and K. E. Linsenmair. Ground spider diversity at natural boundaries: A comparison between subtropical and temperate ecosystem. (in preparation)

Appendix



SECOND PRIZE

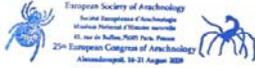
Best Talk

Samuel Yu-Lung Hsieh

presented during the

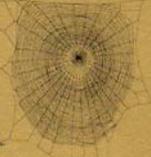
25th EUROPEAN CONGRESS OF ARACHNOLOGY

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in the field of Behaviour, Ecology and Faunistics to

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awarded during the 18th International Congress of Arachnology,
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Marek Żabka
Organising Committee



Nikolaj Scharff
ISA President

Zu Gast an der Uni

Angefangen hat er mit Walen - jetzt untersucht er Spinnen. Der Taiwanese Samuel Hsieh.

Ein Taiwanese im Sailershausener Universitätsforst: Samuel Hsieh schreibt in Würzburg seine Doktorarbeit und erforscht hier die deutsche Fauna. (Foto privat)



Eigentlich ist Samuel Hsieh ein Mensch wie jeder andere auch: Der Taiwanese liebt die Natur, er legt Wert auf den Umweltschutz und er hat seine Vorlieben, denen er nachgeht. Spätestens hier hören die Gemeinsamkeiten auf: Hsieh liebt nämlich Spinnen und verbringt einen Großteil seiner Zeit mit diesen Langbeinern. Der Grund? Der Stipendiat des Deutschen Akademischen Austauschdienstes untersucht in seiner Doktorarbeit die Frage: „Wie verändern sich mit der Zeit Lebensgemeinschaften in der Baumkrone?“. Und zu diesen Lebensgemeinschaften gehören nun mal auch Spinnen. Seit 2004 forscht Samuel Hsieh am Lehrstuhl für Tierökologie und Tropenbiologie. Seine Dissertation betreut Professor Karl Eduard Linsenmair zusammen mit dem Förster Hans Stark.

Zur Person

Samuel Yu-Lung Hsieh wurde 1977 in Taipeh im Norden von Taiwan geboren. An der National Taiwan Universität studierte er Biologie; sein Studium schloss er 2001 mit dem Master ab. Seit 2004 forscht er in Würzburg als Stipendiat des Deutschen Akademischen Austauschdienstes für seine Doktorarbeit.

Dass der Taiwanese Baumkronen als Forschungsort gewählt hat, ist kein Zufall: Schon während seiner Kindheit auf dem Dorf fühlte er sich stark mit der Natur verbunden. Eine Verbundenheit, die noch heute ihren Ausdruck findet, wenn er Landschaften, Pflanzen und Tiere mit Aquarellfarben auf Papier bringt. „Ich liebe die Forschung im Freien“, sagt er begeistert und fährt fort: „Ich liebe es, in der Natur zu sein, mich dort zu entspannen und nachzudenken. Die Natur hat auf mich einen sehr positiven Einfluss. Sie sorgt für gute Laune“.

Noch vor wenigen Jahren, als er in Taiwan lebte, war nicht abzusehen, dass Hsieh sich einmal so intensiv mit Spinnen befassen würde. Damals studierte er Biologie und schrieb seine Bachelorarbeit über Delphine und Wale. Kein leichter Job: „Es ist schwer, Wale zu erforschen, weil man lange auf eine Genehmigung der Behörden warten muss“, sagt Hsieh. Deshalb orientierte er sich neu und beobachtet seitdem Spinnen. Nachdem er schließlich seinen Master abgeschlossen hatte, entschied er sich dazu, in Deutschland zu promovieren. Dabei reizte ihn vor allem die Chance, seine Beobachtungen aus Taiwan mit den zukünftigen aus Deutschland zu vergleichen. Schließlich leben in Deutschland ganz andere Spinnenarten als in Taiwan. „Während in Taiwan überwiegend große Spinnen wie die Vogelspinne vorkommen, findet man in Deutschland vor allem kleinere

Spinnen“, sagt der 30-Jährige. Zudem gehört Taiwan zu den subtropischen Klimazonen, während Deutschland in einer gemäßigten liegt.

