

Trait diversity and spider community composition are associated with lower herbivory in young forest plantations

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HIGHLIGHTS

- Spiders can reduce forest pests and herbivory.
- Forest pest suppression by spiders could be context-dependent.
- The effect of spiders can depend on pest type, herbivory, forest type, and season.
- Spider diversity and community composition are crucial for forest pest suppression.

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ABSTRACT

Spiders constitute a numerically dominant group of generalist predators in forest ecosystems, but their biocontrol function in forest plantations is not well understood. The biocontrol potential of spiders may depend upon interaction among pest type, forest type, season, trait composition, and spider community diversity. Using a correlative approach, we addressed this gap in knowledge in young (10–15 years) oak (*Quercus* spp.) and ash (*Fraxinus* spp.) forest plantations. We sampled (N = 103 samples) foliage-dwelling arthropods and leaves during late spring and autumn. We then measured traits of spiders (body size and hunting strategy) and examined two indicators of herbivory (leaf damage and leaf dry biomass). In oak plantations, abundances of Hemiptera negatively correlated with functional diversity of spiders consistently during the two seasons. Abundances of caterpillars negatively correlated with abundances of ambushers and marginally with abundances of orb-web building spiders during late spring. Abundances of herbivorous Coleoptera negatively correlated with functional evenness of spiders in autumn. Moreover, herbivory negatively correlated with abundances of Space-web builders and functional diversity of spiders in spring but with mean spider body size in autumn. In ash plantations, herbivory negatively correlated with spider abundances in autumn. Our findings provide indirect evidence that foliage-dwelling spiders can be useful for the biological control of forest pests. The biocontrol potential of spiders seems to depend on both functional diversity and identity. Therefore, forest pest management should focus not only on spider community composition but also functional trait diversity of spiders.

1. Introduction

Forests harbour the majority of Earth's terrestrial biodiversity (Harrison et al., 2022) and play a crucial role in the provisioning of ecosystem functions and services, including biological control of pests (Brockhoff et al., 2017). Forest covers today face deforestation, degradation, and fragmentation due to human activities (FAO, 2016), leading to biodiversity loss and changes in the forest (Foley et al., 2005;

Seibold et al., 2019). Methods of sustainable forest management (SFM) are being implemented in planted forests worldwide with the goals, among others, to conserve and restore biodiversity while sustaining high productivity for future needs. Commercial forest plantation involving monocultures or polycultures of various tree species on degraded land can be consistent with SFM (Chazdon, 2008). Most forest plantations are intensively managed through such various silviculture practices as site preparation, thinning, and harvesting (Brockhoff et al., 2008). As a

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result of forest management, a shift in community structure of invertebrate predators has been observed for various taxonomic groups (Niemelä et al., 1996; Paillet et al., 2010; Košulić et al., 2021). To achieve the goals of SFM, there is great need to understand the consequences of these alterations for ecosystem functioning and services.

There is increasing evidence that functional composition and diversity in a community can help to predict further impact on processes shaping the ecological dynamics (Cadotte et al., 2011; Mason & de Bello, 2013; Gagic et al., 2015). Functional community composition can be characterized by the relative and/or absolute abundances of functional groups and by community weighted mean, which is quantified as the mean value of a trait weighted by the species' relative abundance in a community (Lepš et al., 2006). Functional diversity consists of several primary components that, when examined collectively, provide valuable insights into community structure (Mason et al., 2005). Foremost among these is the RaoQ index, which is measured as the mean trait dissimilarity between each pair of species in a community weighted by their relative abundances (de Bello et al., 2016). Second, functional evenness is expressed as the regular distribution of species traits in the functional niche space. Finally, functional divergence index refers to the extent to which the distribution of species abundances maximizes divergence in functional traits within a community (Mason et al., 2005). The ability of these indices to predict ecological functions and services of communities of generalist predators in forest plantations, however, remains poorly understood.

Spiders are among the most abundant and diverse predators across terrestrial ecosystems, including forest habitats (Nyffeler & Sunderland, 2003; Gallé et al., 2017). Although spiders play a significant role in decomposition, nutrient fluxes, and productivity in forest ecosystems (Strickland et al., 2013; Liu et al., 2015), their biocontrol potential in forest plantations is unknown (Nyffeler & Benz, 1987; Michalko et al., 2019a). In agroecosystems, meanwhile, the matter of biocontrol of pests by spiders remains controversial because not only positive effects but also negative and neutral effects have been reported (Michalko et al., 2019a,b). Spiders use a wide variety of hunting strategies (Nyffeler, 1999; Cardoso et al., 2011) and vary in body size (Mammola et al., 2017), and these variations in both traits ensure differential utilization of diverse prey types (Birkhofer et al., 2022). It is therefore possible that spiders' biocontrol potential will depend on the functional composition and diversity of a spider community as defined by body size and hunting strategy (Jonsson et al., 2017; Michalko et al., 2019b).

