Microhabitat conditions affect web-building spider communities and their prey independent of effects of short-term wildlife fencing on forest vegetation

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Abstract.   Spiders play a key role in forest food webs, where they regulate decomposer populations and may act as predators of pests and disease vectors. Spider community composition is determined in part by vegetation structure. Therefore, the exclusion of large mammals, such as deer and wild boar, through wildlife fencing may affect the composition of spider communities and their prey in forest ecosystems. Web-building spiders and their prey were hand-collected in plots that had been fenced for three years, as well as adjacent unfenced plots in a mixed temperate forest in north-eastern Germany. Additionally, spiders in the leaf litter were sampled in fenced and unfenced subareas by sieving litter. Wildlife fencing did not significantly affect spider densities or community composition per microhabitat. However, fencing affected the cover of different microhabitats significantly as there was a higher density of larger trees and higher leaflitter cover in fenced plots while there was a higher percentage of bare ground and deadwood in unfenced plots. Spider communities and their prey composition differed significantly between microhabitats (deciduous trees, coniferous trees, dead wood, understory vegetation, leaf litter) independent of fencing. Thysanoptera prey was mainly caught by spiders on coniferous trees and in the understory vegetation. Heteroptera prey were captured most frequently in the understory vegetation while Hymenoptera (excl. Formicidae) prey were mostly caught on deciduous trees. Several spider species showed a preference between deciduous and coniferous trees in the mixed forest. Wildlife fencing alters the vegetation structure of mixed forests and has indirect effects on spider communities and their role in forest food webs due to alteration of microhabitat availability.

Keywords: Araneae, browsing, predator-prey interactions, prey composition, vegetation structure

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Spiders play a key role as predators in natural (Birkhofer & Wolters 2012) and managed (Michalko et al. 2019) terrestrial ecosystems as they kill 400–800 million tons of prey globally each year (Nyffeler & Birkhofer 2017). In forests, spiders play an important role in the detrital food web, where they can regulate decomposer populations (Lawrence & Wise 2000). Forest spiders may also be important predators of some pest species and disease vectors such as Lepidoptera in temperate and boreal forests, as they reach average biomasses of 0.4 g m^{-2} and kill between 2–10 g of prey per m^2 and year (Nyffeler & Birkhofer 2017). An improved understanding of their trophic ecology in forest ecosystems therefore provides important insights about energy flow through the food chain.

Spider community composition in local habitats is determined by abiotic and biotic factors and is sensitive to both anthropogenic and natural disturbances (Bonte et al. 2002; Ziesche & Roth 2008). Structural heterogeneity usually increases the range of potential web sites and may result in more diverse spider communities (Uetz 1991) highlighting the potential of web-building spiders as bioindicators for habitat change (Marc et al. 1999; Dennis et al. 2001, 2015; Prieto-Benítez & Mendez 2011). Habitat heterogeneity also affects the feeding behaviour (Staudacher et al. 2018) and prey composition (Arvidsson et al. 2020) of spiders. In temperate forests, wildlife fencing is used to exclude mammal species, like deer, to prevent them from browsing on young shoots (Côté et al. 2004). Excluding large herbivores affects the vegetation structure of fenced areas, particularly in the understory stratum and can indirectly affect a wide range of taxonomic groups (Fuller & Gill 2001). The rooting behaviour of wild boars (*Sus scrofa*), for example, can lead to large patches of exposed humus, mineral soil, rocks and roots, and the destruction of understory vegetation (Welander 2000). Grazing by deer alters the forest structure (Augustine & Decalesta 2003), and tree composition and canopy closure in temperate forests affect spider communities (Ziesche & Roth 2008). Patchy disturbances by mammalian herbivores in forests create a habitat mosaic that may increase biodiversity by providing a greater variety of microhabitats (Sereda et al. 2014; Stein et al. 2014) but may also reduce the number of appropriate sites for web building spider species.