Seine Forschung betreibt Samuel Hsieh im Sailershausener Universitätsforst, 70 Kilometer von Würzburg entfernt. Dort sammelt er systematisch und mit einer ausgeklügelten Technik Spinnen und andere Gliederfüßer aus den Baumkronen. Ein erstes Zwischenergebnis seiner Arbeit kann der Doktorand schon präsentieren. „Oftmals teilen sich verschiedene Insekten den Lebensraum in den Baumkronen“. So, wie in einer Stadt unterschiedliche Berufsgruppen den Alltag organisieren, leben dort unterschiedlich spezialisierte Tierarten nebeneinander. Das heiße aber auch: „Sobald ein Baum gefällt wird, geht in relativ kurzer Zeit ein ganzes Insektendorf zugrunde“.

Ein für einen Naturliebhaber ungewöhnliches Hobby hat sich Samuel Hsieh in Deutschland zugelegt: Das Jagen in altdeutscher, traditioneller Tracht. Dies mache er bewusst, um eine „deutsche Tradition“ kennen zu lernen, wie er sagt. Sogar eine Ausbildung hat er dafür absolviert. Mit Erfolg: Vor zwei Monaten wurde Hsieh zum Jäger geschlagen und somit in „die Großfamilie der Jäger“ aufgenommen. Nebenbei hat er in dieser Zeit sein Deutsch deutlich verbessert – vor allem was so manche regionale Gepflogenheit betrifft. Dass Semmel „Brötchen“ bedeutet, war für ihn nämlich anfangs genauso unklar wie der unterfränkische Dialekt.

In zwei Jahren wird Samuel Hsieh voraussichtlich mit seiner Doktorarbeit fertig sein. Bis dahin gilt es noch zu forschen und Berichte zu schreiben. Den nächsten will er im Jahr 2008 an der Cambridge University vorstellen. Mag seine Liebe zu Spinnen für viele exotisch anmuten: Den Exotenstatus verliert Samuel Hsieh spätestens dann, wenn Wiener Würstchen, Schweinshaxen und Bier aufgetischt werden. An der deutschen Küche habe er nämlich mindestens so viel Gefallen gefunden wie an Natur und Jagdhorn blasen.

Christian Schmied

Winzige Krabbler prasseln leise auf die Plane

Baumkronenforscher Samuel Hsieh sammelt sein Forschungsmaterial im Sailerhäuser Wald

Von unserer Mitarbeiterin
RUTH MAHR-HAAS

SAILERSHAUSEN Die Baumkronen bilden einen der letzten noch unerforschten Lebensräume. Weil sie nur schwer zugänglich sind, weiß die Wissenschaft erst seit wenigen Jahren, dass hoch oben in den Bäumen eine reichhaltige Insekten-Fauna lebt, die viele Prozesse in Ökosystem des Waldes entscheidend beeinflusst. Der Taiwanese Samuel Hsieh schreibt seine Doktorarbeit zum Thema Baumkronenforschung an der Uni Würzburg. Seine Forschungsgrundlage holt sich der Biologe dabei direkt von Bäumen im Sailerhäuser Universitätsforst.

Noch versneit und eisig liegt der Wald von Sailershausen. Auf einem einsamen Waldweg ist ein junger Mann samt Handwagen unterwegs. In seinem Gepäck hat Samuel Hsieh viele Plastikplanen, eine seltsam aussehende Maschine und kleine Becher. Der Mann ist „Baumkronenforscher“ und will diesmal im Auftrag der Wissenschaft sechs Bäume einnebeln.