Body size has received much attention for how it determines the strength of interactions between predators and prey within food webs (Rusch et al., 2015; Jonsson et al., 2017; Michalko et al., 2017). For example, variation in predator body size can promote intraguild predation among predators (Jonsson et al., 2017), because smaller predator species can serve as intraguild prey for larger predators (Birkhofer et al., 2008). A shift in body size distribution in spider community can also influence predator-prey interactions as body size determines a spider's prey size, prey type, and per capita capture rate (Nentwig & Wissel, 1986; Pekár et al., 2015; Birkhofer et al., 2022). Another important functional trait in spiders is hunting strategy, and this also can determine pest control services provided by spiders (Michalko & Pekár, 2016; Kersch-Becker et al., 2018; Birkhofer et al., 2022). For instance, web-building spiders are more effective in capturing a highly mobile prey while hunting spiders are more effective in capturing an immobile prey (Nyffeler 1999; Michalko & Pekár, 2016). Spiders' hunting strategies can therefore alter their efficiency in suppressing different pest groups.

Foresters are most interested in whether spiders can reduce damage to trees and not just in the potential to decrease the density of pests. Lower pest densities might not necessarily translate into diminished tree damage because there exist several factors that can prevent that from occurring (Burghardt & Schmitz, 2015). Among these factors, for example, are food-chain length and trees' defensive mechanisms against herbivores (Paine, 1980). For instance, plants can be tolerant to herbivory and produce biomass faster than herbivores are able to consume

it (Burghardt & Schmitz, 2015). In such a case, there would be no trophic cascade (Burghardt & Schmitz, 2015). On the other hand, the impact of spiders can even increase down through the food chain and spiders can have relatively stronger indirect effect on plants than on pests (Michalko et al., 2019a). This can happen when spiders exert not only consumptive effect on pests but also non-consumptive effect and reduce pests' feeding rates (Bucher et al., 2014).

The impacts of spiders on herbivores and herbivory may vary among plantation types. Different tree species can, for example, differ in bark structure. More complex bark structure can serve as microhabitat, source of alternative prey, and refuge from predation (Sunderland & Samu, 2000; Gratton & Denno, 2003), and this can weaken antagonistic interactions among spiders while increasing their pest suppression efficiency (Langellotto & Denno, 2006). A study by Michalko et al. (2021) highlighted that different forest types varied not only by the prey composition of spiders but also by spiders' effectiveness in capturing specific prey types. Changes in the functional structure of a spider community can therefore have a substantial impact on the functioning of forest ecosystems (Sanders et al., 2015).

Using a correlative approach, we investigated how functional diversity and composition of spider communities affect suppression of herbivores and herbivory in young oak and ash plantations. We expected that i) spider community will suppress herbivores and this will consequently translate into lower herbivory. We further hypothesized that ii) suppression efficacy of spider communities will be associated with both functional identity as well as diversity (Gagic et al., 2015). With regard to functional identity, we specifically expected that iii) spiders with different hunting strategies will be efficient in suppressing different herbivore groups because their capture efficacy is varied among different prey types (Michalko & Pekár, 2016). We also expected that iv) the pest suppression efficacy of a spider community will improve with increasing mean body size because larger spiders have higher capture rates (Rusch et al., 2015). With regard to functional diversity, we expected that v) suppression efficacy will increase with measures of functional diversity as niche complementarity among predators boosts their suppression efficiency (Gagic et al., 2015; Greenop et al., 2018).

2. Material and methods

2.1. Study site

The study was conducted within an area of floodplain forest in the vicinity of Vranovice (48°57'57 N, 16°36'23E; Fig. 1), a municipality in the South Moravian Region of the Czech Republic. This territory belongs to the Pannonian bioregion and its altitude ranges between 170 and 360 m. The average annual temperature is within the range 8–10 °C and the mean annual precipitation is between 450 and 500 mm. The studied site is mainly covered by hardwood floodplain forest (*Fraxino pannonicae-Ulmetum* vegetation type). The studied plots were in young oak (*Quercus robur*) and ash (*Fraxinus excelsior*) plantations (10–15 years of age).

