



Non-native Douglas fir promotes epigeal spider density, but has a mixed effect on functional diversity

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Received: 1 August 2022 / Revised: 24 January 2023 / Accepted: 25 January 2023 /

Published online: 10 February 2023

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Abstract

With climate change altering ecosystems worldwide, forest management in Europe is increasingly relying on more adaptable non-native tree species, such as Douglas fir (*Pseudotsuga menziesii*). However, the ecological consequences of the increased utilization of Douglas fir on arthropod diversity and ecosystem functioning are not fully known. Here we assessed how non-native Douglas fir as well as large- and small-scale differences in the environmental context, affect epigeal spider abundance, biomass, taxonomic and functional diversity, and community structure in Central European forests. Our study sites were divided into two regions with large differences in environmental conditions, with seven replicates of five stand types, including monocultures of native European beech (*Fagus sylvatica*), non-native Douglas fir and native Norway spruce (*Picea abies*), as well as two-species mixtures of European beech and each of the conifers. Contrary to our expectations, Douglas fir promoted small-scale spider diversity, and abundance and biomass (activity density). On the other hand, it decreased spider functional divergence and altered spider community structure. Microhabitat characteristics had opposing effects on spider diversity and activity density, with more open stands harboring a more diverse but less abundant spider community. Overall, our findings suggest that increasing Douglas fir utilization at the expense of Norway spruce does not necessarily decrease the diversity of epigeal arthropods and may even promote local spider diversity and activity density. However, care needs to be taken in terms of biodiversity conservation because typical forest spider species and their functional divergence were more strongly associated with native beech than with coniferous stands.

Keywords Community structure · Forest specialists · Microhabitat variability · Mixed-species forestry · *Pseudotsuga menziesii* · Top-down control

Communicated By Akihiro Nakamura

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Introduction

Climate induced stress is substantially altering ecosystems worldwide (Scheffers et al. 2016), inducing changes in invertebrate diversity (Marta et al. 2021), as well as tree dieback (Menezes-Silva et al. 2019). In forest ecosystems specifically, management responses to climate change face multiple challenges trying to balance ecological and economic demands from forests (Ruckelshaus et al. 2015; Albert et al. 2020). For instance, the recent dieback of Norway spruce (*Picea abies*) in Central Europe because of extreme weather and spruce bark beetle (*Ips typographus*) outbreaks (Krejza et al. 2021; Mezei et al. 2017) is likely to lead to increased utilization of more adaptable tree species. One of these species is non-native Douglas fir (*Pseudotsuga menziesii*), the ecological consequences of which, however, are not fully known (Schmid et al. 2014). Potential negative ecological consequences could be tempered by planting Douglas fir in mixtures with native trees, which might combine both climatic stability and ecological sustainability (Tognetti et al. 2010). Nonetheless, such assumed mixture effects are often not well understood in real-world ecosystems and require further empirical evidence (Ammer et al. 2018). This is particularly the case when it comes to effects on the diversity and ecosystem functioning of arthropods, which play important ecological roles in forests (Schowalter et al. 2018).

A crucial ecosystem function performed by arthropods is top-down control, which may be heavily influenced by the diversity of arthropod predator communities (Jonsson et al. 2017). In most terrestrial ecosystems spiders are the dominant predators (Wise 1993). They fill many different niches due to their diversity in predatory tactics (Entling et al. 2007). Moreover, they have been shown to lower the abundance of herbivores and smaller predatory arthropods (Michalko et al. 2019) as well as indirectly lower the decay rate of litter by preying on decomposers (Lawrence and Wise 2000). According to the “enemies hypothesis” top-down control is considered to be positively correlated with tree diversity as a result of higher habitat diversity and prey availability (Root 1973). However, recent studies have shown ambiguous effects of tree species richness on arthropod predator communities (see Staab and Schuldt 2020). Spiders, for instance, have been shown to be more affected by tree identity than tree diversity at relatively short tree diversity gradients in temperate forests in Europe (Oxborough et al. 2012; Oxborough et al. 2016), where the relative contribution of each tree species in the species pool is large (Nadrowski et al. 2010). In this context, our knowledge of how native/non-native tree identity affects spider communities is limited (Oxborough et al. 2016; Ingle et al. 2020). However, it has been generally shown that replacing native forests with non-native plantations leads to a loss in arthropod biodiversity (Brocknerhoff et al. 2008). This could be the result of structural changes in understory vegetation and loss of associated species directly dependent upon the native tree species for their existence (Ennos et al. 2019). When it comes to the effect of Douglas fir on spider diversity and biocontrol potential in Central European forests, recent studies have shown contrasting results depending on stand age, stratum and the spatial scale studied. On one hand, Douglas fir presence was found to strongly decrease epigeal spider abundance and biomass (activity density) in young mixed-species plantations of a tree diversity experiment (Schuldt and Scherer-Lorenzen 2014). On the other hand, arboreal spiders at the same sites had higher abundance on Douglas fir than European beech (*Fagus sylvatica*) at the tree-level, but arboreal spider species richness and activity density decreased in monocultures and mixed stands with higher Douglas fir proportion (Matevski and Schuldt 2021).

Data from intermediate-aged Douglas fir stands showed no significant difference in epigeal spider abundance and diversity in comparison to native trees (Finch and Szumelda 2007). Additionally, data from more mature forest stands is largely lacking, with studies so far focusing on a few sites and not including mixtures with native tree species (Ziesche and Roth 2008). A general understanding of how such non-native tree species and their effects in monocultures versus mixtures influence the diversity of predators such as spiders therefore requires more extensive research.

Such a general understanding also necessitates stronger consideration of the environmental context of tree species and mixture effects. At larger spatial scales, climatic conditions have been shown to influence such effects (Ampoorter et al. 2019). At the local scale habitat features that are in part independent of tree species identity and strongly determined by forest management can play important roles (Penone et al. 2019). Spider community structure depends on vegetation structure, as different feeding guilds have different habitat requirements (Uetz 1991). The addition of fine woody debris has been shown to have a positive effect on spider abundance (Seibold et al. 2016). Furthermore, increasing the amount of other forms of detritus, such as leaf litter, has shown a stronger impact on spider diversity and abundance than altering the plant community (Langellotto and Denno 2004). Lastly, changes in canopy openness are known to alter spider community structure (Cernecká et al. 2020), with peaks in abundance in more open canopies, while functional diversity peaked at more closed canopies (Košulič et al. 2016). Disentangling the effects of habitat structure from tree identity effects can provide insight into developing more balanced forest management decisions.

Here we utilized a set of 35 managed forest stands to determine how stand type, tree species composition and habitat structure affect epigeal spider taxonomic and functional diversity, abundance, biomass and community composition for three of the economically most important tree species for Central European forestry: European beech, Norway spruce and Douglas fir. This species pool allowed us to test the effects that the increased utilization of Douglas fir in Central European forests, promoted by the recent Norway spruce dieback (Krejza et al. 2021), may have on spider diversity and spider-mediated ecosystem functions. The presence of the phylogenetically close Norway spruce enabled us to test if effects of Douglas fir are similar to that of native coniferous species. This provides us with information on how ecologically relevant the ongoing replacement of Norway spruce by Douglas fir will be for the biodiversity of associated forest organisms. Furthermore, having two-species mixtures of European beech with each of the conifers can shed light on whether planting conifers in mixtures would temper any conifer effects, especially effects of Douglas fir. Since our study sites are distributed in two distinct regions differing in environmental conditions, we can test the relative importance of site conditions and tree species identity for the structuring of spider communities. Lastly, by including tree species composition (tree proportions and neighborhood diversity) and habitat structure (herb complexity, litter cover, deadwood cover and canopy openness) in our analyses, we are considering the heterogeneity among stands of the same type to better understand how tree species composition and habitat structure may modify or outweigh the influence of stand type.

We hypothesized that (i) Douglas fir monocultures harbor lower spider diversity, abundance, and biomass than native stands, with this effect being partially alleviated in mixtures. Moreover, (ii) we expected that differences in local tree proportions and habitat structure, that better encapsulate the heterogeneity among and between stand types, have higher

explanatory power than just stand type in explaining spider diversity and composition. Lastly, (iii) regional and local differences in environmental conditions were also expected to play a strong role in structuring spider communities.

Materials and methods

Study sites and plot design

We performed this study on 35 mature temperate forest plots, each covering an area of 0.25 ha. The plots were arranged in 7 quintets (for a schematic of a quintet see Schuldt et al. 2022), covering a range of stand ages, tree proportions and site conditions in the federal state of Lower Saxony, Germany (Table S1). Four of the quintets were situated in the higher altitude, nutrient rich southern half of the state, while three were situated in the lower elevation, nutrient poor northern half of the state (Foltran et al. 2021; Fig S1). Each quintet was composed of five forest stands: (1) monoculture of European beech, (2) monoculture of Douglas fir, (3) monoculture of Norway spruce, (4) mixture of European beech and Douglas fir and (5) mixture of European beech and Norway spruce.

Data collection

Spiders were sampled with pitfall traps between 16.03.-20.09.2019. We set 8 pitfall traps at each plot in two rows of 4 traps each, with 10 m distance between traps and at least 10 m distance from the plot edge (Fig S2). Traps were transparent 500 mL plastic cups with a diameter at entry of 9.4 cm and a depth of 10 cm, placed flush to soil and covered with a metal mesh with a mesh width of 1.5 cm to prevent capture of small vertebrates. A 150 mL 50% propylene glycol solution, with an added odorless detergent to reduce surface tension, was used as trapping solution. Traps were emptied in 3-week intervals for 9 periods resulting in a total of 2520 samples. All adult spiders were determined to species level using the identification key by Nentwig et al. (2021), following the nomenclature of the World Spider Catalog (2021). After identification the biomass of all spider species was estimated by using mean species body length values for both sexes separately (Nentwig et al. 2021) and calculating their biomass (in mg) by using the body length-biomass equations of Penell et al. (2018). Spider functional guilds according to Cardoso et al. (2011), and the phenological length (in months) of adult activity (Nentwig et al. 2021) were used as traits for further analyses of functional diversity. These traits have been shown to significantly affect resource use of spiders and are therefore important in determining their functional effect (Cardoso et al. 2011; Schuldt et al., 2014). Moreover, we distinguished between species strictly associated with forests (either with a preference for forests in general, or for open or closed forests, respectively) and those not strictly associated with forests (occurring in both forests and open habitats) or primarily associated with open habitats based on habitat use data from Dorrow et al. (2019).

We used multiple predictors to explain the differences in spider abundance, biomass, and diversity within and between plots, including stand type, region (northern and southern plots), tree diversity, tree proportions, as well as microhabitat characteristics such as vegetation complexity, canopy openness, litter cover and deadwood cover. We used proportions

of the three target tree species in a 10 m radius around each trap, to describe the local tree community composition in a more detailed way than the categorical distinction of the five forest stand types. Furthermore, since oak (*Quercus* spp.) was present in some of our plots, we used oak proportion to see if it affected spider communities. Tree proportions were calculated from maps of the area potentially available (APA; Gspaltl et al. 2012) to each of the target tree species (in m²). In APA-maps, the stand area is divided into adjacent patches that are assigned to individual trees. Each point in a plot is assigned to a tree by smallest distance between point and tree, weighted by tree crown radii, which were estimated from tree diameters with species-specific allometric equations (Pretzsch et al. 2015). We tested species identity effects of the target conifers (Douglas fir and Norway spruce) and oak using their APA, excluding European beech due to high collinearity with the APA of conifers (variance inflation factor, VIF > 10). Tree diversity was quantified with a novel spatially specific index of neighborhood diversity called NDiv (Glatthorn 2021). Using APA maps, this index defines the diversity of the neighborhood surrounding individual trees. From these measurements we calculated the tree diversity in a 10 m radius around each trap. This allows for a spatially specific, small-scale measure of tree diversity, with higher NDiv values in stands with random species distribution than patch distribution, even if they have identical mixture proportions.

The microhabitat characteristics in a 100 m² square area centered around each trap were assessed in 05.-07.2019. The percentage of litter cover was visually estimated at the beginning of May, while the percentage of fine deadwood cover with a diameter lower than 7 cm was visually estimated at the end of July. Visual cover estimations were performed by dividing the 100 m² square area around each trap into 4 quartiles of equal size (25 m²) and visually estimating the coverage to a percent by walking through the quartile, one cover type (litter, deadwood) at a time. Furthermore, we measured vegetation complexity in June by setting up two 60 cm tall metal spikes at a distance of 30 cm from each other in four vegetation patches around each trap. These spikes were connected with strings at heights of 10, 20, 30, 40 and 50 cm. All the points where plant material touched the different strings as well as all the plant material that intersected the area between two strings were counted. The sum of all touches and intercepts was in turn used as a measure of herb vegetation complexity. Lastly, canopy openness was measured above each trap using a Solariscope (SOL 300) in July 2019.

Statistical analyses

We analyzed all data at the trap level. Only the distance-based redundancy analysis (dbRDA) was done at the plot level. Due to 8.7% of the samples being missing (e.g. destruction of traps due to wild boar), and traps being open for different time periods (15–24 days per sampling period) owing to field restrictions, spider abundance and biomass were calculated on a per trap/day basis. Furthermore, species diversity was calculated using coverage-based rarefaction and extrapolation of species diversity (Hill numbers) with the iNEXT R package (Hsieh et al. 2016). Functional diversity indices were calculated at the trap level using the species' biomass, guild and phenological length (in months) of adult activity. The functional diversity indices used were functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al. 2008), as well as functional dispersion (FDis) (Laliberté and Legendre 2010), calculated with the R package FD (Laliberté et al. 2014).

Table 1 Structure of linear mixed effect models used

Model	Dependent variables	Independent variables	Random effect
Stand type	Spider abundance, biomass, species richness (Hill numbers 0–2), FRic, FDis, FEve, FDiv	Stand type, region, and the interaction between them	Plot nested in site
Plot characteristics		Douglas fir, Norway spruce and oak proportions, NDiv, vegetation complexity, canopy openness, litter and deadwood cover, region, and the interaction between region and all previously mentioned variables	

We used abundance and biomass per trap/day, community weighted mean (CWM; average biomass of individual adult spiders) biomass, Hill numbers ($q=0, 1, \text{ and } 2$), FRic, FEve, FDiv and FDis as response variables in linear mixed effects models with study plot nested in study site quintet as a random effect. All response variables with the exception of the functional diversity indices were $\log(x + 1)$ transformed to improve modeling assumptions. The linear modeling was done in two successive steps to account for the fact that forest stand and plot characteristics were not completely independent of each other (Table 1). We estimated all models with the nlme R package (Pinheiro et al. 2020) and subsequently performed a stepwise selection procedure based on AICc (Burnham and Anderson 2010) in order to acquire the most parsimonious models with the best model fit. Afterwards, we confirmed that multicollinearity between variables was low using VIF (≤ 5), calculated with the R Package car (Fox and Weisberg 2018). Lastly, we calculated overall effects of individual factors with the R Package car (Fox and Weisberg 2018), followed by a post hoc test of estimated marginal means in the emmeans package to test for significant differences ($p < 0.05$) in response variables among stand types and regions (Searle et al. 1980). Model simplification was conducted based on maximum likelihood estimation. The final models were updated based on restricted maximum likelihood estimation.

Furthermore, we analyzed the similarity between spider assemblages at the plot level with distance-based redundancy analysis (dbRDA). Similarity was based on the Morisita-Horn index of square root-transformed abundance data (Jost et al. 2011). We tested for correlations of the ordination axes with canopy openness, vegetation complexity, litter and deadwood cover as environmental vectors using distance-based redundancy analysis (Legendre and Anderson 1999), and region, site and stand type as environmental factors using permutational multivariate analysis of variance using distance matrices (Anderson 2001) in the *vegan* R package. Lastly, the indicator values (IndVal) per region, site, and stand type, for all spider species and guilds were calculated using the IndVal procedure (Dufrêne and Legendre 1997). We used significant IndVal values > 0.25 as a threshold (Dufrêne and Legendre 1997). All analyses and figures were made in R 4.0.2.

Results

We captured a total of 21,911 spiders, 16,213 (74%) of which were adults, belonging to a total of 130 species. Sheet web weavers dominated with 9896 adult individuals belonging to 44 species, followed by ground hunters (2729 individuals belonging to 19 species) and other hunters (2650 individuals belonging to 44 species) (Table S2). By far the most abundant species was the agelenid sheet web weaver *Coelotes terrestris* with 3851 individuals (24% of all adult spiders; Table S2). Of the recorded species, two were in the Red List of German spiders (Blick et al. 2016): *Walckenaeria mitrata* labeled with G (Endangerment of unknown extent) and *Xysticus luctuosus* labeled with 3 (Endangered) (Table S3). Of the total catch, 107 species with 15,897 individuals (98% of all adults) were typical forest species. Forest specialist species patterns were highly correlated with the overall catch for all metrics ($r > 0.75$, $P < 0.001$) and thus we only tested patterns in the overall catch. Some exceptions are discussed in the discussion.

Effects of stand type and region

Stand type influenced microhabitat characteristics, with canopy openness being highest in both conifer monocultures (Table S4).

Regarding spider response variables, both region and stand type had significant effects (Table 2, S5-6). In terms of regional effects, spider abundance (Fig. 1 A) and biomass per trap/day (Fig. S3A), as well as spider CWM biomass (Fig. S3B) were higher in the southern sites than in the northern sites (Table 2, S5-6). Concerning stand type effects, spider abundance and biomass per trap day, CWM biomass, Hill numbers 1 and 2, as well as FDiv, FEve and FDis were not significantly different between stand types (Table 2, S5-6). On the other hand, both conifer monocultures harbored higher spider functional richness (FRic) than European beech monocultures (Fig. 1B; Table 2, S5-6). Rank-abundance curves showed that abundance distributions differed to some extent among the stand types, with beech monocultures and the mixtures tending to show a slightly more even distribution with lower dominance of the most abundant species, especially in comparison to Norway spruce monocultures (Fig. 1 C; Table 2, S5-6).

Effects of plot characteristics

Models using plot characteristics including tree diversity, tree proportions and microhabitat characteristics (Table S7), explained a higher variance (R^2) on average but had a consistently lower model fit (AICc). The only exception to this pattern were models where spider species richness (Hill number 0) was used as a response, where models using plot characteristics also had a higher model fit (Table S6-7).

Conifer tree proportions significantly influenced spider response variables (Table S7). Increasing Douglas fir proportion promoted spider abundance (Fig. 2 A) and biomass (Fig. S4A) per trap/day, as well as functional richness (Fig. 2B). Moreover, increasing Norway spruce proportion promoted spider species richness (Hill number 0) (Fig. S4B) and functional richness (Fig. S4C) in the northern plots. Lastly increasing the proportion of both conifers resulted in less functionally divergent spider assemblages (Fig. 2 C).

Table 2 Overall effects of individual factors (stand type, region and their interaction) on spider abundance, biomass and diversity based on mixed-effects model analyses. Statistically significant relationships indicated in bold

	Log (Spider abundance per trap/ day+1)			Log (Spider biomass per trap/ day+1)			Log (Hill number q=0 +1)			Log (Hill number q=1 +1)					
	x ²	Df	P	x ²	Df	P	x ²	Df	P	x ²	Df	P			
Stand type															
Region	19.002	1	<0.001	32.613	1	<0.001	6.678	4	0.154	2.365	1	0.124	3.197	1	0.073
Stand type: Region							9.047	4	0.060						
							FRic						FDiv		
							x ²						x ²		
Stand type	2.466	1	0.116				16.105	4	0.003						
Region				31.037	1	<0.001							2.323	1	0.128

Furthermore, microhabitat characteristics influenced spider response variables (Table S7), with stands with higher canopy openness having lower spider abundance (Fig. 2D) and biomass (Fig. S4D) per trap/day, but higher spider diversity (Hill number 0–2) (Fig. 2E, Table S8) and functional dispersion (Fig. S4E). Additionally, canopy openness had a marginally significant effect ($p=0.073$) on functional richness in our models, which became significant ($p=0.038$) when only canopy openness was included in the model. On the other hand, stands with higher litter cover had higher spider abundance (Fig. S4F) and biomass (Fig. S4G) per trap/day, but lower spider functional evenness (Fig. S4H). Lastly, sites with more deadwood cover had lower richness of dominant species (Hill number 2) (Fig. 2 F).

Spider community structure

Using dbRDA we analyzed how region, site and stand type affected spider community assemblages, and checked if any species or guilds were closely connected to a specific region, site or stand type with IndVal analysis (Fig. 3; Table S8–9). In terms of species composition, there was a significant difference in assemblages among different regions and sites (Table S9). The southern sites were dominated by larger, more abundant sheet web builders (IndVal=0.613, $p=0.001$), while the northern sites were dominated by the relatively smaller and less abundant ground (IndVal=0.639, $p=0.001$) and ambush hunters (IndVal=0.589, $p=0.001$). *Coelotes terrestris* (sheet web builder) with 3851 individuals was the most dominant in the southern plots (IndVal=0.794, $p=0.001$), while *Tenuiphantes flavipes* (sheet web builder) with 1644 individuals was the most dominant in the northern plots (IndVal=0.949, $p=0.001$). Furthermore, other species and guilds had high indicator values for different regions, sites, and stand type (Table S8). Moreover, there was a regional difference in the species habitat preference, with more forest specialists in the southern plots (IndVal=0.576, $p=0.001$) and more species with no strict preference for forests or open habitats in the northern plots (IndVal=0.949, $p=0.001$; Table S8). Concerning stand types, stands containing Douglas fir were the only ones harboring spider species with high indicator values, with *Diplocephalus latifrons* (IndVal=0.386, $p=0.001$) and *Walckenaeria atrotibialis* (IndVal=0.256, $p=0.001$) being indicators for Douglas fir monocultures, while *Pardosa saltans* (IndVal=0.260, $p=0.041$) was an indicator for European beech/Douglas fir mixtures (Table S8). In terms of stand types, species with no strict habitat preference dominated in Douglas fir monocultures (IndVal=0.333, $p=0.025$), while forest specialists with no strict preference for closed or open forests dominated in European beech monocultures (IndVal=0.357, $p=0.029$).

Discussion

Contrary to our expectations, stands with higher local proportions of Douglas fir promoted epigeal spider activity density. Stands with higher proportion of both conifers harbored assemblages with higher functional richness but lower functional divergence. Moreover, regional differences in environmental conditions modified tree identity effects on spider diversity and were the most important factor in structuring spider assemblage structure. Local environmental context, especially canopy openness and litter cover, further modified spider diversity but played a less significant role than tree identity. Overall, our findings

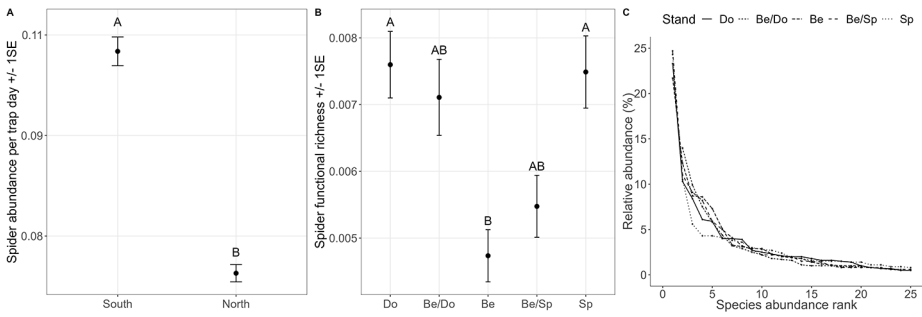


Fig. 1 Effects of region (North and South) and stand type (Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture) on spider abundance and functional richness based on results of linear mixed effects models. Differences in mean \pm SE abundance (A) per trap day. Differences in mean \pm SE spider functional richness between stands (B). Rank-abundance distribution of spider assemblages of different stand types (D). Significant differences calculated with a post hoc test of estimated marginal means with significant differences marked with different letters. X axis of panel C truncated at 25 to better see differences between stands. Note that the response variables for panel A and B were log + 1 transformed to improve model fit, and the Y-axes show back-transformed values

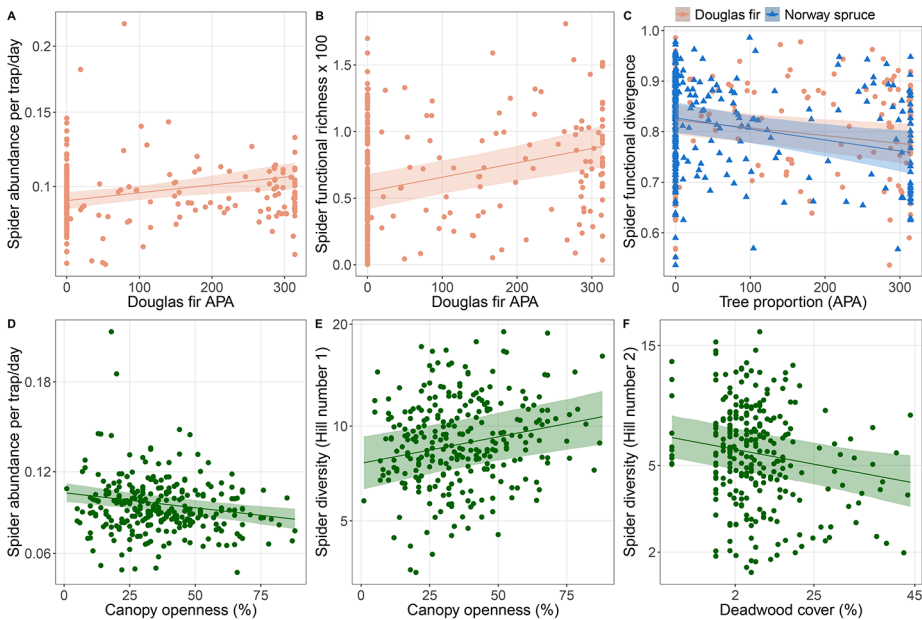


Fig. 2 Effects of local (10 m radius around traps) conifer proportions and microhabitat characteristics on spider abundance, taxonomic and functional diversity. Based on results of linear mixed effect models. Differences in spider abundance per trap/day (A) and functional richness (B) in plots with different Douglas fir proportion, as well as spider functional divergence (C) in plots with different proportions of both conifers. Differences in spider abundance (D) per trap/day, and spider diversity (Hill number 1) (E) in plots with different canopy openness. Differences in spider diversity (Hill number 2) (F) in plots with different deadwood cover. Bands represent 95% confidence intervals. Y-axis values show data adjusted for covariates in the final mixed models for panels A, D, E. Note that the response variables in panels A, D-F were log + 1 transformed to improve model fit. Furthermore, deadwood cover was log (x + 1) transformed. X and Y-axes show back-transformed values

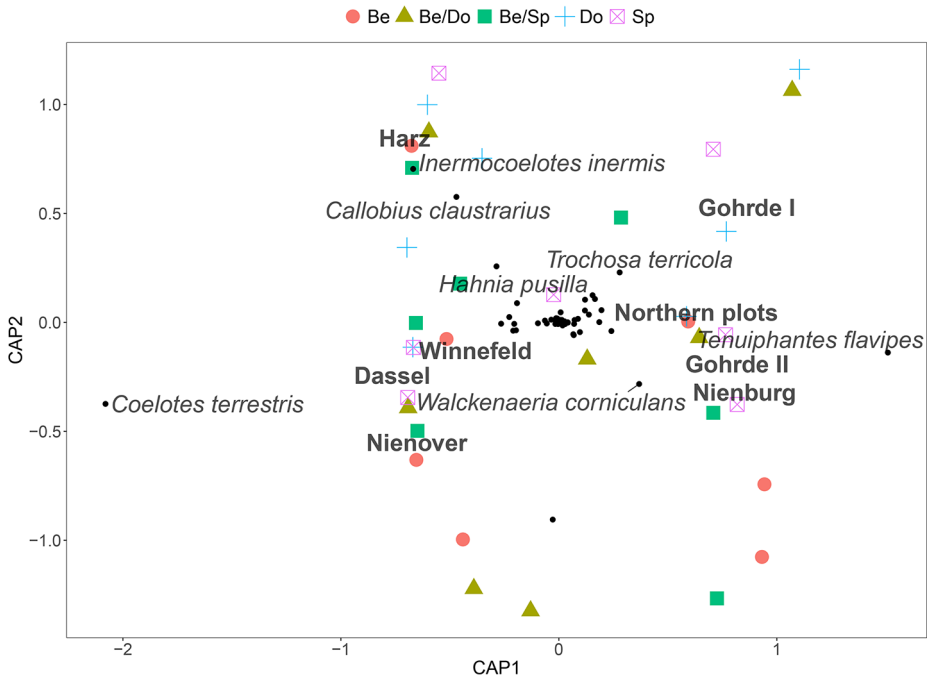


Fig. 3 dbRDA ordination plot (Morista-Horn index) of spider species across 35 study plots, grouped by stand type (Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture). Species are represented by black points. Only species with IndVal values > 0.5 for region or site are labeled with their names in italics. Bold text labels represent significant ($p < 0.05$) effects of site and region

suggest that increasing Douglas fir utilization in Central European forests does not necessarily negatively affect the biodiversity of epigeal spiders and may even potentially benefit spider-associated top-down control. However, it is important to note that forest specialists were particularly associated with native European beech monocultures, highlighting the role of beech forests for biodiversity conservation.

Tree identity effects depend on spatial scale

As expected, tree identity had a stronger impact on spider activity density and diversity than tree diversity (Oxborough et al. 2012; Oxborough et al. 2016). Additionally, no difference between monocultures and mixtures was registered. Differences between monoculture stand types were much more pronounced than differences between monocultures and mixtures. The main difference was that functional richness was significantly higher in conifer monocultures than in native European beech monocultures. This could be a result of the dense beech canopies during the summer which can lower habitat diversity via lower variability in insolation, microclimate and herb layer vegetation (Michalko et al. 2021). Thus, these dense beech canopies can have a negative effect on the functional diversity of arthropods (Perry et al. 2018).

Interestingly, the registered effect of Norway spruce on functional richness was present only in the warmer (lower elevation), nutrient poor northern sites. In general, several of the effects we observed on spider diversity and abundance were strongly affected by study region. This is particularly an issue when it comes to evaluating the ecological effects of Douglas fir in Europe, as many studies investigating how this tree species affects biodiversity were strongly limited in their geographic extent (Finch and Szumelda 2007; Ziesche and Roth 2008; Matevski and Schuldt 2021). Our study design, with sites distributed across a wider environmental gradient, therefore provides a more comprehensive picture on how and under which environmental conditions Douglas fir influences biodiversity. Potentially, the regional effects we observed could again, at least in part, be related to canopy openness and its effects on forest floor environmental conditions, as the difference in canopy openness between Norway spruce and European beech monocultures was only significant in the north (Table S10) and canopy openness had a positive effect on all measures of spider species diversity (Hill numbers 0–2). The difference in canopy openness between the regions could be due to higher drought stress in the warmer, drier northern region (Table S11), as drought stress has been connected to lower canopy closure in forests (Pfeifer et al. 2019).

Unlike the plot-level, where Douglas fir had no significant effect on spider activity density, increasing local Douglas fir proportion (tree proportions in a 10 m radius around each trap) promoted spider activity density. This cannot be attributed to an expected positive effect of canopy openness on spider activity density (Košulič et al. 2016), as results of local canopy openness showed the opposite effect on abundances and local Douglas fir proportion and local canopy openness were not highly correlated (Pearson's $r=0.148$; $p<0.001$). As this result is not related to any environmental variable we measured and was only present at the local scale, further research on Douglas fir's effects on local environmental variables is necessary to understand this species' effects on local spider activity density. These abovementioned differences in results from the plot and local scale indicate that integrating biodiversity concerns into forest management can benefit from the consideration of multiple spatial scales.

Our results of plot-level increases in spider diversity and local-scale increases in abundance with higher Douglas fir proportions add to recent research on the same study sites showing beneficial effects of Douglas fir on ground beetle diversity and top-down control (Kriegel et al. 2021; Matevski et al. 2021), especially in monocultures. Such results indicate that planting Douglas fir is not necessarily detrimental to the diversity of such forest floor-associated taxa, even when this tree species is planted in monocultures. However, these results should be tempered with the fact that planting Douglas fir in mixtures with phylogenetically distant tree species such as European beech has some potential benefits when it comes to other ecosystem functions. These include overyielding (Thurm and Pretzsch 2016) and herbivory reduction (Matevski et al. 2022).

Lastly, functional divergence was lower in stands with higher local conifer proportion showing that, even though increasing local conifer proportion benefits the overall trait richness of spiders, the trait space becomes more dominated by species with similar traits. These findings suggest that while coniferous stands might accumulate functionally different species, many of these are rare occurrences and the dominant species are functionally rather similar. Previous studies have suggested that non-native tree species and species planted outside their natural range (as is the case for Norway spruce in our study, as it would naturally only occur at higher elevations outside our study region) can lead to functional homog-

enization of animal communities because it is easier for generalist species to adapt to such tree species (Pereira et al. 2012; Gossner 2016, Schuldt et al. 2022). Thus, planting both conifers in mixtures with European beech could preserve the biodiversity of forest specialists and reduce functional homogenization.

Local habitat context differentially affects spider diversity and activity density

Some tree identity effects, such as the conifer effect on spider functional richness and Norway spruce effect on species richness (Hill number 0), could be better attributed to micro-habitat characteristics such as local canopy openness. Local canopy openness consistently promoted spider taxonomic (all Hill numbers) and functional richness (marginal effect, $p=0.073$). Furthermore, it promoted functional dispersion and had a marginally positive effect on functional evenness ($p=0.058$) showing that increasing local canopy gaps would promote most aspects of spider taxonomic and functional diversity. This is concordant with recent research showing that increasing canopy openness in stands promotes spider taxonomic and functional richness, as increasing canopy gaps improves niche variability due to increased environmental heterogeneity (Vymazalová et al. 2021).

On the other hand, increasing local light availability led to a decrease in spider activity density. Furthermore, litter cover had a negative effect on the activity density of spiders with no strict preference for forests or open habitats (Table S12). Additionally, the effect of local litter cover on abundance was present only in the southern sites due to a dominance of sheet web weavers that benefit the most from increased local litter cover (Roberts 1993), emphasizing the role of litter cover. This dominance of one functional group of spiders is also the reason for the negative effect of local litter cover on functional evenness in the southern sites. Lastly, local fine deadwood cover had a negative effect on spider species richness, when taking into account the most abundant species (Hill number 2). As most measures of diversity were higher in more open stands, it makes sense that they would be negatively affected by forest-related variables such as fine deadwood cover (Oxbrough et al. 2005), although previous research has shown that such fine deadwood can increase the abundance of individual spider species (Castro and Wise 2010).

The contrasting response of spider activity density and diversity to open and forest-associated variables shows a tradeoff, with taxonomic and functional diversity being higher in open stands with less fine deadwood cover, while stands with higher canopy closure and litter cover had higher spider activity density. Therefore, thinning forest stands and increasing canopy gaps could promote spider diversity, while managing forests with higher canopy closure would promote spider activity density.

Community structure is mostly affected by regional differences

Spider community structure was mostly influenced by large scale differences in environmental conditions (climate, soil quality). The colder, nutrient rich southern sites harbored more and larger spiders, while the warmer, nutrient poor northern sites harbored smaller, less abundant spiders. Sheet web weavers and forest specialists dominated in the south, while the north was dominated by ground hunters and species with no strict preference for forests or open habitats. Between-stand differences in community structure were not pronounced, with differences between coniferous monocultures and other stands being larger

in the northern than the southern sites. This could be a result of larger differences in canopy openness between coniferous and other stands in the north, as canopy openness has been shown to explain most of the variation in spider community structure (Ryndock et al. 2012; Košulič et al. 2016). However, spiders with different habitat preferences preferred different stand types. Douglas fir monocultures only benefited species with no strict habitat preference, while native European beech monocultures benefited forest specialists with no preference for open or closed forests. These results suggest that planting Douglas fir in mixtures with European beech could temper any negative effects on forest specialist spiders.

It is important to note that our study is based on relatively small plots (0.25 ha) within larger forest expanses, which are a mix of European beech and coniferous patches at the landscape scale. Such a composition might allow exchange and dispersal between different stand types and could contribute to the small observed differences among stand types for many of the response variables including community composition. This means that although our results are valid for Central European Forest management, further research is required to test how large-scale monotonous conditions of pure conifer stands would affect local spider communities and whether similar or deviating patterns are found in the forest canopy, which might be a less contiguous habitat for spiders than the forest floor.

Conclusion

Contrary to our expectations, Douglas fir, especially local Douglas fir proportion within stands, promoted epigeal spider diversity and activity density in both northern and southern plots. Our findings presented here, alongside other research that showed positive effects of Douglas fir on carabids (Kriegel et al. 2021) and prey caterpillar attack rates at the same study sites (Matevski et al. 2021), indicate that increasing Douglas fir utilization is not necessarily detrimental to forest floor-associated generalist predators and might potentially promote their top-down effects. Norway spruce had similar effects on spider diversity, but only in the warmer, nutrient poor northern sites. This finding, alongside litter cover effects being present only in the southern sites, suggests that regionally different approaches are necessary to promote spider diversity and abundance. In addition to litter cover, other forest-associated local microhabitat characteristics, that can be altered with forest management, such as local canopy openness and fine deadwood cover, emerged as additional predictors of spider diversity and activity density. Our findings suggest that increasing Douglas fir utilization at the expense of Norway spruce may not negatively affect overall species numbers and activity density of ground-living arthropod predators. At the same time, we identified an important role of native beech for functional divergence and community composition of typical forest spiders. Therefore, the consequences of increased utilization of non-native trees such as Douglas fir needs to be looked at not only through the lens of climate adaptability and other potential benefits such as increased top-down control. We should also be cognizant of probable loss of native arthropod fauna, especially specialists, since non-native trees such as Douglas fir harbor a low diversity of herbivorous arthropods and feature, in general, mostly generalist and common arthropod species (Schmid et al. 2014). Thus, planting Douglas fir at low proportions in mixtures with native European beech may be a more secure option than monocultures when considering the conservation of specialist spiders.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-023-01233-1>.

[org/10.1007/s10531-023-02547-5](https://doi.org/10.1007/s10531-023-02547-5).

Author contributions AS conceived the research, DM collected, processed, analyzed the data, and drafted the initial version of the manuscript, with AS substantially contributing to later versions of the manuscript.

Funding D.M. acknowledges funding by Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 316045089/GRK2300.

Open Access funding enabled and organized by Projekt DEAL.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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