Hsieh breitet die 46 Quadratmeter großen Planen sorgfältig auf dem Waldboden unter den alten Bäumen aus. „Vorsicht! Jetzt wird es sehr laut,“ warnt der 28-Jährige. Kurz danach legt er rote Kopfhörer an, schnallt sich eine Maschine um und hält sie nach oben Richtung Baumkronen. Das Ding macht einen Höllenlärm. Ein dichter weißer Nebel steigt langsam nach oben. Er bringt vielen kleinen Tierchen den Tod in die verschnittenen Baumkronen.

Sammeln mit dem Handbesen

Lebt da oben überhaupt noch was bei der Kälte? Die Antwort kommt umgehend von oben. Winzige Krabbler prasseln leise auf die Pla-



Der Forscher sammelt seine Beute auf den Plastikplanen ein und verpackt sie in Becher. Zurück im Labor an der Universität werden die Tiere dann bestimmt.
FOTO RUTH MAHR-HAAS

nen. Raupen, Spinnen, Fliegen und kleine Käfer liegen dort bereits. Der junge Forscher wartet noch zwei Stunden, bis das Gift richtig wirkt und das Getier von der Krone auf die Plane gefallen und schließlich tot ist. Danach schnappt sich Hsieh einen kleinen Handbesen, kehrt sorgfältig die Plane ab und füllt seine Beute in die mitgebrachten Becher ab.

„Die Hauptarbeit kommt dann erst in Würzburg,“ macht der zurückhaltende junge Mann deutlich. Der Doktorand sitzt dann an einem Mikroskop im Zoologischen Institut an der Uni Würzburg und wertet seine Proben aus. Sein Hauptinteresse gilt dabei den Spinnentieren. Mit denen habe er sich schon in seiner tropischen Heimat beschäftigt und seine Diplomarbeit darüber geschrieben. „In meiner Heimat Taiwan sind die Spinnen allerdings viel größer als hier,“ lacht Hsieh. Betreut wird seine Dissertation von Prof. Dr. Eduard Linsenmaier und von Förster Hans Stark, der ihn bei seiner praktischen Arbeit in Sailershausen unterstützt.

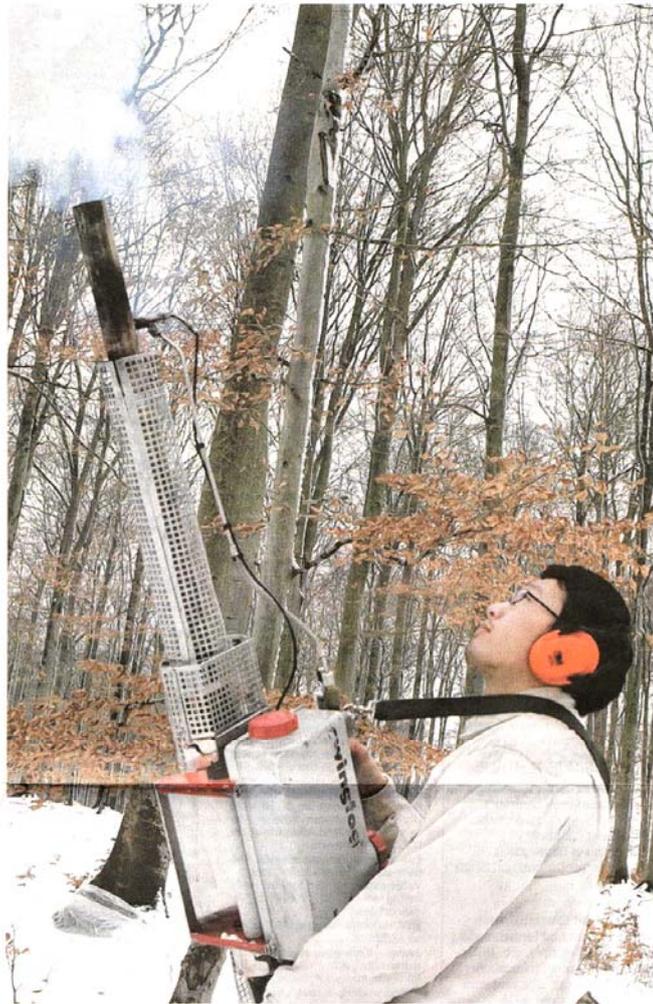
Tiere werden „benebelt“

Um die Tiere aus den Wipfeln der Bäume in sein Labor zu holen, scheue der Wissenschaftler am Lehrstuhl für Tierökologie und Tropenbiologie an der Universität Würzburg keine Mühe, erzählt Stark, der hin und wieder bei dem jungen Forscher vorbeischaut.