2.2. Sampling Design

Sampling was performed twice, once during late spring (from the middle to the end of June 2019) and once in autumn (start to middle of October 2019). Four stands per each forest type were selected. In each oak stands, 9–11 samples were randomly collected during late spring (N = 40) and three to four samples during autumn (N = 14). In each ash stand, 6–10 samples were randomly collected during late spring (N = 35 samples) and two to four samples during autumn (N = 14 samples). A sample was uniformly created by 10 s of beating branches of a single tree. Beating was performed over a sheet of standardized size (surface: 1 × 1 m). All collected arthropods were preserved in 75 % ethanol. To estimate herbivory, 10 compound leaves of ash and 10 leaves of oak were picked randomly from the beaten branches in each sample, then dried and preserved in the laboratory.

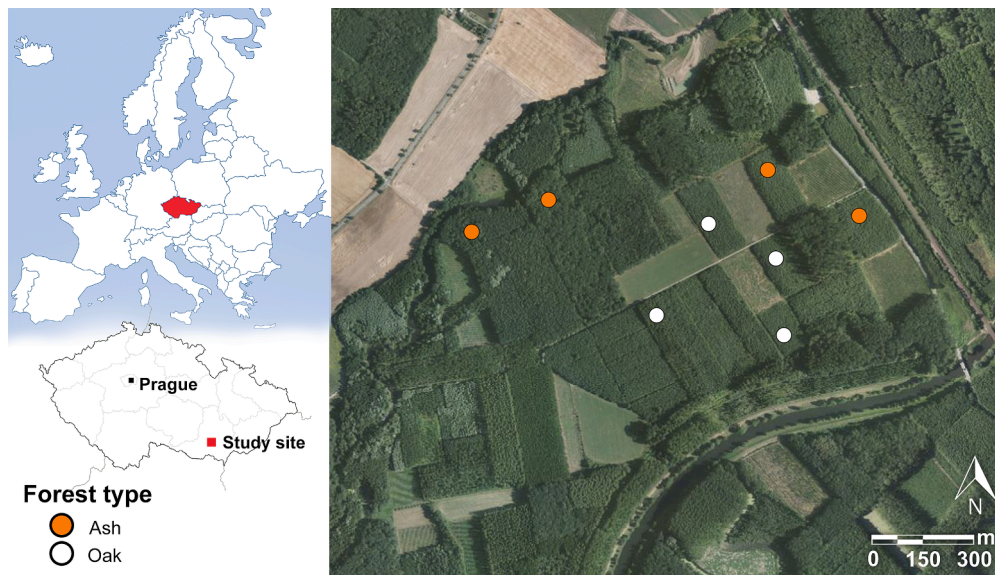


Fig. 1. Location of site and area of selected stands.

2.3. Arthropod identification

We determined all arthropods using a dissecting microscope. Insects were determined to order or suborder level. Those insect groups including both herbivores and predators (e.g. Hemiptera, Coleoptera, and Hymenoptera) were identified to such level that enabled identification of their trophic groups. We also distinguished larval vs adult stage in holometabolic insects because different life stages may be exposed to different predators. There were only three predator groups with sufficiently high abundances to enable statistical evaluation, namely spiders, ants, and earwigs. We treated predator groups (spiders, earwigs, and ants) separately in all analyses due to their different degrees of omnivory. Each individual spider was identified to the lowest possible level, meaning species (adults) or genus (juveniles) (Nentwig et al., 2018). In each spider individual, we also noted body size (carapace length and width; precision 0.01 mm) and hunting strategy (hunters, ambushers, orb-web spiders, space-web spiders, and sheet-web spiders; Cardoso et al., 2011) as functional traits.

2.4. Herbivory estimation

We estimated two indicators of herbivory – percentage leaf damage and dry leaf biomass – that can provide complementary insight on the effects of herbivores with different feeding strategies (i.e. chewing vs. sap-feeding insects; Zvereva et al., 2010; Johnson et al., 2016). We used a standardized method to quantify leaf damage (Johnson et al., 2016). We visualized 10 leaves of oak per sample ($N = 480$ leaves / season) and 30 leaflets of 10 ash leaves per sample ($N = 1440$ leaflets / season). The percentage damage of an oak leaf was quantified as follows: The leaf was divided into 3 parts and the percentage damage in each part was estimated visually. The damage per oak leaf was then taken as the average percentage damage across the three parts (Johnson et al., 2016). The percentage damage of an ash compound leaf was quantified as the average damage across three randomly selected leaflets from the compound leaf (Johnson et al., 2016). A digital milligram scale was used to weigh leaf biomass with precision of 0.1 mg. The biomass was measured by weighing 30 small dried leaflets from 10 ash compound leaves and 10 dried leaves of oak per sample. To obtain the dry leaf biomass, we weighed whole leaves or leaflets.

2.5. Statistical analyses

All statistical analyses were performed within the R environment (R Core Team, 2022). First, we computed the sample coverage to estimate the sampling completeness of spider genera using the R package “iNEXT” (Hsieh et al., 2016). As both, diversity and community composition are important for top-down control, we investigated the effects from various measures of these two community components. As measures of diversity, we used genus richness (number of spider genera), functional diversity (Rao index), functional evenness (FEve), and functional divergence (FDiv) of spiders. The indices of functional diversity were computed using the R package “FD” (Laliberté et al., 2014). The community composition was investigated by means of abundances of all spiders, abundances of particular spider hunting strategies, and mean body size within a spider community. We also included abundances of earwigs and abundances of ants in the analyses to account for the presence of other arthropod predators. Beside spiders, earwigs and ants were the most abundant arthropod predators in the canopies of the studied plantations.

The functional traits to measure the functional diversity and composition of spider communities were hunting strategy (see 2.3., Arthropod identification) and body size of spiders. To reduce dimensionality, we conducted principal component analysis using two measures of spider body size (carapace width and length) and extracted coordinates of each individual on the first axis. We then used the coordinates to compute indices of functional diversity and mean body size in spider communities.

Before running the structural equation models (SEMs), we pre-selected the potential links by performing piecewise correlation using the Spearman coefficient (Table S2-9). As we were interested in the biocontrol potential of predators, we selected only those moderate and strong correlations ($r > 0.30$; Cohen, 1992; Nakagawa, 2004) indicating top-down control. Top-down control of herbivores by predators was indicated by negative correlation, top-down control of plants by herbivores was indicated by positive correlation with leaf damage and negative correlation with biomass, and positive indirect effect of predators on plants was indicated by negative correlation with leaf damage and positive correlation with biomass. We then ran the SEMs using the preselected links to investigate top-down control of herbivores and herbivory by the arthropod predators. We ran four separate SEMs, one for each forest type and season. The piecewise SEMs were run in the R package “piecewiseSEM” (Lefcheck, 2016).

We used generalized linear mixed models (GLMM) or general linear mixed models (LMM) as the individual component models in the SEMs (Zuur et al., 2015). For leaf weight we used GLMMs with Gamma error structure and inverse link function (GLMM-g). For percentage damage, we used LMMs but the data were logit transformed to approach normal distribution of errors. For abundance data, we used GLMMs with Poisson distribution and log link function (GLMM-p) or negative binomial GLMMs with log link (GLMM-nb) if the data were overdispersed (Zuur et al., 2015). The nonsignificant links in the SEMs were removed by stepwise backward selection based upon critical values and the Akaike information criterion (AIC) and we present the most parsimonious model (Lefcheck, 2016). We tested the goodness of fit of the SEMs using the Fisher's C statistic and associated P-values. P-values > 0.05 indicate a good fit and that no potentially significant missing paths were excluded (Lefcheck, 2016). Data are available in (Khum et al., 2024).

3. Results

Overall, we collected 3162 arthropods (883 spiders, 196 ants, 124 earwigs, and 1959 primary consumers out of which 884 were herbivores) and 1920 leaves. Using beating as the collecting method, spiders were the most numerous predators in both forest types and during both sampling seasons (Fig. 2). The estimated sample coverage of spider genera was 98 % and 95 % for oak and ash stands, respectively

(Table S1). Ants were relatively numerous predators in oak plantations during spring season while earwigs were relatively numerous predators in oak and ash plantations during autumn (Fig. 2). Caterpillars and Hemiptera were numerous herbivores in oak plantations during spring (Fig. 2). Coleoptera were relatively numerous herbivores in both forest stands and during both sampling seasons (Fig. 2).

3.1. Oak plantations

The abundances of ants and earwigs did not strongly correlate with the indicators of herbivory and their abundances did not strongly correlate with the abundances of herbivores ($P > 0.05$; Table S2,3). The SEM model in oak plantations during spring had a good fit (Fisher's C = 24.0, df = 18, AIC = 52.0, $P = 0.155$; Fig. 3A). The various herbivorous groups and herbivory indicators were correlated with different diversity components and with different groups of spiders (SEM, $P < 0.051$; Fig. 3A). Overall leaf damage was negatively correlated with abundance of the space-web building spiders (SEM, $P = 0.036$; Fig. 3A) and functional diversity of spiders (SEM, $P = 0.025$; Fig. 3A). Abundance of Hemiptera was negatively correlated with functional diversity of spiders (SEM, $P = 0.014$; Fig. 3A). Abundance of caterpillars was negatively correlated with abundances of ambushers (SEM, $P = 0.012$; Fig. 3A) and marginally with abundances of orb-web building spiders (SEM, $P = 0.051$; Fig. 3A).

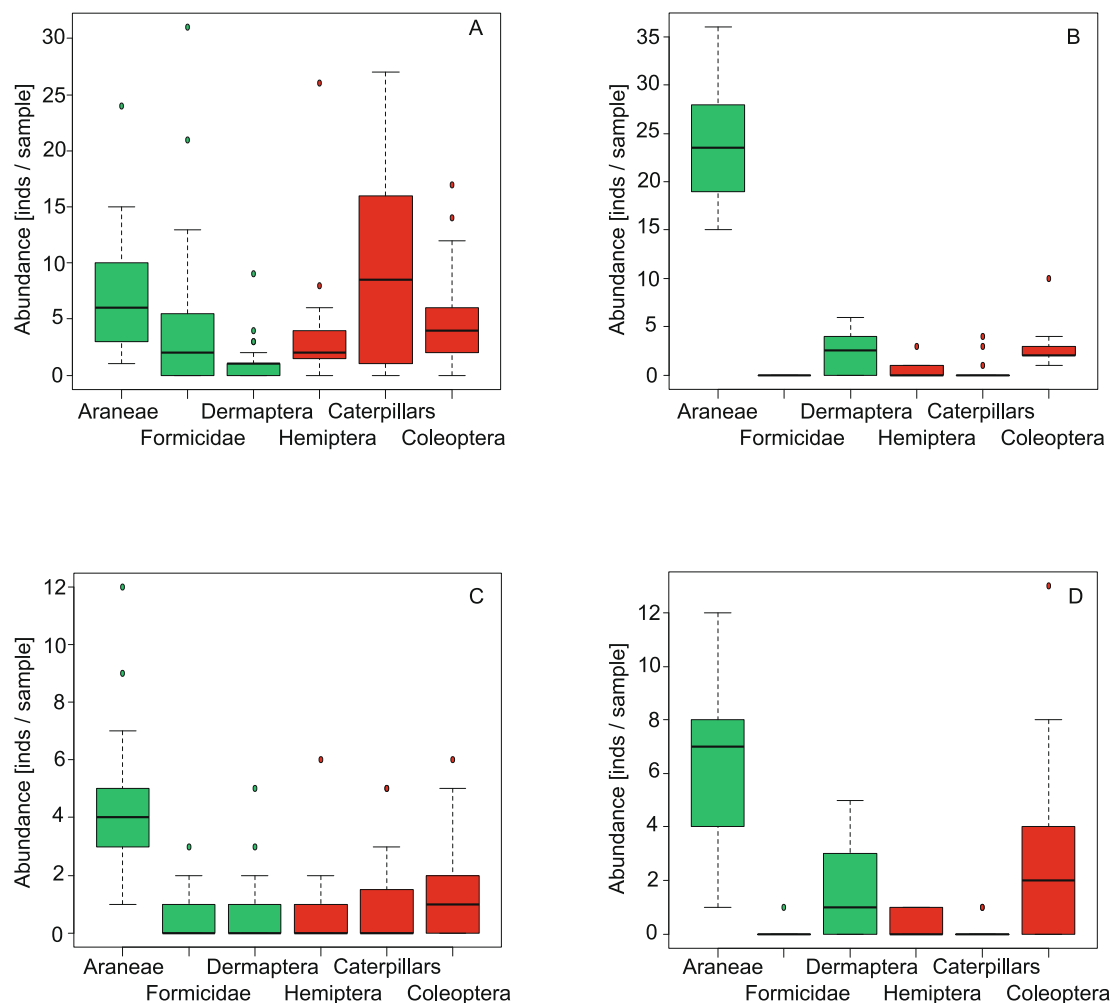
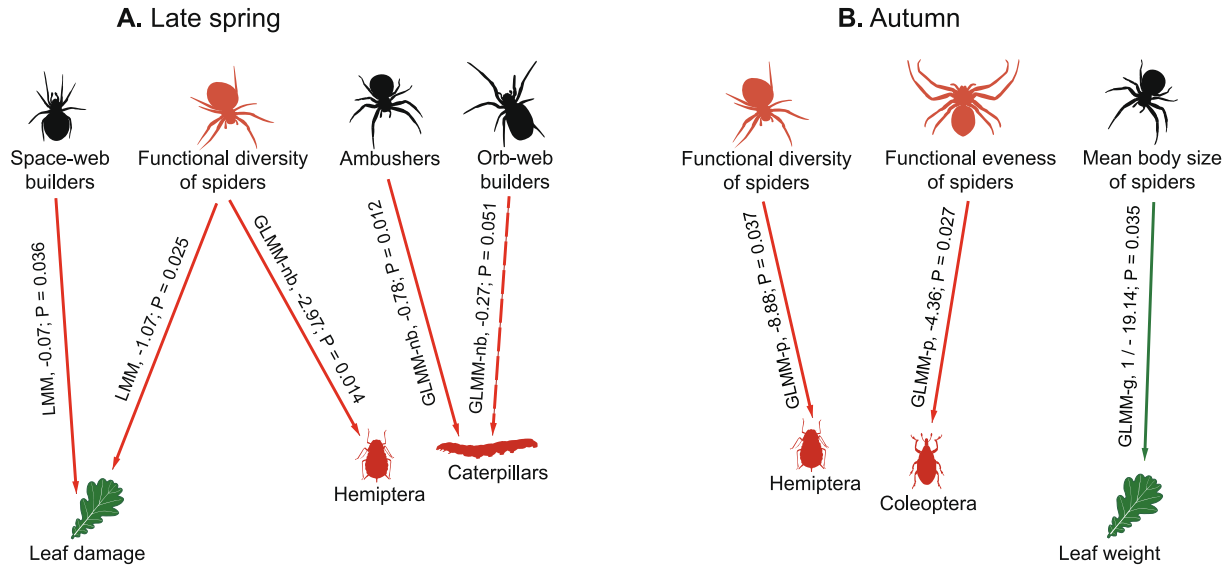


Fig. 2. The abundances of arthropod predators (green colour) and herbivores (red colour) in young oak (A,B) and ash (C,D) plantations during late spring (A,C) and autumn (B,D). The horizontal lines are medians, boxes are quartiles, whiskers are 1.5 times interquartile range, points are outliers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Oak plantations



Ash plantations

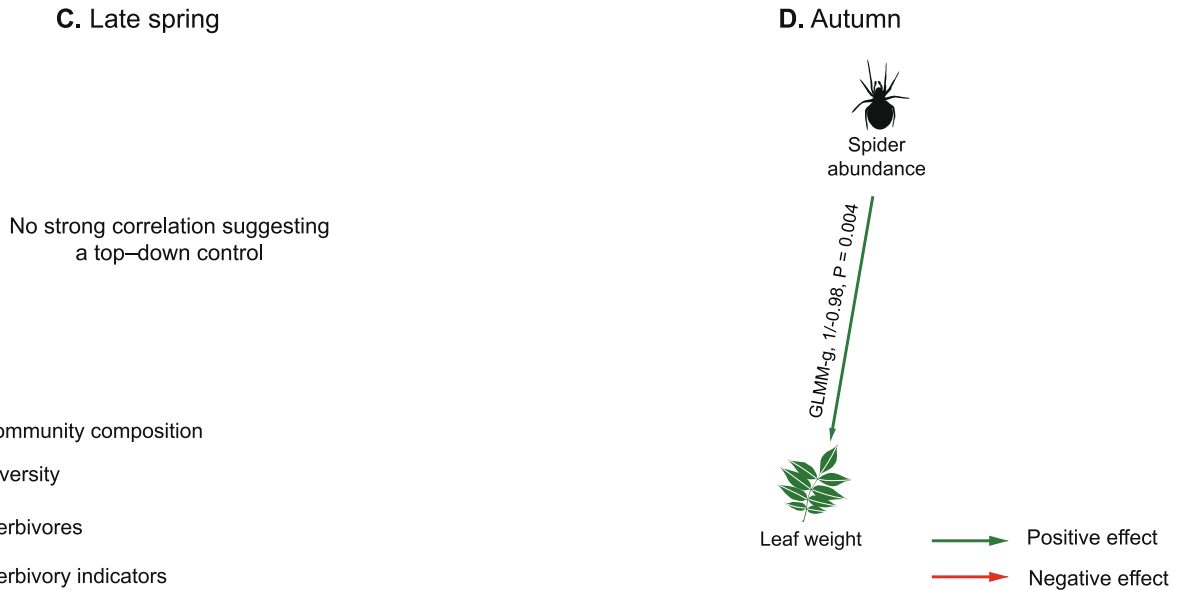


Fig. 3. Structural equation models investigating relationships between oak leaves, ash leaves, herbivores, and spiders in oak plantation (A, B) and ash plantation (C, D). Arrows point from explanatory to response variable. Different colours of significant variables indicate four different parameters, with black indicating community composition of spider, orange spider diversity, red herbivore abundance, and green herbivory. Arrow colours indicate statistical significance, with green signifying positive effect and red negative effect between variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In autumn, the model had a good fit (Fisher’s C = 18.8, df = 18, AIC = 38.8, P = 0.406). Only leaf weight as an herbivory indicator was positively correlated with increasing mean body size of spiders (SEM, P = 0.034; Fig. 3B). Abundances of Hemiptera were negatively correlated with increasing functional diversity of spiders (SEM, P = 0.037; Fig. 3B). Abundances of Coleoptera were negatively correlated with functional evenness of spiders (SEM, P = 0.027; Fig. 3B).

3.2. Ash plantations

In late spring, there was no strong correlation that would suggest a top-down control by spiders, earwigs, or ants (P > 0.05; Table S6,7). The SEM model investigating top-down control in autumn was just identified as saturated SEMs with zero degrees of freedom (SEM, Fisher’s

C = 0, df = 0, P = 1), as the only significant link suggesting a top-down control of herbivory was increasing leaf weight with increasing spider abundances (SEM, P = 0.004; Fig. 3D).

4. Discussion

Using a correlative approach, we investigated whether the functional diversity and composition of spider community, abundances of earwigs, and abundances of ants are correlated with lower abundances of herbivores and lower herbivory in young forest plantations, namely oak and ash. In accordance with our first hypothesis, we found that spiders had a potential to suppress pests and reduce herbivory in both forest types. There was no such correlation that would indicate a biocontrol potential of other dominant arthropod predators, namely earwigs and ants. In

accordance with our second hypothesis, the results indicate that both diversity and community composition of spiders significantly affected the potential of spiders to suppress herbivores and herbivory. We found support also for the third hypothesis that spiders' specific hunting strategies will differ in their efficiency for suppressing different herbivore groups, as abundances of orb-web builders and ambushers negatively correlated with abundances of caterpillars. Our fourth hypothesis was supported as leaf biomass positively correlated with body size of spiders in oak plantations during autumn. Our fifth hypothesis was also supported, as functional diversity of spiders was negatively correlated with abundances of Hemiptera and leaf damage, while functional evenness was negatively correlated with abundances of Coleoptera in oak plantations.

Abundances of caterpillars were negatively correlated with densities of ambush hunters and marginally also with orb-web building spiders in oak plantations during late spring. A previous study by [Marc and Canard \(1997\)](#) had found that caterpillars are mainly captured by cursorial spiders, including ambush species, in orchard trees. This may explain why ambushers decreased the abundance of caterpillars. On the other hand, abundances of Hemiptera and Coleoptera in the oak plantations were negatively correlated with overall functional diversity and functional evenness of spiders instead of with abundances of spiders having any particular hunting strategy. Hemiptera represents a substantial part of the diets of spiders across all hunting strategies ([Michalko & Pekár, 2016](#)) and with various body sizes ([Birkhofer et al., 2022](#)), while Coleoptera are important part of the diets of space-web building spiders and ambush hunters ([Michalko & Pekár, 2016](#)). Differences in hunting strategies and body size enable not only trophic niche separation but also microhabitat separation ([Cardoso et al., 2011](#)). This microhabitat complementarity among spiders with distinct hunting strategies and body sizes might facilitate predation on Hemiptera and Coleoptera ([Jonsson et al., 2017](#)).

There were several links connecting spiders directly to lower herbivory without interconnections to lower densities of herbivores. Spiders can influence prey not only through consumptive effects, whereby prey is utilized directly, but also through non-consumptive effects, where prey respond to predation risk ([Michalko et al., 2019b](#)). For example, herbivorous insects are known to decrease their foraging activity to minimize detection by spiders, and consequently this can lead to lower herbivory without an impact on pest densities ([Bucher et al., 2014](#); [Beleznai et al., 2015](#)). Similar to consumptive effects, non-consumptive effects were driven by spider community diversity as well as composition. During autumn in ash plantations, there was a positive correlation between spider abundances and plant biomass, probably because herbivores reduced their foraging in patches with higher predation risk. During late spring in oak plantations, functional diversity of spiders negatively correlated with leaf damage caused by chewing insects. This might be because spiders with different hunting strategies are spatially complementary ([Cardoso et al., 2011](#)), collectively diminishing enemy-free space for the pests and consequently reducing their foraging activity ([Hlivko & Rypstra, 2003](#)). During autumn in oak plantations, there was a positive correlation between leaf biomass and the mean body size of spiders. Larger spiders present greater predation risk than do small spiders, and herbivores might thus reduce their foraging more in places with higher predation risk ([Hlivko & Rypstra, 2003](#); [Binz et al., 2014](#)).

Apart from the consistent correlation observed between Hemiptera and the functional diversity of spiders, the correlation patterns varied notably between the two seasons. These seasonal changes can largely be attributed to phenological shifts in the trait composition of spider communities. In late spring, the majority of spiders are relatively large adults and sub-adults ([Nentwig et al., 2023](#)), which exhibit high capture rates and pose a significant threat to their prey. By autumn, however, most spider species consist of small to medium-sized juveniles ([Nentwig et al., 2023](#)), whose lower capture rates result in a reduced predatory threat compared to adults ([Binz et al., 2014](#); [Pekár et al., 2015](#)).

Our results have implications for forest management. Given that the biocontrol potential of spiders correlates with both functional diversity and identity, forest management strategies should aim to conserve highly diverse and abundant spider communities that would encompass all the diversity components and particular hunting strategies. For example, implementing mixed-species stands rather than monocultures can enhance habitat complexity and resource availability, thus supporting a wider array of spider species and hunting guilds ([Samu et al., 2014](#)). Additionally, maintaining structural diversity within the forest, such as by retaining deadwood, leaf litter, and varying canopy cover, provides essential microhabitats and prey resources for different spider species ([Wise, 1993](#); [Košulič et al., 2021](#)). These conditions can be maintained through coppice-with-standards management, particularly within oak forests, which has been shown to be an effective method for supporting overall spider taxonomical and functional diversity indicators ([Košulič et al., 2016](#); [Vymazalová et al., 2021](#); [Weiss et al., 2021](#)). Periodic disturbances, such as controlled burns or selective thinning, can mimic natural forest dynamics, thereby promoting habitat heterogeneity and preventing competitive exclusion of certain spider species ([Pinzon et al., 2013](#)). Moreover, ensuring connectivity between forest patches within otherwise homogeneous forest plantations through ecological corridors can facilitate spider dispersal and colonization, thus enhancing genetic diversity and resilience of spider populations ([Fischer et al., 2013](#); [Gurr et al., 2016](#)). Incorporating a mosaic of successional stages within forest landscapes can also be beneficial, as different spider species may prefer dissimilar stages of forest succession ([Bonte et al., 2003](#); [Hamřík et al., 2023](#)). This approach supports the persistence of both early-successional species and those requiring mature forest conditions. Furthermore, minimizing the use of pesticides and adopting sustainable management methods with a stronger ecological focus, including integrated pest management practices that prioritize the use of selective pesticides, especially in the management of young forest plantations, can help reduce negative effects on spider communities ([Košulič et al., 2021](#)), thereby preserving their ecological roles as natural pest control agents ([Michalko et al., 2019a,b](#)).

5. Conclusion

In conclusion, our correlative approach provides indirect evidence that spiders in forest canopies can contribute to reducing forest pests and herbivory. However, the biocontrol efficacy of spiders in forest plantations is highly context-dependent, shaped by functional identity, diversity, and their interactions with pest type, herbivory indicators, forest type, and season. This highlights the importance of not only preserving spider diversity but also understanding changes in functional community composition to optimize their pest suppression potential. Future studies should aim to identify the specific functional traits of spiders that enhance biocontrol effectiveness under varying environmental and management conditions. For example, research could investigate how different hunting strategies or body sizes influence pest suppression across forest types and successional stages, with particular emphasis on young forest stands, which are especially vulnerable to pest infestations.

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CRedit authorship contribution statement

Warbota Khum: Writing – review & editing, Writing – original draft, Visualization, Investigation. **Ondřej Košulič:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation. **Radek Michalko:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2024.105666>.

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