Few studies have addressed the effects of mammal grazing or foraging on spider communities in forest ecosystems. Ground-dwelling spider species richness and abundance varies with tree canopy coverage. Canopy gaps in plantation forests support a higher species richness and abundance than areas with closed canopy (Oxbrough et al. 2006). Landsman & Bowman (2017) found that deer exclusion resulted in higher structural habitat complexity, but reduced species richness of hunting and web-building spider communities locally. Bucher et al. (2021) showed pronounced effects of deer exclusion on vegetation properties, with lower abundances of sheet-web weavers in enclosures. Both previous publications highlight the effect of deer fencing on spider and potential prey communities (Landsman & Bowman 2017; Bucher et al. 2021) but did not analyse the actual effects of fencing on spider prey composition. Current increases in wildlife fencing in Europe, partly due to the construction of fences to prevent the spread of the African Swine Flu (Jori et al. 2021) and partly to protect newly planted deciduous trees from browsing (Löf et al. 2010) emphasize the need to better understand the effects of fencing on non-target species that play a dominant role in forest food-webs.

Exclusion of mammalian herbivores could result in structurally more complex habitats with a higher diversity of available microhabitats for web-building spiders, thereby potentially increasing their abundance and richness. Reduced disturbance, on the other hand, could also lead to a more uniform forest structure with a reduced variety of microhabitats and lower spider species richness. The current study aimed to answer the following questions: (1) how does deer fencing affect spider community composition after three years? and (2) does fencing affect the availability and composition of prey caught by web-building spiders? We hypothesize that fencing (H1) increases the vegetation structure and directly promotes the richness and abundance of local web-building spider communities, and that (H2) prey availability and composition of prey are more diverse in fenced areas.

METHODS

Research site.—The study was conducted in a mixed forest in the Havelland district in north-eastern Germany (Federal state of Brandenburg, coordinates: 52° 54′ 66″ N, 12° 06′ 47″ E). The studied forest area is located next to the field station Linde owned by the Zwillenberg-Tietz Foundation (https://www.zwillenberg-tietz-stiftung.de/). The forest is dominated by Scots pine (*Pinus sylvestris*) growing on sandy soil. Three deer species are present in the study area: European fallow deer (*Dama dama* (Linnaeus, 1758)), Red deer (*Cervus elaphus* Linnaeus, 1758) and Roe deer (*Capreolus capreolus* (Linnaeus, 1758)). Fenced plots were established throughout the forest as part of a previous research project, and fences had been in place for three years at the time of spider sampling. Fences were constructed of chain link fencing wrapped around wooden poles and had a total height of 2 meters. To measure the effect of fencing on spiders, a total of 11 fenced treatment plots and 11 adjacent unfenced control plots of the same size were established. All plots had a size of 10×10 meters and the control plots were always paired with directly adjacent treatment plots in order to reduce confounding effects of large-scale habitat differences.

Sampling.—Sampling was conducted between the 12th of May to the 21st of June, 2019 as a peak season for adult spiders. In order to estimate the microhabitat and vegetation structure of each plot, vegetation data was collected in a standardized way. Five 1×1 meter quadrats were randomly placed inside each plot and eight microhabitat properties were recorded as the percentage coverage with (1) leaf litter, (2) grass, (3) herbs, (4) mosses, (5) deadwood and (6) bare ground by visual estimation. In addition, (7) the number of trees with a height above 2 meters was counted and the (8) tree diameter at breast height (DBH) was recorded for all trees in the 10×10 m plots. Large disturbances in the plot, such as fallen trees and soil disturbance by animals, were also recorded.

Web-building spiders and their prey were collected by visually searching each plot for 45 minutes at each of two separate occasions throughout the sampling season. Hand-collected spiders and their prey were searched for in the following microhabitats: (1) bark and branches of deciduous trees, (2) bark and branches of coniferous trees, (3) deadwood and (4) understory vegetation. Each microhabitat type was investigated for a similar amount of time in a rotating scheme as follows: a location was picked randomly and each spider-web visible in the vicinity was investigated further. The spider was first located and collected with a pooter, then the web with prey remains was subsequently collected and put in a vial together with the spider and a label with information on the microhabitat. Pairs of treatment plots and control plots were always searched consecutively on the same date. In order to also survey spider species living in the leaf litter, additional sampling was carried out with a litter sieve once per plot. Three 1×1 meter areas with at least 50% leaf litter coverage were selected in each study plot and all of the leaf litter inside was sieved for spiders. No prey records are present for these leaf-litter inhabiting spiders.

Identification.—All spiders and their prey were identified with the use of a stereo microscope (Leica Stereo Zoom S9) with magnifications between 15–90 times. Adult spiders were identified to species level using identification keys from araneae.unibe.ch (Nentwig et al. 2021) and Roberts (1996). Prey remains were identified to the following levels allowing a reliable classification: Acari, Araneae, Auchenorrhyncha, Brachycera, Coleoptera, Collembola, Diplopoda, Formicidae, Heteroptera, Hymenoptera, Lepidoptera, Nematocera, Opiliones, Psocoptera, Stenorrhyncha and Thysanoptera (also see Arvidsson et al. 2020). Rare spider species were classified according to Platen et al. (1999).

Statistical analysis.—Permutational multivariate analysis of variance (PERMANOVA; Anderson 2014) was used to analyse all dependent variables in univariate (total spider abundance (adults and juveniles) & effective number of species (Chao et al. 2010), number of prey items per web and taxonomic richness of prey) and multivariate (vegetation structure, spider species composition & prey composition) models. The dependent variables for univariate models were transformed into resemblance matrices with pairwise distances between all samples based on Euclidean distances. The spider and prey composition data were transformed into resemblance matrices with pairwise distances between all samples based on Bray-Curtis similarities. Vegetation structure was transformed into a resemblance matrix with pairwise distances between all samples based on Gower similarities to account for the different scales of measurement in individual vegetation properties. By using Gower similarities, all vegetation properties were internally standardized to a range from 0–1 (Gower & Warrens 2014). The random factor "Plot" (11 levels) and the fixed factors "Fence" (2 levels: with or without) and "Microhabitat" (5 levels: litter, deadwood, understory vegetation, coniferous and deciduous tree) were specified for the PERMANOVA models. PERMANOVA was then performed with type III sums of squares and 9999 permutations of residuals under a reduced model. Fixed factors with significant effects on spider species or prey order composition were further analysed for homogeneity of multivariate dispersions with distance-based tests using the same resemblance matrices as for the respective PERMANOVA model. Non-parametric rank-based Kruskal-Wallis tests were used to compare differences between microhabitats for individual prey order groups. Principal coordinates ordination (PCO) was used to visualize differences in vegetation structure and spider species composition based on the respective resemblance matrix. Spider species or microhabitat properties (see section sampling) with multiple correlation coefficients larger than 0.3
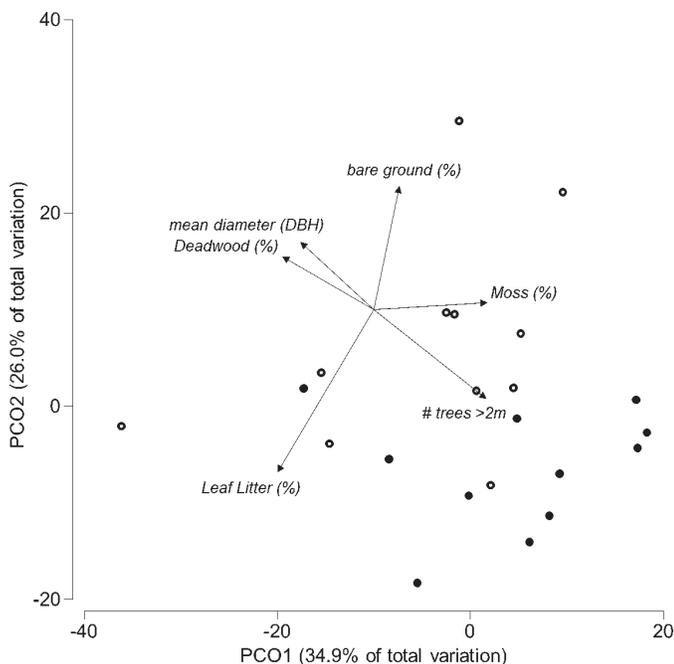
Figure 1.—Principal coordinates ordination (PCO) based on a Gower similarity matrix of eight vegetation properties in fenced (•) and unfenced (○) study plots. Vegetation properties with a multiple correlation coefficient > 0.4 are superimposed as vectors: percentage cover with deadwood, bare ground, moss or leaf litter and mean diameter and number of trees higher than 2m in study plots.

with PCO axes scores were considered as characteristic or common for certain factor levels. PERMANOVA models and ordinations were calculated with PRIMER 7 version 7.0.13 and the PERMANOVA add-on (PRIMER-e, Quest Research Limited, Auckland, New Zealand).

RESULTS

Vegetation.—The fence treatment affected the vegetation structure in the study plots significantly ($F_{1,10} = 4.72$; $P = 0.010$). Fenced plots on average had a higher density of trees with a height above 2m (mean ± standard deviation: 23.6 ± 9.5 vs. 15 ± 4.1 trees) and a higher percentage cover with leaf litter (47.6 ± 16.0 vs. 43.2 ± 19.1), but a lower percentage of bare ground (1.1 ± 1.8 vs. 5.8 ± 6.1) or deadwood cover (9.4 ± 4.2 vs. 14.5 ± 7.2) compared to unfenced plots (Fig. 1).

Spiders.—A total of 940 spiders from 75 species plus 136 unidentified juvenile individuals were collected from different microhabitats (deciduous or coniferous trees, deadwood, understory vegetation (all by hand-collection) or litter (by litter sieving)). The total abundance of spiders was not significantly affected by the presence of a fence ($F_{1,31} = 1.50$; $P = 0.259$), but differed significantly between microhabitats ($F_{4,31} = 37.89$; $P < 0.001$). The average number of spiders declined from litter (23.9 individuals) to deciduous tree (10.6) to understory (9.2) to deadwood (4.6) and coniferous tree (1.4) microhabitats. The effective number of spider species was not significantly affected by the presence of a fence ($F_{1,31} = 1.05$; $P = 0.331$), but differed significantly between microhabitats ($F_{4,31} = 74.29$; $P < 0.001$). The average number of effective
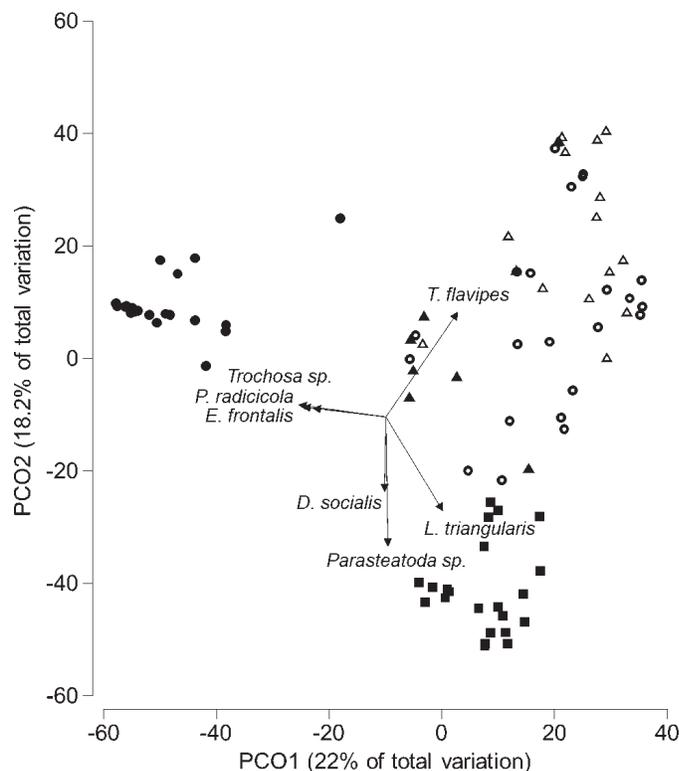

Figure 2.—Principal coordinates ordination (PCO) based on a Bray-curtis similarity matrix of log(x+1)-transformed abundance data of 75 spider species sampled in litter (•), understory vegetation (○), deciduous tree (■), coniferous tree (▲) or deadwood (△) microhabitats. Spider species with a multiple correlation coefficient > 0.3 are superimposed as vectors.

species declined from litter (8.4 species) to deciduous tree (4.1) to understory (3.0) to deadwood (2.3) and coniferous tree (1.2) microhabitats. The species composition of spider communities did not differ significantly between fenced and unfenced plots ($F_{1,31} = 1.65$; $P = 0.112$), but differed significantly between microhabitat types ($F_{4,31} = 14.64$; $P < 0.001$; Fig. 2). Differences between spider communities in microhabitats did not primarily result from heterogeneity of multivariate dispersions ($F_{1,93} = 2.76$, $P = 0.056$) indicating that communities primarily differed in species composition and not in the magnitude of variation between plots.

Several spider species, including some from non-web building families, were frequently (in at least 10 study plots) and exclusively collected from litter microhabitats (due to the different sampling method): *Abacoproeces saltuum* (L. Koch, 1872) (Linyphiidae), *Euophrys frontalis* (Walckenaer, 1802) (Salticidae), *Hahnia ononidum* Simon, 1875 (Hahniidae), *Neon reticulatus* (Blackwall, 1853) (Salticidae), *Pelecopsis radicicola* (L. Koch, 1872) (Linyphiidae), *Phrurolithus festivus* (C. L. Koch, 1835)(Phrurolithidae)*, Scotina celans* (Blackwall, 1841) (Liocranidae) and *Trochosa* sp., whereas *Drapetisca socialis* (Sundevall, 1833) (Linyphiidae) and *Parasteatoda lunata* (Clerck, 1757) (Theridiidae) were exclusively collected from deciduous tree microhabitats in at least 10 study plots. *Linyphia triangularis* (Clerck, 1757) (Linyphiidae) was more common in deadwood and deciduous tree microhabitats than in the other three microhabitat types. *Tenuiphantes flavipes*
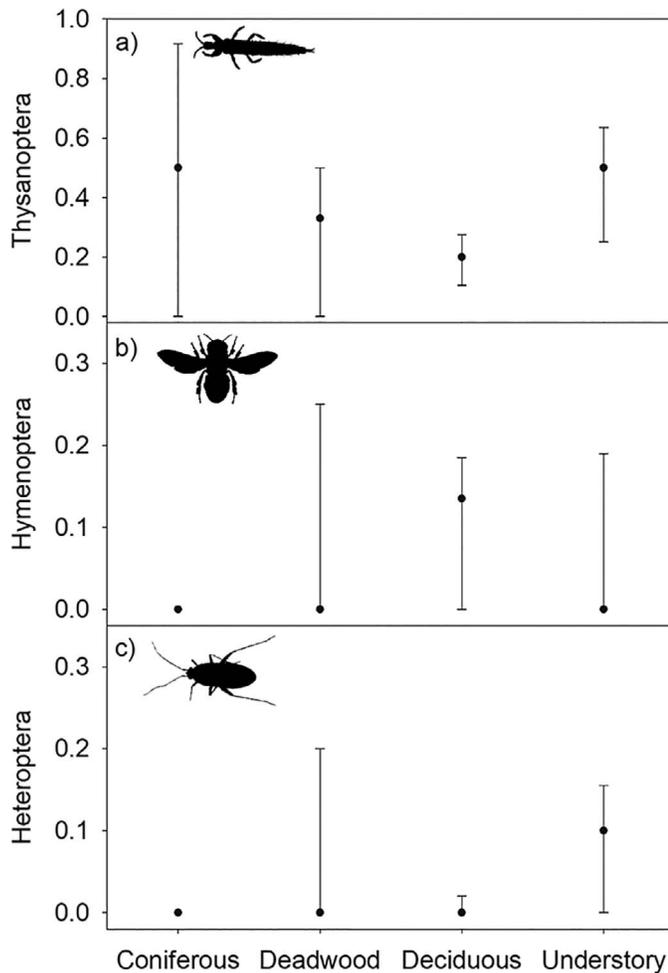
Figure 3.—Medians and 75th and 25th percentiles for the number of prey items per spider web for (a) Thysanoptera, (b) Hymenoptera excluding Formicidae and (c) Heteroptera prey in coniferous tree, deadwood, deciduous tree and understory vegetation habitats.

(Blackwall, 1854) (Linyphiidae) was more common in deadwood and understory vegetation microhabitats than in litter or coniferous microhabitats and absent from deciduous tree microhabitats. Two red listed species were caught: *Gnaphosa bicolor* (Hahn, 1833) (Gnaphosidae), listed as endangered, and *Xysticus luctuosus* (Blackwall, 1836) Thomisidae, listed as critically endangered.

Prey.—A total of 639 prey items were collected from spider webs from the following taxonomic groups: Acari (111 prey items), Araneae (5), Auchenorrhyncha (14), Brachycera (12), Coleoptera (16), Collembola (43), Diplopoda (1), Formicidae (29), Heteroptera (26), Hymenoptera (excl. Formicidae, 55), Lepidoptera (5), Nematocera (72), Opiliones (1), Psocoptera (4), Stenorrhyncha (110) and Thysanoptera (135) plus 191 unidentifiable prey items from 400 spider webs. In total, 74.8% of all identified prey items were insects.

The number of prey items per spider web was not significantly affected by the fence treatment ($F_{1,19} = 1.58$; $P = 0.246$) or microhabitat ($F_{3,19} = 0.84$; $P = 0.495$). The average taxonomic prey richness per web differed significantly between microhabitats ($F_{3,17} = 8.42$; $P = 0.002$), but was not

significantly affected by the fence treatment ($F_{1,17} = 0.15$; $P = 0.709$). The prey composition in spider webs differed significantly between microhabitats ($F_{3,17} = 2.01$; $P = 0.011$), but not between fence treatments ($F_{1,17} = 0.10$; $P = 0.990$). Differences in prey composition at least partly resulted from heterogeneity of multivariate dispersion between microhabitat types ($F_{3,66} = 5.28$, $P = 0.012$) with the prey composition in understory vegetation being significantly more homogenous than in deadwood (t = 3.11, $P = 0.009$) or coniferous tree (t = 4.22, $P = 0.001$) habitats. The number of Thysanoptera (Kruskal-Wallis H = 14.34, $P = 0.003$) and Hymenoptera excl. Formicidae (Kruskal-Wallis H = 8.40, $P = 0.038$) prey items differed significantly between microhabitats. The number of Heteroptera prey items tended to differ between microhabitats (Kruskal-Wallis H = 6.51, $P = 0.089$). Thysanoptera prey were most common for spiders in the understory vegetation and on coniferous trees and least common for spiders on deciduous trees (Fig. 3a). Hymenoptera prey, excluding Formicidae, was most common for spiders on deciduous trees, less common for spiders on deadwood or in understory vegetation and absent from spider webs on coniferous trees (Fig. 3b). Heteroptera prey was most common in spider webs in the understory vegetation, less common in webs on deadwood and deciduous trees and absent from webs in coniferous trees (Fig. 3c).

DISCUSSION

Wildlife fences affected the structure of vegetation significantly, with more trees and a higher litter cover, but a lower bare ground and deadwood cover in fenced plots. The observed structural differences were expected, due to younger trees being protected from grazing and the ground being undisturbed by wild boars in fenced areas (see also Kirby 2001; Morecroft et al. 2001). Differences in vegetation structure were hypothesized to affect web-building spider assemblages, since web-building spider species often have different preferences for vegetation structure (Uetz 1991). These expectations were confirmed in the current study comparing web-building spider communities between different microhabitats. The limited effects of fencing on spider communities at the plot level in our study at least partly results from the standardized sampling protocol for web-building spiders and their prey. Microhabitats were not sampled proportionally to their occurrence in fenced and unfenced study plots, but sampling was standardized to similar sampling time for each microhabitat. The litter microhabitat had the highest spider abundance and diversity and a unique set of species exclusively occurred in the litter layer. Given the significantly higher litter cover in fenced plots, these diverse and unique communities would benefit from fencing at the plot level. In previous studies, the exclusion of deer also led to a higher abundance of understory vegetation and thereby to a greater abundance of web-building spiders (Takada et al. 2008; Roberson et al. 2016, but see Landsman & Bowman 2017). Bucher et al. (2021) however, observed lower abundances of sheet-web weavers in fenced plot that had higher understory vegetation. In the current study, however, the coverage of understory vegetation (grasses and herbs), did not differ significantly between fenced and unfenced plots and web-building spiders in these habitats always had a relatively high number of Thysanoptera prey items independent of the

presence of a fence. These results document the complexity of responses by forest-inhabiting spiders to wildlife fencing and highlight the importance to consider different vegetation properties from the litter layer (this study) to understory vegetation (Takada et al. 2008; Roberson et al. 2016) and vegetation heterogeneity and height up to 200 cm (Bucher et al. 2021) in future studies.

Fenced plots, however, had significantly fewer deadwood microhabitats. Activity of large mammals in unfenced plots may have caused this pattern due to direct damage to trees. Additionally, removal of deadwood during the construction of fences may have contributed to this difference. A range of web-building spider species benefited from the presence of deadwood microhabitats, further supporting its high value for arthropod diversity in general (Jabin et al. 2004), but also highlighting the context dependency of deadwood effects on arthropods (Floren et al. 2014). Webs of *Tenuiphantes flavipes*, for example, were frequently found on the lower parts of deadwood pieces, suggesting that unfenced plots support this species due to higher availability of suitable microhabitats. If deadwood was located close to the ground its rigid structure supported the construction of webs by larger species such as *Agelena labyrinthica* (Clerck, 1757) (Agelenidae) and *Eratigena atrica* (C. L. Koch, 1843) (Agelenidae). If the area around deadwood offered open spaces, orb-web species such as *Cyclosa conica* (Pallas, 1772) (Araneidae) and *Zilla diodia* (Walckenaer, 1802) (Araneidae) utilized these microhabitats. Hymenoptera (excl. Formicidae) and Heteroptera prey was less frequently observed in webs of spiders in deadwood microhabitats. Hymenoptera and Heteroptera primarily utilize plant associated resources and therefore preferred understory vegetation as a microhabitat. In deadwood microhabitats, Thysanoptera prey was mainly observed in webs of orbweavers (Araneidae) or larger sheet-weavers (Linyphiidae). Compared to, for example, Hymenoptera prey (excl. Formicidae), Thysanoptera are often more randomly distributed in local habitats, as they are transported by wind and are not good, active fliers (Mound 1983).

Several common, forest-inhabiting spider species have rather broad habitat preferences, such as *Linyphia triangularis* and *Neriene peltata* (Wider, 1834) (Linyphiidae). Both species build rather large sheet webs attached to branches of trees and were therefore observed in both fenced and unfenced plots. The density of taller trees was significantly higher in fenced compared to unfenced plots, probably due to the lower intensity of browsing on saplings inside the fenced plots. *Linyphia triangularis, Parasteatoda* sp. and juvenile *Drapetisca socialis* showed preferences for deciduous trees. *Parasteatoda sp.* webs were often observed between separate trunks of the same tree, while *D. socialis* was almost exclusively observed close to single small branches sticking out with a 90° angle from the main branch. Both these tree properties were more common for deciduous trees. *Lepthyphantes minutus* (Blackwall, 1833) (Linyphiidae), on the other hand, was only collected from the bark of coniferous trees. Korenko et al. (2011) in the Czech Republic and Halaj et al. (1998) in the US observed preferences of *Linyphia triangularis* for coniferous rather than deciduous trees. These results contradict observations in the current study in Germany and observations from Sweden (Arvidsson pers. obs.). According to Roberts (1996),

Linyphia triangularis constructs webs on bushes or trees with sufficiently stable foliage and frequently occurs in both forest types. Microhabitat preferences of this common, cosmopolitan species may depend on geographic location and the availability of alternative habitats. Spiders in deciduous tree microhabitats captured a large number of hymenopteran prey while spiders in coniferous tree microhabitats did not. The previously explained preferences of web-building spider species for structural properties of deciduous trees may facilitate the construction of webs that are more suitable to capture larger flying prey.

Two closely related species with overlapping habitat preferences in the genus *Linyphia* co-occurred throughout study plots. During the beginning of the fieldwork in May adult individuals of *Linyphia hortensis* Sundevall, 1830 (Linyphiidae) were observed in the upper stratum of the understory vegetation, and individuals of the larger, co-occuring *Linyphia triangularis* were juvenile at this time and primarily occupied web sites at the bottom of understory vegetation. During the second sampling period in June, there was a complete shift in stratum utilization between these two species.

Conclusion.—While spider community or prey composition per microhabitat did not differ significantly between fenced and unfenced plots in the current study, it is evident that wildlife fencing altered the litter cover and vegetation structure of forests and will have indirect effects on spider communities and their role in forest food webs due to alteration of microhabitat availability. The abundance and diversity of spiders was highest in the litter layer and on deciduous trees and significantly higher litter coverage and more deciduous trees were observed in the fenced plots. These results suggest that herbivores may negatively affect spider communities due to effects on litter cover and younger deciduous trees. The studied forest showed a high value for spider conservation, including two red listed species, as it offered a wide range of microhabitats including deadwood as a valuable microhabitat for several spider species. The rather unique properties of temperate forest on sandy soil in the state of Brandenburg allowed heat-loving spider species (e.g., *A. saltuum, Tapinocyba praecox* (O. Pickard-Cambridge, 1873) (Linyphiidae) to co-occur with species which require more shaded or moist habitats (e.g., *P. radicicola, Trochosa terricola* Thorell, 1856 (Lycosidae).

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