Die Samel-Methode von Samuel Hsieh nennt sich „Benebeln“ oder „Fogging“. Dazu wird die Baumkrone mit dem Gliedertiergift Pyrethrum eingesprüht. „Pyrethrum zerfällt in wenigen Stunden und hinterlässt keine Spuren im Ökosystem,“ versichert Stark. Bei dem Projekt werden ein Jahr lang monatlich 28 Bäume untersucht. 108 solcher Benebelungen hat der Biologe schon durchgeführt. Jede liefert das Bild einer Baumkronen-Lebensgemeinschaft zu einem bestimmten Zeitpunkt im Jahr.

Es gibt schon einige Zwischenergebnisse: Oftmals teilen sich viele Tausende Spinnen und Insekten den Lebensraum einer einzigen Baumkrone in luftiger Höhe. Eine gigantische Wohngemeinschaft von Gliedertieren (Arthropoden) mit mehreren Hundert Arten. Die häufigsten sind Mücken und Fliegen, die bis zu 40 Prozent aller Individuen ausmachen. Danach folgen Käfer und Rindläuse.

„Die Baumkronenforschung ist von unschätzbarem Wert für die Waldökologie“, sagt Hsieh. Dabei vergleicht er Baumkronen von jun-



Feuer frei! Mit einem Höllenlärm schießt Samuel Hsieh das Gift nach oben in die Baumkronen. Bald darauf fallen die toten Insekten auf die Erde herab.
FOTO RUTH MAHR-HAAS

gen, mittelalten und alten Bäumen. Für ihn überraschend fand Hsieh ausgerechnet in den Baumkronen mittelalter Bäume die meisten Arthropoden und Spinnentiere. Wenn jetzt also viele mittelalte Bäume ge-

fällt würden, dann verlören viele Tiere ihren Lebensraum.

Der Tod nützt vielen

Und wie vertragen sich Gift-einsatz und Wissenschaft? Der

junge Forscher bringt es auf den Punkt: Er opfert wenige Tierchen, um mit seiner Forschungsarbeit längerfristig viele davon am Leben erhalten zu können.



Nach mehrmonatiger Ausbildung entließ Lehrgangsführer Eugen Bieber (links) 23 Schüler in Veitshöchheim mit Jägerschlag auf die freie Pirsch.
FOTO OLGA GLEISER

Neugierig auf deutsche Jagdtradition

Auch der junge Taiwanese Samuel Hsieh bestand die Jägerprüfung

VEITSHÖCHHEIM (ca) Der Heilige Hubertus ist der Patron der Jäger, Forstleute und Schützen. Der adelige Lebewann traf auf der Pirsch auf einen Hirschen mit strahlendem Kreuz im Geweih und entsagte seinem alten Leben. Alljährlich feiern die Jäger seinen Gedenktag, den 3. November. Der Hubertushirsch ist den Jägern auch heute noch Mahnung zur Demut gegenüber der Natur. Für den Kreisvorsitzenden des Bayerischen Landesjagdverbandes (BLJV), Manfred Ländner, ist die Hubertusfeier ein „Tag des Innehaltens und der Besinnung“ in einer Zeit „ständigen

Wandels“. Viele Menschen kennen Tier- und Pflanzenwelt des Waldes nicht mehr, dem Großstädter ist er nur noch Freizeitraum. „Der Respekt vor der Natur reduziert sich auf das Haustier.“ Um so wichtiger ist es, dass der Jäger „wie von jeher dem Wild gegenübertritt- pflegend, hegend, aber auch jagend“. Lehrgangsführer Eugen Bieber entließ auch heuer wieder mit dem Jägerschlag mehrere Schüler in die Gemeinschaft der Jäger. Doch nicht allein im Bestehen der schwierigen, zentral gestellten Jägerprüfung sieht er das Ziel des 120-stündigen Kurses, sondern darin, die „Natur zu begrei-

fen“ und den „Kreislauf und ständigen Wechsel der Natur“ kennen zu lernen. Das große Einmal-Eins des Jägerlateins bereitete dem Taiwanese Samuel Hsieh keine Probleme. Begriffe wie Sau, Keller oder Firsching gehen ihm flüssig über die Lippen. Seit drei Jahren lebt und studiert er in Deutschland. Seine Doktorarbeit in der Biologie führt ihn regelmäßig in die Hasberge, wo der Forstmeister, mit dem der Spinnenforscher zusammenarbeitet, die Neugierde auf die „deutsche Jagdtradition“ weckte. Hsieh bewunderte, wie es in Deutschland gelingt, „Naturschutz und Waldnutzung aus-

zugleichen“. Auch wenn seine Familie zu Hause seine Leidenschaft nicht versteht, für ihn ist mit dem Jägerschlag ein Traum in Erfüllung gegangen. Für 40-jährige Zugehörigkeit zeichnete Manfred Ländner die Jäger Fritz Glos, Franz Hartwig, Arthur Mecklein sowie Hetner und Peter Vogel, für 50-jährige Mitgliedschaft Gerhard Burk, Otto Seidelmayr sowie Host und Willy Spanheimer mit der Ehrennadel aus. Das Jagdhornbüscherscorps unter Peter Kraus, die Parforcehornbläser unter Markus Friedrich sowie das Trio Frankonia umrahmten den Abend musikalisch.

Prüfungszeugnis

Herr
Samuel Yu-Lung Hsieh

geboren am 24.01.1977 in Taipeh

hat die

Jägerprüfung

gemäß § 15 Abs. 5 des Bundesjagdgesetzes und
Art. 28 Abs. 1 des Bayerischen Jagdgesetzes

am 1. Oktober 2007 mit Erfolg abgelegt.

Der Nachweis der erforderlichen Kenntnisse für die Ausübung der Jagd mit Fallen gemäß
Art. 28 Abs. 1 des Bayerischen Jagdgesetzes wurde bei der Anmeldung erbracht.

Vorsitzendes Mitglied
des Prüfungsausschusses

Für die
Prüfungsbehörde
i. A.



(Rützel)

(Baumeister)

Chapter X

Ehrenwörtliche Erklärung

Gemäß § 4, Absatz 3, Ziffer 3, 5 und 8 der Promotionsordnung für die Fakultät für Biologie der Bayerischen Julius-Maximilians-Universität Würzburg vom 15. März 1999, zuletzt geändert durch Satzung vom 12. August 2009, erkläre ich hiermit ehrenwörtlich, dass ich die vorliegende Dissertation selbstständig angefertigt habe und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe. Die Dissertation hat keinem anderen Prüfungsverfahren vorgelegen, weder in gleicher noch in ähnlicher Form. National Taiwan University in Taipeh hat mir den Titel "Master of Science" verliehen. Weitere akademische Grade habe ich weder erworben noch zu erwerben versucht.

Würzburg, 5. September 2011

Mitglieder der Promotionskommission

Vorsitzender: Prof. Dr. Georg Krohne

Gutachter: Prof. Dr. Karl Eduard Linsenmair

Gutachter: Prof. Dr. Jürgen Tautz

Eingereicht am: 07. Sep. 2011

Tag des Promotionskolloquiums: 23. Nov. 2011

(Dissertation: 1.0; Promotionskolloquium: 1.0)

Doktorurkunde ausgehändigt am: