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Consequences of enriching European beech forests with non-native Douglas fir for generalist arthropod predator diversity, abundance and pest control

Dissertation
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“*Never confuse education with intelligence, you can have a PhD and still be an idiot.*”
— **Richard P. Feynman**

Table of Contents

Summary

As anthropogenic climate induced stress leads to biodiversity loss and an increase in the frequency and severity of pest outbreaks, forest management in Central Europe is looking for ways to balance demands of biodiversity conservation and economic utility. To fulfil these demands Central European forestry is shifting from monoculture plantations to mixtures with phylogenetically distant deciduous and coniferous tree species which have been show to promote biodiversity and top-down control. Furthermore, the utilization of non-native Douglas fir, which combines climate change adaptability and high growth rates, is increasing and Norway spruce dieback is likely to exacerbate this. The ecological consequences of such an increase in non-native Douglas fir utilization are not fully known, but it is likely to lead to diversity and abundance loss of generalist arthropod predators, which in turn could translate to lower top-down control and higher herbivory (**Chapter 1**). In addition to testing this hypothesis, I will study if non-native Douglas fir effects are tempered in mixtures with phylogenetically distant European beech and to what extent Douglas fir effects are similar to effects of the phylogenetically close Norway spruce.

Firstly I studied how Non-native Douglas fir affected the diversity, abundance and biomass of epigeal spiders collected by pitfall traps in mature forest stands (**Chapter 2**). Contrary to my expectations, epigeal spider abundance, biomass and functional richness was higher in stands with higher Douglas fir proportions, with site conditions playing a crucial role in structuring spider communities. Further analysis on arboreal spiders collected by tree beating in young forest stands (**Chapter 3**) showed that arboreal spiders have the highest numbers on individual conifer trees, especially Douglas fir. However, at the plot level spider species richness, abundance and biomass decreased with an increasing proportion of both Douglas fir and Norway spruce due to lower species turnover among coniferous trees (Matevski & Schuldt, 2021). These results suggest that it is important to consider matters of scale, stratum and forest age when discussing Douglas fir effects on spider diversity and top-down control potential.

To see whether Douglas fir effects on spider top-down control potential translate into effects on predation pressure, we assessed clay caterpillar attack rates on the ground and herb layer in mature forest stands (**Chapter 4**). The results from this study (Matevski et al., 2021) showed that Douglas fir monocultures harbored significantly higher ground layer arthropod attack rates than all other stands, except for Norway spruce monocultures. Additional analysis on European beech sapling and mature tree leaf damage in monocultures as well as mixtures with Douglas fir and Norway spruce (**Chapter 5**) showed that stands with higher Douglas fir proportion suffered less sapling and mature European beech leaf damage. The results of these two manuscripts show that Douglas fir effects on spider diversity and community composition translate into effects on arthropod-mediated top-down control.

All in all, my thesis suggests that, at least in the context of generalist arthropod predator diversity and ecosystem functioning, Douglas fir effects are mostly congruent with forest management demands by promoting diversity and economic utility (**Chapter 6**). Nonetheless, these results are dependent on stand age, site conditions, stratum and spatial scale studied, highlighting the importance of considering these factors when studying tree diversity and identity effects on arthropod diversity and ecosystem functioning.

Contributions to the research chapters

Chapter 2. Local spider diversity and density are promoted by non-native tree introduction

Dragan Matevski[1], Andreas Schuldt[1]

Authorship: DM collected the data, analyzed the data and led the writing of the manuscript, AS conceived the ideas and designed the methodology. All authors contributed critically to writing the manuscript and gave final approval for publication.

Chapter 3. Tree species richness, tree identity and non-native tree proportion affect arboreal spider diversity, abundance and biomass (published)

Dragan Matevski[1], Andreas Schuldt[1]

Authorship: DM collected the data, analyzed the data and led the writing of the manuscript, AS conceived the ideas and designed the methodology. All authors contributed critically to writing the manuscript and gave final approval for publication.

Chapter 4. Non-native Douglas fir (*Pseudotsuga menziesii*) promotes sentinel prey attack rates in Central European forests (published)

Dragan Matevski[1], Jonas Glatthorn[2], Peter Kriegel[3], Andreas Schuldt[1]

Authorship: DM collected the data, analyzed the data and led the writing of the manuscript, JG collected the data and analyzed the data, PK collected the data, AS conceived the ideas and designed the methodology. All authors contributed critically to writing the manuscript and gave final approval for publication.

Chapter 5. Introduction of non-native Douglas fir reduces leaf damage on both saplings and mature trees in European beech forests (submitted)

Dragan Matevski[1], Estela Foltran[4,5], Norbert Lamensdorf[5], Andreas Schuldt[1]

Authorship: DM collected the data, analyzed the data and led the writing of the manuscript, EF collected the data and analyzed the data, NL conceived the ideas and designed the methodology, AS conceived the ideas and designed the methodology. All authors contributed critically to writing the manuscript and gave final approval for publication.

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Chapter 1

General introduction

1.1 Forest management in a changing climate

Silviculture is facing multiple challenges given the increasing need to promote both biodiversity and economic utility (Albert et al., 2020; Ruckelshaus et al., 2015), which can sometimes be at odds with one another (Schmid et al., 2014). Such demands are exacerbated by the profound effects of anthropogenic climate change and other anthropogenic stressors (Millar & Stephenson, 2015) that lead to biodiversity loss of both invertebrates (Marta et al., 2021) and vertebrates (Ceballos et al., 2015), as well as dieback of tree species (Menezes-Silva et al., 2019).

To better cope with the changing climate, Central European forest stands are transitioning from monocultures to mixed-species forest stands (Pretzsch, 2019), with phylogenetically diverse mixtures of deciduous and coniferous trees (Knoke et al., 2008). However, despite tree species richness showing positive effects on biodiversity, ecosystem functioning and economic value of forests (Ampoorter et al., 2020; Huang et al., 2018; Knoke et al., 2008, Scherer-Lorenzen, 2014), forest management is still extensively relying on monoculture plantations (Chazdon & Brancalion, 2019). Furthermore, adapting forests to climate change is likely to lead to an increase in the utilization of non-native Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), as it combines high growth rates with potentially better adaptation to climate change than typical native European tree species (Dyderski et al., 2018). Douglas fir currently accounts for only 2–3% of the forest area in several European states (Schmid et al., 2014), but the area is expected to increase making it likely to become the third most important conifer in German forests after Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) (Höltermann et al., 2008). This trend is likely to increase as a consequence of the recent dieback of Norway spruce in Central Europe due to drought, storms, temperature maxima and the Eurasian spruce bark beetle *Ips typographus* (Krejza et al., 2021; Mezei et al., 2021). The ecological consequences of such a trend are not yet fully known (Schmid et al., 2014). However, the introduction of exotic species is considered one of the main reasons for the loss of biodiversity (IUCN 2000). Non-native conifers have been shown to be among the most problematic non-native plant species with efforts being made to understand their impact (Sapsford et al., 2020). In this context, Douglas fir plantations are particularly deleterious from a nature conservation point of view when they replace species-rich and threatened ecosystems such as forest glades and heathlands (Fagundez, 2013). Such negative biodiversity effects could be tempered by planting Douglas fir in mixtures with native trees, which could combine both climatic stability and ecological sustainability (Tognetti et al., 2010). Nonetheless, our knowledge of the ecological consequences of these trends in forest management is limited and requires further empirical evidence (Ammer et al., 2018).

In particular, there is an increased need to consider how forest management practice would affect arthropod diversity and arthropod-mediated ecosystem functions (Schowalter et al. 2018), as arthropods play crucial roles in biodiversity conservation and ecosystem functioning of forests (Schowalter, 2012). Moving from monocultures to more diverse tree mixtures of phylogenetically distant tree species has been show to increase the resistance of forests to natural disturbances such as herbivore and pathogen attack (Jactel et al., 2017; Jactel et al., 2021) and increasing plant diversity has been shown to promote the biodiversity and top-down control potential of generalist arthropod predators (Haddad et al., 2009; Root, 1973). On the other hand, the introduction of non-native Douglas fir in native forests has been shown to have negative effects on the diversity and abundance of arthropods (Roques et al., 2006; Schuldt & Scherer-Lorenzen, 2014) and as a result may impact arthropod-mediated ecosystem functions such as predation and herbivory. In order to reach a better understanding on how current trends of forest management may affect biodiversity and ecosystem functioning, the consequences of enriching European beech (*Fagus sylvatica* L.) forests with Douglas fir on generalist arthropod predator diversity and arthropod-mediated functions will be studied in this thesis.

1.2 Generalist arthropod predator communities

A crucial function performed by generalist arthropod predators is pest control, which may heavily rely on the diversity and community composition of generalist arthropod predators (Jonsson et al., 2017). According to the “enemies hypothesis” arthropod predator abundance as well as pest control is considered to be positively correlated with more diverse plant communities as a result of higher habitat diversity and prey availability (Haddad et al., 2009; Root, 1973). However, a recent review of the “enemies hypothesis” has shown that it is not a concept that can be applied to all taxa and study systems and might not unambiguously apply to forests (Staab & Schuldt, 2020). Spiders, a highly abundant and species rich group of generalist arthropod predators that is important in both the forest floor and canopy food webs, for example, have been shown to be more strongly influenced by tree identity than tree diversity. This is especially true for managed forests in Central Europe where the diversity gradients are short (Oxborough et al., 2012; Oxborough et al., 2016) and the relative contribution of each tree species in the species pool is significant (Nadrowski et al., 2010).

In the scope of tree identity effects, our knowledge of whether spider communities are significantly different in non-native vs native forests is limited (Ingle et al., 2020; Oxborough et al., 2016). However research so far has generally shown that replacing native forest stands with non-native plantations leads to a loss in arthropod biodiversity (Brockerhoff et al., 2008), possibly as a result of changes in understory vegetation structure and loss of associated species directly dependent upon the lost native trees for their existence (Ennos et al., 2019). When it comes to the effect of non-native Douglas fir on spider abundance, diversity and biomass in Central European forests, recent research has shown contrasting results depending on stand age. Douglas fir presence has been shown to strongly decrease epigeal spider abundance and biomass in young mixed-species plantations of a tree diversity experiment (Schuldt & Scherer-Lorenzen, 2014). On the other hand, data from intermediate-aged Douglas fir stands showed no significant difference in epigeal spider abundance and diversity in comparison to native trees (Finch & Szumelda, 2007), while data from more mature forest stands is lacking, focused on few sites and doesn’t include mixtures with native tree species (Ziesche & Roth, 2008). Research on canopy spiders in this context is scarcer, even though tree-associated predator communities can be assumed to make a significant contribution to arthropod predator diversity and functioning that differs significantly from conditions on the forest floor (Basset et al., 2015). Therefore, a general understanding of how non-native tree species and their effects in monocultures versus mixtures influences the diversity and community composition of generalist arthropod predators such as spiders requires more extensive studies.

For such a general understanding to be achieved it is important to account for the environmental context and the spatial scale of the observed tree diversity and non-native tree identity effects. At larger spatial scale climatic conditions have been shown to influence tree diversity and identity effects on spider diversity and community structure (Ampoorter et al., 2019). Unfortunately, studies on non-native tree Douglas fir effects on spider diversity and community structure have been mainly restricted to (small sets of) individual study sites (Finch & Szumelda, 2007; Ziesche & Roth, 2008) and knowledge on Douglas fir effects at larger spatial scales is limited. Additionally, canopy research can allow us to address predator-herbivore interactions at different spatial scales. For instance, direct interactions between predators and herbivores, and therefore top-down control, might be primarily determined at the individual tree level (Muiruri et al., 2016) and can be modulated by the local neighborhood tree diversity (Setiawan, 2016). In contrast, predator biodiversity and therefore measures for conservation might be structured more strongly at the plot level, through turnover of predator species among trees (Zhang et al., 2017). Moreover, at the local scale of individual forest stands, habitat features that are partially independent of tree species identity and strongly determined by forest management and the resulting forest structure can play important roles (Penone et al., 2019). Effects of habitat structure such as vegetation complexity, deadwood coverage, litter properties and canopy openness have previously been shown to modulate tree identity effects on spider diversity and community structure (Janssen et al., 2007; Košulič et al., 2019; Seibold et al., 2016). Different spider guilds require different vegetation structure (Uetz, 1991), with ground hunters requiring heterogeneous vegetation with open patches to search for prey and patches of taller vegetation for refuge (Maelfat & Dekeer, 1990), while web building spiders require more structurally complex vegetation that provides increased web attachment points (Diehl et al., 2013). Other aspects of habitat structure such as deadwood and litter cover can also affect spider communities. The addition of deadwood has been shown to promote prey abundance, as well as the abundance of spiders, with spiders being strongly affected specifically by fine woody debris such as branches (Seibold et al., 2016). Interestingly, 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 (Langellato and Denno, 2004; Uetz, 1975). Lastly, changes in canopy openness are known to modify spider community structure (Cernecká et al., 2016), with peaks for abundance, as well as conservation indicators such as conservation value and degree of rareness in more open canopies, while functional diversity peaked in stands with lower canopy openness (Košulič et al., 2019). Unraveling the effects of spatial scale and habitat structure from tree diversity and identity effectscan provide insight into forest management practices that would be better suited to balancing ecological and economic demands.

1.3 Arthropod-mediated ecosystem functions

As tree mortality increases due to large-scale insect-pest outbreaks triggered by climate induced stress (Ammer et al., 2018; Jacquet et al., 2012; Netherer et al., 2019), it is important to go beyond researching how forest management practices alter arthropod diversity and community structure and see if these changes translate to alterations of arthropod-mediated ecosystem functions such as herbivory and predation. This can be done by assessing the link between predator densities and predation pressure by studying sentinel prey attack rates, and seeing if higher predation pressure contributes to lowering herbivory damage. Recent ecological research suggests that, in general, increasing tree diversity improves the resistance of a forest stand to natural disturbances such as herbivory and pathogen damage (Jactel et al., 2017; Jactel et al., 2021). Decreasing herbivory with increasing tree diversity has been found to be most pronounced for mixtures with phylogenetically distant tree species (Jactel et al., 2021). Such a pattern of associational resistance is particularly common for damage caused by specialists (Jactel et al., 2021), because heterospecific neighbors lower the chance of host detection by reducing host frequency (resource concentration hypothesis; Root, 1973), mixing of cues (host apparency hypothesis; Castagneyrol et al., 2013), non-host tree preference (decoy hypothesis; Ruttan & Lortie, 2015), or promotion of top-down control by natural enemies (enemies hypothesis; Root, 1973, but see Staab & Schuldt, 2020). On the other hand, some specialist herbivores (Plath et al., 2012) and most generalist herbivores cause more damage in mixtures (Jactel & Brockerhoff, 2007; Schuldt et al., 2010). Such an associational susceptibility effect is a result of generalists benefiting from the broader diet range (Unsicker et al., 2008) and spill-over from highly preferred to less-preferred hosts (White & Whitham, 2000) in mixtures. A general understanding of the influence of tree diversity on natural disturbances and top-down control is further complicated by the effects of tree identity and environmental context (Castagneyrol et al., 2014; Muiruri et al., 2016; Pinzon et al., 2018; Jactel et al., 2021).

The effects of tree identity and composition and the need for a better understanding of their modifying role are particularly relevant when it comes to non-native tree species such as Douglas fir. In terms of forest pests, Douglas fir has shown distinct incompatibilities, as even polyphagous herbivores such as black arches (*Lymantria monacha* L., 1758) have difficulties coping with a diet of Douglas fir needles (Gruppe and Goßner, 2006). Additionally, Douglas fir has not yet been victim to larger pest outbreaks in Europe (Roques et al., 2006). On the other hand, there are concerns over the negative effects of planting Douglas fir on the abundance and biomass of natural enemies (Finch and Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014), as well as possibilities of accumulating introduced herbivores, and native herbivores performing a host jump, over time (Roques et al., 2006). Planting Douglas fir in mixtures may alleviate some of these concerns with enemy to prey ratios being higher in mixtures than in monocultures due to a higher alternative prey availability, complementary food resources and microhabitats (Björkman et al., 2015).

For such mixture types, an important research issue is the need to understand the spatial scales and environmental context at which impacts of tree diversity and tree identity are effective (Chase et al., 2018). At large spatial scales climate has been shown as an important factor for predation pressure in forests with predation pressure decreasing with elevation and increasing with latitude (Lövei & Ferrante, 2017; Roslin et al., 2017). Additionally, predation pressure can vary by the stratum studied, with arthropod attack rates being highest at the ground level (Lövei & Ferrante, 2017). On the other hand, community-level tree species composition and tree species proportions may be important drivers of tree mixture effects on leaf damage (e.g. Hantsch et al., 2014; Muiruri et al., 2018), while local tree neighborhoods may strongly influence diversity effects by modifying host apparency and environmental conditions (Castagneyrol et al., 2013; Grossman et al., 2018). Environmental variation can be considered an important moderator of tree diversity and tree identity effects on arthropod-mediated ecosystem functions, e.g. via modifications on resource availability for tree growth and ontogenetic development, as well as alterations of microclimate and microhabitats which can alter predator densities (Basset et al., 2001; Hughes, 2005; Kollberg et al., 2014; Nigel & Pinzon et al., 2018; Zvereva et al., 2020). As such it is important to consider effects of tree diversity and non-native trees in the context of scale and environmental context.

1.4 Study design and scope

This dissertation was performed in the framework of the research training group (RTG) 2300 -"Enrichment of European beech with conifers – impacts of functional traits on ecosystem functioning". In this RTG eleven closely linked subprojects focus on whether mixtures show higher functional diversity than European beech monocultures and whether conifer effects on ecosystem functioning are more pronounced in mixtures with Douglas fir (Glatthorn et al., 2021). The research of the RTG was performed on 40 mature temperate forest stands of 0.25 ha (50 m × 50 m) each, all differing in stand age, mixture proportions and site conditions. The forest stands comprised three of the most commercially important species in Europe: the broadleaved native European beech, as well as the coniferous native Norway spruce and non-native Douglas fir. Plots were organized into eight 'quintets', across the federal state of Lower Saxony in Germany, with 4 nutrient rich, higher elevation quintets with higher precipitation in the southern half of the state and 4 nutrient poor, drier, lower elevation quintets in the northern part. The quintets were used to avoid bias due to regional clustering of stand types. Each quintet contained one monoculture plot of each tree species and two European beech-conifer (European beech/Norway spruce and European beech/Douglas fir) mixtures. The cutoff point for stands being classified as mixtures was tree proportions of at most 85% of the more dominant target species and at least 15% of the other target species. Classifying the stands in such a way is more meaningful from the perspective of forest management (plots were selected together with foresters) since this is how these stand types look like in practice.

In addition to data from the RTG plots, this thesis used data from the BIOTREE-SPECIES sites near Kaltenborn, Thuringia, Germany, which are a part of the BIOTREE biodiversity and ecosystem functioning experiment (Scherer-Lorenzen et al., 2007). The BIOTREE-SPECIES sites consist of 16 young forest plantations (12 year old trees at time of sampling) of 0.58 ha (124 m × 48 m) that include the three target species of the RTG in the species pool, with the addition of sessile oak (*Quercus petraea* Liebl.) as the fourth target tree species. Tree species composition and tree species richness treatments were distributed randomly across the 16 plots. Four of the plots were monocultures of every tree species present in the species pool, six plots represented all possible 2-species mixtures, while four plots represented all possible 3-species permutations and two plots were 4-species mixtures containing all tree species studied. Since in some instances fast-growing and slow-growing tree species were planted in the same plot, tree individuals were planted in 8 m × 8 m monospecific cells (size of the cells was based on the canopy properties of full-grown tree individuals), to avoid early outcompeting of less competitive species.

In the scope of the RTG, I investigated arthropod diversity and functioning as part of Subproject 6 – "Arthropod diversity and functioning in mixed vs pure stands", where I focused mainly on generalist arthropod predator (spider) diversity and community structure as well as arthropod-mediated ecosystem functions such as predation and herbivory. The underlying hypothesis of this dissertation is that Douglas fir monocultures stands would harbor lower spider diversity and biomass of epigeal and canopy spiders than native forest stands, which would result in lower predation pressure and possibly higher herbivory. Furthermore, such non-native Douglas fir effects would be lessened in mixtures which would benefit both biodiversity and economic utility. I firstly investigated how tree diversity, tree identity and plot characteristics affect spider diversity, abundance and biomass using pitfall trap data from the RTG sites (**Chapter 2**). Then, I used data from the BIOTREE experiment to see if tree diversity and identity effects are similar in the canopy of younger forest stands with a longer diversity gradient, as well as to see if spatial scale (tree vs plot-level) and local neighborhood (surrounded by homospecific or heterospecific trees) have an effect on spider diversity, abundance and biomass (**Chapter 3**). In order to see if the previously detected effects of scale, tree diversity, tree identity and plot characteristics translate into changes in arthropod-mediated ecosystem functions I assessed predation and herbivory at the RTG sites (**Chapters 4-5)**. Herbivory was assessed by assessing leaf damage on European beech saplings and mature trees in monocultures and mixtures with conifers, checking if soil nutrient capacity might modulate effects of tree diversity, tree identity and microhabitat characteristics (**Chapter 4**). Predation was assessed by setting up a sentinel prey experiment at the ground and herb layer, checking for effects of tree diversity, tree identity and microhabitat characteristics (**Chapter 5)**. Overall, this set of studies contributes to a better understanding of how generalist arthropod predator diversity and arthropod-mediated functions are affected by spatial scale, tree diversity, tree identity and plot characteristics focusing mainly on the possible consequences of increased utilization of Douglas fir in Central European forests.

Chapter 2

Local spider diversity and density are promoted by non-native tree introduction

Dragan Matevski, Andreas Schuldt

Abstract

As climate change is altering ecosystems worldwide, forest management is increasingly relying on more adaptable non-native tree species, such as Douglas fir (*Pseudotsuga menziesii*) in Europe. 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, influened by large and small scale differences in the environmental context, affect 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 (climate and soil quality) 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*), and two-species mixtures of European beech and each of the conifers. Contrary to our expectations, Douglas fir promoted spider diversity and activity density, indicating that increasing Douglas fir utilization may result in increased top-down control. Norway spruce had similar effects on spider diversity, but the effects were limited to the warmer, nutrient por northern region, highlighting the importance of spatial context. Microhabitat characteristics such as local canopy openness, litter cover and fine deadwood cover had opposing effects on spider diversity and activity density, with more open stands harboring a more diverse but less abundant spider community. All in all, our findings suggest that increasing Douglas fir utilization at the expense of Norway spruce may promote local spider diversity and density.

2.1 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 adaptation face multiple challenges trying to balance ecological and economic demands from forests (Albert et al., 2020; Ruckelshaus et al., 2015). For instance, the recent dieback of Norway spruce (*Picea abies* (L.) H. Karst.) in Central Europe as a result of extreme weather and bark beetle outbreaks (Krejza et al., 2021; Mezei et al., 2021) is likely to lead to increased utilization of more adaptable tree species such as non-native Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), the ecological consequences of which, however, are not fully known (Schmid et al., 2014). Potentially 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 pest control, which may be heavily influenced by the diversity of arthropod predator communities (Jonsson et al., 2017). According to the "enemies hypothesis" pest 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 & 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 (Ingle et al., 2020; Oxborough et al., 2016). However it has been generally shown that replacing native forests with non-native plantations leads to a loss in arthropod biodiversity (Brockerhoff et al., 2008), possibly as a consequence 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 non-native 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 has been shown to strongly decrease epigeal spider abundance and biomass 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* L.) at the tree-level, but arboreal spider species richness, abundance and biomass decreased with increasing Douglas fir proportion at the plot-level (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), while data from more mature forest stands is lacking, focusing on 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 influences 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), while 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). Differences in spider community structure with vegetation structure have been linked with foraging strategies (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 (Langellato and Denno, 2004). Lastly, changes in canopy openness are known to alter spider community structure (Cernecká et al., 2016), with peaks for abundance in more open canopies, while functional diversity peaked at more closed canopies (Košulič et al., 2019). Disentangling the effects of habitat structure from tree identity effects can provide insight into forest management practices that would be better suited to balancing ecological and economic demands.

Here we utilized a set of 35 managed forest stands to determine how stand type, tree species composition and habitat structure affect spider taxonomic and functional diversity, abundance 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 allows us to test the effects that the increased utilization of Douglas fir in Central European forests, as a result of 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 non-native Douglas fir are similar to that of a native coniferous species, which provides information on how ecologically relevant 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 both conifers can shed light on whether planting Douglas fir in mixtures would temper any effects by Douglas fir. Moreover, 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 taking into account 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) non-native Douglas fir monocultures harbor lower spider diversity, abundance and biomass than native stands, with this effect being partially alleviated in mixtures due to higher habitat heterogeneity. 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, with regional differences in environmental conditions also having a strong impact on structuring spider communities. Lastly (iii), in terms of community composition we expected lower beta diversity, and lower rare species diversity in conifers due to lower turnover among conifers (Matevski & Schuldt, 2021), especially in non-native plantation of Douglas fir, possibly as a consequence of structural changes in understory vegetation in comparison to native forests (Ennos et al., 2019).

2.2 Materials and methods

2.2.1 Study site 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, covering a range of stand ages, tree proportions and site conditions in the federal state of Lower Saxony, Germany (Table A1). 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 2.1). Each quintet was composed of five forest stands: European beech, Douglas fir and Norway spruce monocultures, and two-species mixtures with European beech and each of the two conifers.

2.2.2 Data collection

Spiders were sampled with pitfall traps between 16.03-20.09.2019. We set 8 pitfall traps at each plot in a 2x4 grid with 10 m distance between traps. 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 mammals. 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 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). Additionally, we classified the spider species to functional guilds according to Cardoso et al. (2011), and collected information on the phenological length (in months) of the activity period of adults from Nentwig et al. (2021), 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 associated and species not associated with forests based on habitat use data from Blick et al. (2016) and Nentwig et al. (2021).

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 *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 m^2). 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 and 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 distribution of tree species than patch distribution, even if they have identical mixture proportions.

The microhabitat characteristics in a 5 m radius around each trap were assessed from May to July 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. 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.

2.2.3 Statistical analyses

We analyzed the data at the trap level with the exception of the non-metric multidimensional scaling (NMDS) which was done at the plot level. Due to 8.7% of the samples being missing (e.g. loss of traps due to wild boar), spider abundance and biomass were calculated on a per trap/day basis and species diversity was calculated using coverage based rarefaction and extrapolation of species diversity (Hill numbers) using the *iNEXT* R package (Hiesh 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).

We used abundance and biomass per trap/day, community weighted mean (CWM; average biomass of individual adult spiders) biomass, Hill numbers (q=0-2), 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 modelling 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 from each other. Firstly we tested for effects of stand type and region (northern vs. southern sites, see above) by including stand type, region and their interactions as predictors in the model. In the second step we replaced stand type with plot characteristics that better encompass the within- and among-stand heterogeneity of our forest stands. This latter model included NDiv, the proportions of European beech, Norway spruce and Oak, vegetation complexity, canopy openness, as well as litter and deadwood cover. We estimated all models with the *nlme* R package (Pinheiro et al., 2020) and subsequently performed a stepwise selection procedure based on AICc (Burnham & 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 & Weisberg, 2018). Lastly, we used the Tukey HSD (honest significant difference) post-hoc test and p-values adjusted with the Holm-method using the *multcomp* R package (Hothorn et al., 2008) to test for significant differences ($p < 0.05$) in response variables among stand types and regions. Model simplification was conducted based on maximul 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 non-metric multidimensional scaling (NMDS). Similarity was based on the Morisita-Horn index of square root-transformed abundance data (Jost et al., 2011). A stable solution was computed from multiple random starting points on the basis of three reduced dimensions (20 random starts). We tested for correlations of the ordination axes with canopy openness, vegetation complexity, litter and deadwood cover as environmental vectors, and region, site and stand type as environmental factors. Additionally, we calculated the multiplicative diversity partitioning (Jost, 2007) with the *vegan* R package to check for differences in the beta diversity compartments (diversity among traps, sites and regions) among stand types. Lastly, the indicator values (IndVal) per region, site, stand type, as well as tree species presence in the plot, 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.

2.3 Results

We captured a total of 21,911 spiders, 16,213 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 A2). By far the most abundant species was the agelenid sheet web weaver *Coelotes terrestris* (Wider, 1834) with 3851 individuals (Table A2). Of the recorded species, two were in the Red List of German spiders (Blick et al., 2016):

Walckenaeria mitrata (Menge, 1868) labeled with G (Endangerment of unknown extent) and *Xysticus luctuosus* (Blackwall, 1836) labeled with 3 (Endangered) (Table A3). Of the total catch, 107 species with 15,897 individuals were typical forest species. Forest 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.

2.3.1 Effects of stand type and region

Stand type influenced microhabitat characteristics with deadwood cover being higher in European beech/Douglas fir mixtures than Norway spruce monocultures, while canopy openness was highest in both conifer monocultures (Table A4). Regarding spider response variables both region and stand type had significant effects (Tables A5-6). In terms of regional effects, spider abundance (Fig. 2.1A) and biomass per trap/day (Fig A2A) as well as spider CWM biomass (Fig A2B) was higher in the southern sites than the northern sites (Tables A5-6). Concerning stand 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 (Tables A5-6). On the other hand, Norway spruce monocultures harbored higher spider diversity (Hill number 0) than European beech monocultures only in the northern sites (Fig. 2.1B; Tables A5-S6), while both conifer monocultures harbored higher spider functional richness than European beech monocultures (Fig. 2.1C; Tables A5-S6). The abundance distribution of species also differed between stand types, with the highest dominance of abundant species being in Norway spruce monocultures, closely followed by European beech/Norway spruce monocultures, then Douglas fir and European beech monocultures, with European beech/Douglas fir mixtures having the lowest dominance of abundant species (Fig. 2.1D; Tables A5-S6). Additionally, the abundance distribution in Norway spruce monocultures showed lower evenness among spider species than other stand types.

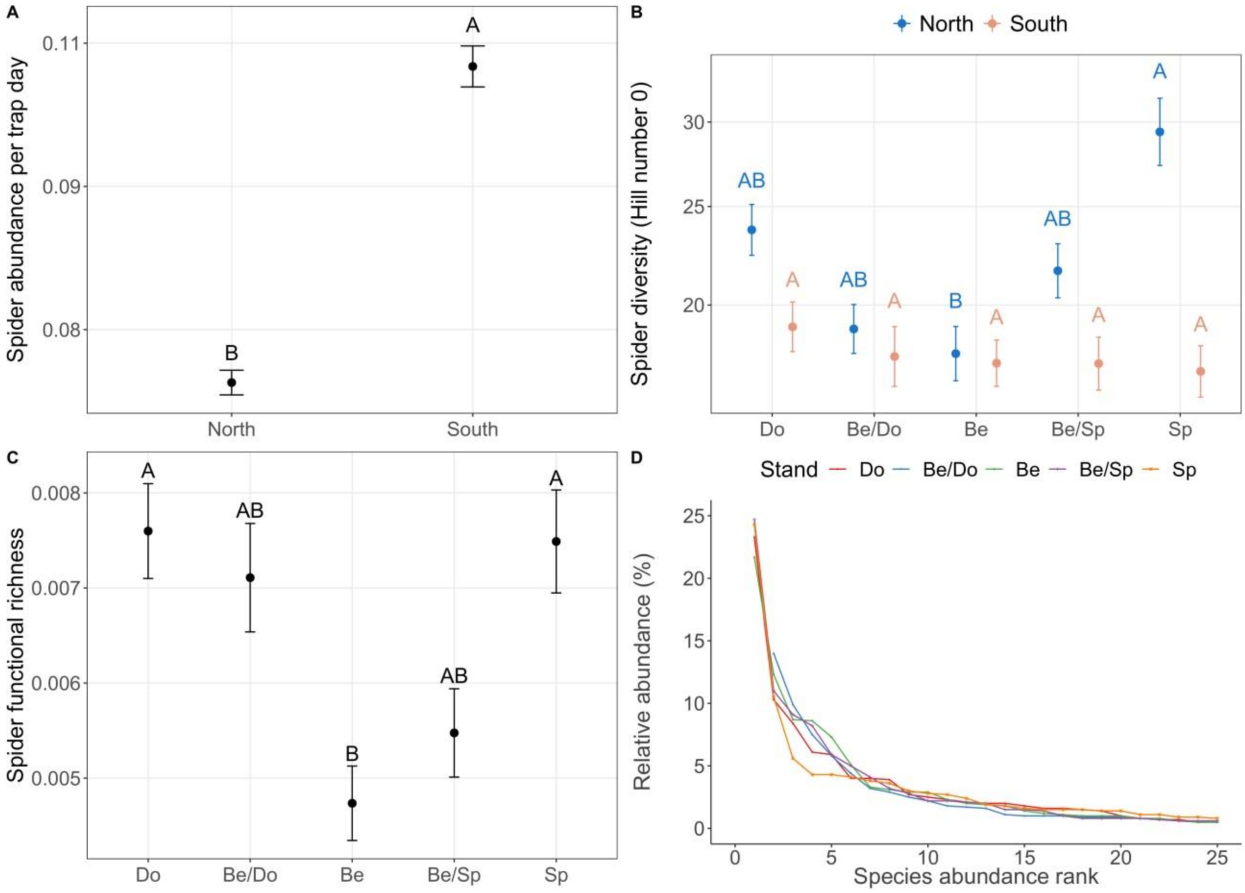

Fig. 2.1 Effects of region (North and South) and stand type (Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture) on spider abundance, biomass and diversity. Differences in mean ± SE abundance (A) per trap day (note that traps were open for up to 183 days in total). Differences in mean ± SE spider diversity (Hill number 0) between stands of different regions (B) and differences in mean ± SE functional richness between stands (C). Rank-abundance distribution of spider assemblages of different stand types (D). Significant differences calculated with Tukey HSD post-hoc with p-values adjusted with the Holm-method marked with different letters. For panel B only significant differences within region are presented. X axis of panel D truncated at 25 to better see differences between stands. Note that the response variables for all panels except for C were log+1 transformed to improve model fit, and the Y-axes show back-transformed values.

2.3.2 Effects of plot characteristics

Models using plot characteristics including tree diversity, tree proportions and microhabitat characteristics (Table A7), explained a higher variance but had a lower model fit. The only exception to this pattern were models where spider diversity (Hill number 0) was used as a response, where models using plot characteristics also had a higher model fit (Table A6-7).

Conifer tree proportions significantly influenced spider response variables (Table A7), with Douglas fir proportion promoting spider abundance (Fig. 2.2A) and biomass (Fig. 2.2B) per trap/day, Norway spruce proportion promoting spider diversity (Hill number 0) (Fig 2.2C) and functional richness (Fig. 2.2D) only in the northern plots, while both conifers promoted less functionally divergent (Fig. 2.2E) but more functionally rich (Fig. 2.2F) spider assemblages.

Furthermore, microhabitat characteristics influenced spider response variables (Table A7), with stands with higher canopy openness having lower spider abundance (Fig. 3A) and biomass (Fig. 2.3B) per trap/day, while more spider diversity (Hill number 0-2) (Fig. 2.3C, Table A8) and functional dispersion (Fig. 2.3D). Additionally, canopy openness had a marginally significant effect (p= 0.073) on functional richness in our models, which becomes significant (p= 0.038) if only canopy openness is in the model. On the other hand, stands with higher litter cover had higher spider abundance (Fig. 2.3E) and biomass (Fig. 2.3F) per trap/day, but lower spider functional evenness (Fig. 2.3G). Lastly, sites with more deadwood cover had less spider diversity (Hill number 2) (Fig. 2.3H).

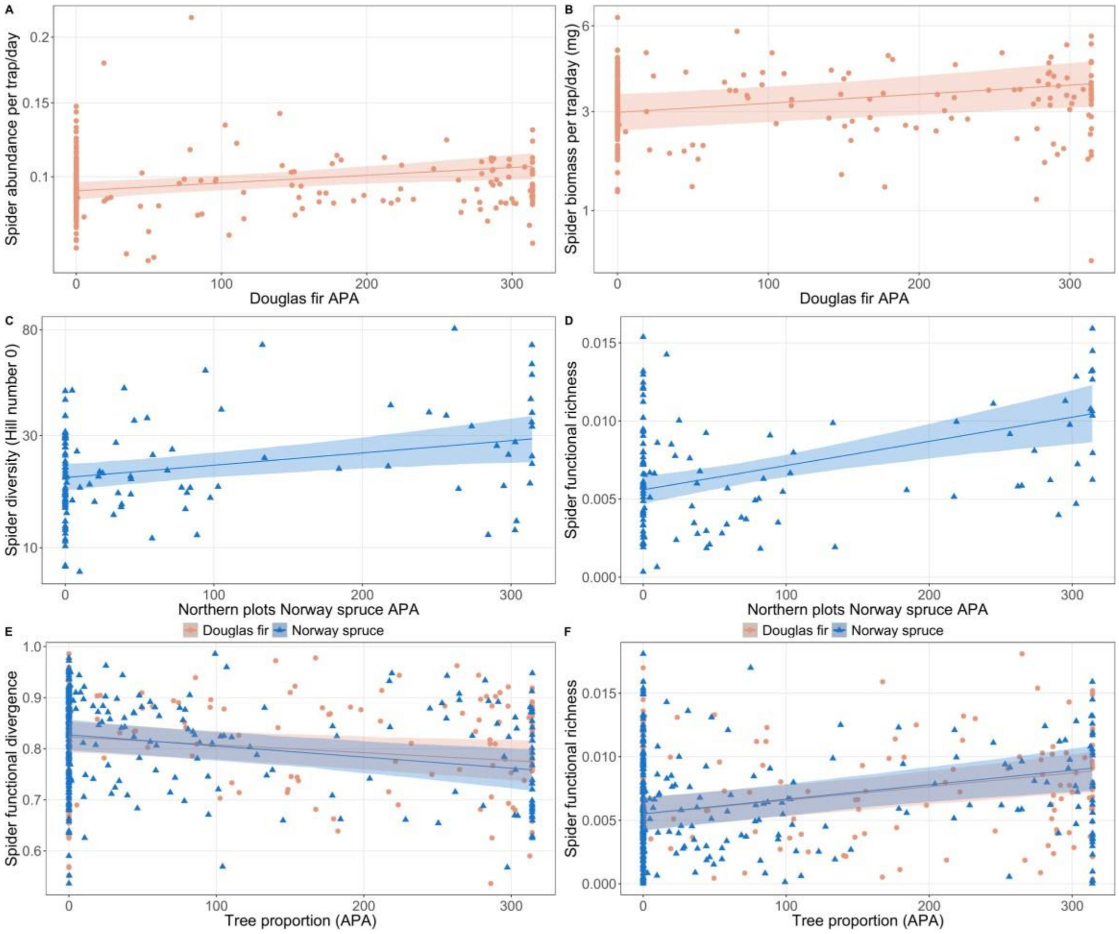

Fig. 2.2 Effects of local (10 m radius around traps) conifer proportions on spider abundance, biomass and diversity. Differences in spider abundance (A) and biomass per trap/day (B) in plots with different Douglas fir proportion, spider diversity (Hill number 0) (C) and functional richness (D) in northern plots with different Norway spruce proportion, as well as spider functional divergence (E) and richness (F) in plots with different proportions of both conifers. Bands represent 95% confidence intervals. Y-axis values show data adjusted for covariates in the final mixed models for panels A and B. Note that the response variables in panels A-C were log+1 transformed in order to improve model fit. Y-axes show back-transformed values.

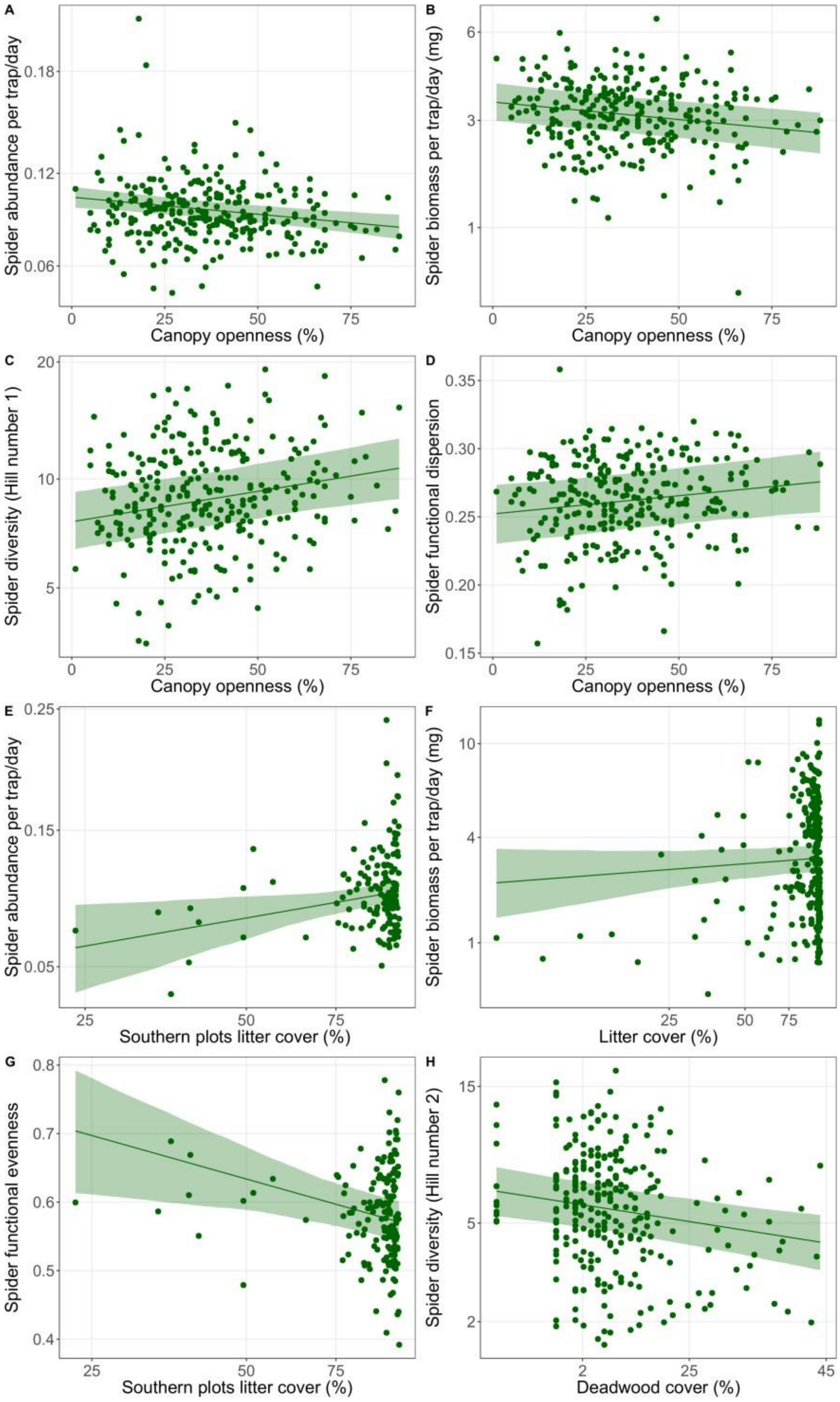

Fig. 2.3 Effects of microhabitat characteristics on spider abundance, biomass and diversity. Differences in spider abundance (A) and biomass (B) per trap/day, spider diversity (Hill number 1) (C), as well as functional dispersion (D) in plots with different canopy openness. Differences in spider abundance per trap/day in the southern plots (E), biomass (F) per trap/day, as well spider functional evenness in the southern sites (G) in plots with different litter cover, as well as spider diversity (Hill number 2) (H) 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-E, and G. Note that the response variables in panels A-C, E, F and H were log (x+1) transformed in order to improve model fit. Furthermore litter cover was log transformed and deadwood cover was log (x+1) transformed. Y and X-axes show back-transformed values.

2.3.3 Spider community structure

Using NMDS we analyzed how region, site and stand type affected spider community assemblages (Fig. 4; Table A8). In terms of species composition, there was a clear difference in assemblages from the northern and southern regions with a less clear difference among sites within the regions. *Coelotes terrestris* with 3851 individuals was the most dominant in the southern plots (IndvaL=0.794, p=0.001), while *Tenuiphantes flavipes* (Blackwall, 1854) with 1644 individuals was the most dominant in the northern plots (IndvaL=0.949, p=0.001), with other species having high indicator values for different regions, sites, stand type and tree presence/absence (Table A8). Concerning stand types, stands containing Douglas fir were the only ones harboring spider species with high IndvaL values with *Diplocephalus latifrons* (O. Pickard-Cambridge, 1863) (IndvaL=0.386, p=0.001) and *Walckenaeria atrotibialis* (O. P.-Cambridge, 1878) (IndvaL=0.256, p=0.001) being indicators for Douglas fir stands, while *Pardosa saltans* Töpfer-Hofmann, 2000 (IndvaL=0.260, p=0.041) was an indicator for European beech/Douglas fir mixtures (Table A8). Differences in spider assemblages among individual study plots and stand types within regions were mainly governed by differences in canopy openness and litter cover, with a greater differentiation between coniferous and deciduous stands in the northern, than the southern region (Fig. 2.4).

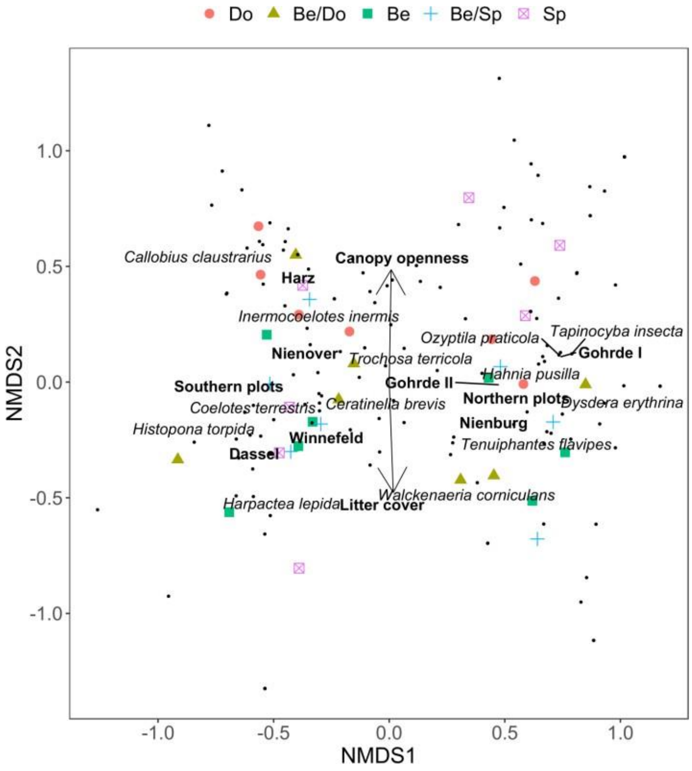

Fig 2.4. NMDS ordination plot (Morista-Horn index) of spider species across 35 study plots, grouped by stand type (Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture). Stress = 0.166. Species are represented by black pionts. Only species with IndvaL values > 0.5 for region or site are labeled with their names in italic. Bold text labels represent significant ($p < 0.05$) effects of microhabitats (vectors), site and region.

2.3.4 Diversity partitioning

When analyzing the partitioning of different measures of diversity (Hill numbers q=0-2), the proportion of alpha diversity rose when going from q=0 to q=2, with among trap beta diversity being the smallest beta diversity partition for all diversity measures (Fig. 2.5A-C).

Furthermore, among site beta diversity was the largest diversity partition for q=0 (Fig. 2.5A), while among region diversity was highest for q=1-2 (Fig. 2.5B-C). Both among site and among region diversity were responsible for a higher proportion of diversity than expected from a random distribution for all stands and measures of diversity (Fig. 2.5A-C). On the other hand, there were differences between stands and measures of diversity when it comes to among pitfall trap diversity (Fig. 2.5A-C). Most stand types had higher diversity than expected except for European beech monocultures and European beech/Norway spruce mixtures for Hill number 0 (Fig, 2.5A), Douglas fir monocultures for Hill number 1 (Fig. 2.5B) and European beech/Norway spruce mixtures for Hill number 2 (Fig. 2.5C).

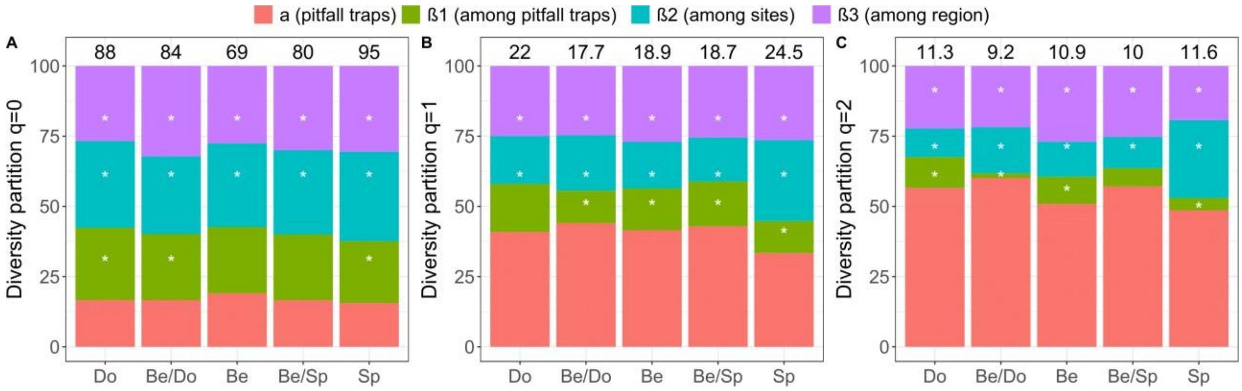

Fig. 2.5 Differences in diversity partitioning of spiders between different stand types (Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture) and measures of species diversity (A-C). The values for Hill numbers for each stand type denoted on the x-axis is indicated by the number at the top of each bar. White asterisks indicate proportions with significantly ($P < 0.001$) higher values than expected from a random distribution.

2.4 Discussion

Contrary to our expectations, stands with higher local Douglas fir proportion promoted spider abundance and biomass. Furthermore, stands with higher proportion of both conifers harbored assemblages with higher functional richness but lower functional divergence. Moreover, conifers did not have lower beta diversity and there were no significant difference in diversity partitioning between the stand types. Regional differences in environmental conditions modified tree identity effects, with Norway spruce promoting spider species (Hill number 0) and functional richness only in the colder, nutrient poor northern sites. Local environmental context, especially canopy openness and litter cover, played an important but less significant role than tree identity. It is important to note that in some cases, namely for spider abundance and biomass, canopy openness had an effect that was independent of tree/stand identity—with canopy openness having a negative effect, while increasing the proportion of Douglas fir, which contributes to more open canopies, had a positive effect. Lastly, in terms of community structure, regional differences were the most important factor in structuring spider assemblages, with the southern sites being dominated by larger, more abundant sheet web builders, while the northern sites were dominated by the relatively smaller and less abundant ground and ambush hunters. Stand differences, especially between coniferous and beech monocultures, were more pronounced in the northern sites, possibly due to a larger difference in canopy openness between stand types. Overall, our findings suggest that increasing Douglas fir utilization in Central European forests could benefit spider-associated top-down control without significant negative effects to all partitions of spider diversity.

2.4.1 Tree identity effects depend on spatial scale

As expected, tree identity had a stronger impact on spider density and diversity than tree diversity (Oxborough et al., 2012; Oxborough et al., 2016), with no registered difference between monocultures and mixtures. Effects of the two mixture types were different, with a pronounced difference in rank abundance structure between European beech/Norway spruce mixtures showing the highest dominance of abundant species and European beech/Douglas fir mixtures showing the lowest. In terms of other stand type effects, differences between monocultures were the most pronounced, with functional richness being significantly higher in both non-native Douglas fir and native Norway spruce monocultures than in native European beech monocultures. This could be a result of significantly higher canopy openness in coniferous than in deciduous monocultures, which can result in direct and indirect changes to habitat diversity, which in turn could benefit functional diversity (Perry et al., 2018). Interestingly, the registered effect of Norway spruce on functional richness, as well as the presence of significantly more spider species (Hill number 0) in Norway spruce monocultures than European beech monocultures was present only in the warmer, nutrient poor northern sites. Such a regional effect could be a result of canopy openness, as the discrepancy in canopy openness between Norway spruce and European beech monocultures was highest in the north 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, as drought stress has been connected to lower canopy closure in forests (Pfeifer et al., 2018)

When looking at tree identity effects at the local scale (10 m radius around each trap), it became obvious that while some local scale results confirmed the previously mentioned stand type results on spider taxonomic and functional richness, others were exclusive to the local spatial scale. Such is the unexpected positive effect of local Douglas fir proportion on spider abundance and biomass. This cannot be attributed to an expected positive effect of canopy openness on spider density (Košulič et al., 2019), as results of local canopy openness showed the opposite effect and local Douglas fir proportion and local canopy openness were not highly correlated. As this result is not related to any environmental variable we measured and is only present at the local scale, further research on Douglas fir’s effects on local environmental variables is necessary to understand Douglas fir’s effects on local spider density. This adds to recent research on the same study sites showing beneficial effects of Douglas fir on top-down control (Kriegel et al., 2021; Matevski et al., 2021), especially in monocultures. Such results indiciate that planting non-native Douglas fir in mixtures may not be necessary to temper any negative non-native tree effects on top-down control, with Douglas fir monocultures being better suited to promote top-down control. However, these results should be tempered with findings that show that planting non-native Douglas fir in mixtures with phylogenetically distant native tree species such as European beech would benefit overyielding (Thurm & Pretzsch, 2016), reduce herbivory (Jactel et al., 2021) and biodiversity (Oxbrough et al., 2016). Lastly, functional divergence was lower in stands with higher local conifer proportion showing that, even though increasing local conifer proportion benefits the total spider trait richness, the trait space becomes more dominated by species with similar traits. The presence of differing plot and local level effects highlights the importance of spatial scale when analyzing tree identity effects, while the presence of regional effects highlights the importance of the environmental context (climate, soil quality etc.) of the study system

2.4.2 Tradeoff between diversity and activity density

Some tree identity effects such as the registered conifer effect on spider functional richness and Norway spruce effect on species richness (Hill number 0) could be better attributed to microhabitat characteristics that can be independent of tree identity like local canopy openness. Local canopy openness consistently promoted spider taxonomic (all Hill numbers) and functional richness (marginal effect). Furthermore, it promoted functional dispersion and had a marginally positive effect on functional evenness showing that increasing local canopy gaps would promote most aspects of spider taxonomic and functional diversity. This is in concordance 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). Additionally, small scale canopy gaps not only promote the diversity of open habitat spiders, but also keep forest generalists and specialists (Košulič et al., 2016).

On the other hand, increasing local light availability led to a decrease in spider abundance and biomass. This could be a result of more closed canopies having more litter cover which benefits the activity density of both large sheet web weavers and cursorial hunters (Uetz, 1979), which were numerically dominant in our study sites. This can be seen from our results of local litter cover where both abundance and biomass was higher in stands with higher local litter cover. When looking at region specific effects, the effect of local litter cover on abundance was present only in the southern sites due to a dominance of large sheet web weavers that benefit the most from increased local litter cover. Moreover, this dominance of one functional group of spiders is 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). 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 abundance and biomass

2.4.3 Community structure is mostly affected by regional differences

Spider community structure was mostly influenced by large scale differences in environmental conditions (climate, soil quality) between the two regions, and to a lesser extent the sites. The warmer, nutrient rich southern sites harbored more and larger spiders, while the colder nutrient poor northern sites harbored smaller, less abundant spiders. Sheet web weavers dominated in the south while the north was dominated by ground hunters. In terms of beta diversity partitioning within region differences were the most important for all diversity measures except the one most sensitive of rare species (Hill number 0), where smaller scale within-site differences provide suitable conditions for the less abundant species. Stand differences in diversity partitioning were minimal, with stands containing conifers not showing lower beta diversity to European beech monocultures as it has been the case for arboreal spiders (Matevski & Schuldt, 2021).

Between stand differences in community structure were not pronounced and were mainly governed by differences in canopy openness and litter cover. However, differences between stand types, especially differences between coniferous monocultures and other stands were larger in the northern than the southern sites. This could be a result or 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 (Košulič et al., 2016; Ryndock et al., 2011). It is important to note that our study is based on relatively small plots (0.25 ha) within larger forest expanses, which are an amalgamation 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 oberved 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.

2.5 Conclusions

Contrary to our expectations, Douglas fir, especially local Douglas fir proportion promoted spider diversity and activity density. Our findings presented here, alongside other research that shows 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 could result in increased top-down control. Norway spruce had similar effects on spider diversity, but the effects were only limited to the colder, nutrient poor northern sites, highlighting the importance of taking into account large scale differences in environmental conditions when trying to generalize tree identity effects. Furthermore, large scale differences in environmental conditions strongly influenced spider community composition with larger and more numerous spiders inhabiting the warmer, more nutrient rich southern sites. Forest-associated microhabitat characteristics that can be altered with forest management such as local canopy openness, litter cover and fine deadwood cover had opposing effects on spider diversity and activity density, with more open stands harboring more diverse but less abundant spider community. All in all, our findings suggest that increasing Douglas fir utilization at the expanse of Norway spruce may lead to increased spider-mediated top-down control without significant negative consequences to spider diversity, while promoting forest-associated microhabitats at the local level would promote spider density but reduce diversity.

Chapter 3

Tree species richness, tree identity and non-native tree proportion affect arboreal spider diversity, abundance and biomass[1]

Dragan Matevski, Andreas Schuldt

Abstract

Sustainable forest management increasingly favors mixtures, but effects on many ecosystem characteristics, such as biocontrol by predators and their biodiversity, are still not well understood. This knowledge gap can be particularly problematic when these mixtures include non-native tree species, such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), which are planted because of their high growth rates and climatic suitability but might have negative effects on forest biota. Available studies have mostly focused on epigeic communities, even though tree-associated predator communities can be assumed to make an important contribution to biocontrol that differs significantly from conditions on the forest floor. Here, we analyzed the responses of spiders, as generalist arboreal predators, along a tree species richness gradient in a young tree diversity experiment in Thuringia, Germany, utilizing four of the most economically important deciduous and coniferous tree species in Europe: European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) H. Karst.), Douglas fir and sessile oak (*Quercus petraea* Liebl.), planted in stands of 1–4 tree species. We tested for effects of tree species richness, tree identity and composition (tree species proportion and position of individual trees) on arboreal spider species richness, functional diversity, abundance, biomass and community structure at both the tree and plot level. Tree species richness promoted arboreal spider species richness and functional richness at the plot level and community-weighted mean spider biomass at the tree level. Tree identity and composition had a stronger influence than tree species richness on structuring spider communities, with arboreal spiders having higher numbers per tree on conifers, especially on Douglas fir. However, at the plot level spider species richness, abundance and biomass decreased with an increasing proportion of conifers due to lower species turnover among coniferous trees. The observed effects of tree species richness, tree identity and tree species proportions early in the establishment of forest stands might influence the strength of top-down control of herbivores in critical stages of development of forest stands. Tree species selection and the proportion in which these trees are mixed with other species should be determined with care in order to concomitantly promote biodiversity and biocontrol. In this context, an important finding of our analyses is that potentially negative effects of non-native Douglas fir on arboreal arthropods were not more severe than effects of native conifers that are planted outside of their natural habitats.

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3.1 Introduction

Biodiversity experiments have advanced our understanding of the linkages between biodiversity and ecosystem functioning (Eisenhauer et al., 2019; Van der Plas, 2019). Recently there has been increasing demand by governments and institutions for utilizing these linkages for more sustainable land use (Albert et al., 2020). However, despite many studies showing positive effects of tree species richness on ecosystem functioning in forests (Ampoorter et al., 2020; Huang et al., 2018; Scherer-Lorenzen, 2014), and an ongoing trend of replacing monocultures with mixtures (Knoke et al., 2008), forest management is still extensively relying on monoculture plantations (Chazdon & Brancalion, 2019). Moreover, adapting forests to climate change is leading to an increased appeal of non-native tree species in many regions, such as Douglas fir (*Pseudotsuga menziesii*) in Central Europe (Schmid et al., 2014). Douglas fir combines high growth rates and potentially better adaptation to climate change than typical native European tree species (Dyderski et al., 2018). However, planting non-native tree species could lead to negative ecological consequences (Schmid et al., 2014), especially when planted in monocultures. Admixing such non-native tree species with native tree species might be a promising approach to combine productivity, climatic stability, and ecological sustainability (Tognetti et al., 2010). However, our knowledge, particularly with respect to the ecological consequences of such mixtures, is limited and requires further research (Ammer et al., 2018). In particular, there is an increased need to consider how forest management affects biodiversity and functions performed by arthropods (Schowalter et al., 2018). Recent studies have shown a decline in arthropod species richness and biomass (e.g. Seibold et al., 2019), and an increased use of non-native tree species, such as Douglas fir, might strengthen these trends because such species might harbor an impoverished subset of native arthropod diversity (e.g. Roques et al., 2006).

A vital function performed by arthropods is pest control, which may heavily rely on the diversity of predator communities (Jonsson et al., 2017). Pest control is frequently considered to be positively correlated with more diverse plant communities (Haddad et al., 2009; Root, 1973). A popular hypothesis concerned with the interaction between plant diversity and higher trophic levels is the "enemies hypothesis", which predicts that predators are more abundant and diverse in species-rich plant communities as a result of higher habitat diversity or a more stable supply of abundant and varied prey (Root, 1973). There is very limited knowledge of how admixtures of non-native tree species influence the relationship between tree species richness and the abundance and diversity of predators. Available studies have mostly focused on epigeic predators at the forest floor (Oxbrough et al., 2016; Schuldt & Scherer-Lorenzen, 2014). Research on arboreal predators in this context is rare, even though tree-associated predator communities can be assumed to make an important contribution to biocontrol and biodiversity conservation that differs significantly from conditions on the forest floor (Basset et al., 2015). Moreover, arboreal research allows addressing matters of spatial scale that have been shown to affect biodiversity-ecosystem functioning relationships in general (Chase et al., 2018), but are not well explored in the context of plant-predator diversity relationships (but see Skarbek et al., 2020). Direct interactions between predators and herbivores, and therefore top-down control, might be determined to a larger extent at the level of individual trees (Muiruri et al., 2016) and can be modulated by the local neighborhood diversity (Setiawan, 2016). In contrast, predator biodiversity and therefore measures for conservation might be structured more strongly at the plot level, through turnover of predator species among trees (Zhang et al., 2017).

Here, we utilized a controlled early-successional forest biodiversity-ecosystem functioning experiment to assess tree diversity, tree composition (tree proportion and local neighborhood diversity) as well as tree identity effects at the plot and tree level on predator diversity, community structure and pest control potential for four of the economically most important tree species for Central European forestry (*Fagus sylvatica* L., *Quercus petraea* Liebl., *Picea abies* (L.) H. Karst. and *Pseudotsuga menziesii* (Mirb.) Franco). We analyzed the species richness, functional diversity, community structure, abundance and biomass of arboreal spiders, which play an important role in the regulation of arboreal insect populations in temperate forests (Floren & Schmidl, 2008) and which respond sensitively to changes in vegetation structure (Halaj et al., 2000). The presence of mixtures of deciduous and coniferous trees and the inclusion of Douglas fir reflects two common trends in Central European forestry, to which our study provides novel insights with respect to biodiversity conservation and biocontrol potential. Although previous studies showed ambiguous effects of tree species richness on arthropod predator communities at the forest floor (Grossman et al., 2018; Staab & Schuldt, 2020), we expected i) a positive effect of tree species richness on spider diversity and abundance at the plot level, because arboreal predator communities might be more specific to the structures and resources provided by different tree species (Mupepele et al., 2014). However, we hypothesized that ii) effects of tree species identity and not plot-level tree species richness play a key role in structuring spider communities at the level of individual trees, with neighborhood diversity modulating this effect. We further expected that (iii) tree identity effects will also modify plot-level relationships (see Schuldt & Scherer-Lorenzen, 2014) and Douglas fir, as a non-native tree species, will support the least diverse spider fauna, which will be similar in community structure to its close phylogenetic relative Norway spruce.

3.2 Materials and methods

3.2.1 Study site and experimental design

We performed our study in the framework of the BIOTREE experiment (Scherer-Lorenzen et al., 2007), on one of the BIOTREE-SPECIES sites near Kaltenborn, Thuringia, Germany (for site details see Table B1, a map of the study site is provided in Scherer-Lorenzen et al., 2007). It comprises 16 study plots of 0.58 ha (124 m × 48 m) each, established on a former agricultural area by planting 3–4 year old seedlings in 2003/2004, and thus representing an afforestation site of an early successional forest (12 year old trees at the time of sampling). The experimental sites were located adjacent to a pine-dominated pine-beech forest.

The tree species pool consists of four of the commercially most important coniferous and deciduous species in Europe: the broadleaved species European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* Liebl.), and the coniferous species Norway spruce (*Picea abies* (L.) H. Karst.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Tree species composition and tree species richness treatments were allocated randomly across the 16 plots. Four of the plots were monocultures of every tree species present in the species pool, six plots represented all possible 2-species mixtures, while four plots represented all possible 3-species permutations and two plots were 4-species mixtures containing all tree species studied. Since in some cases fast-growing and slow-growing tree species were planted in the same plot, tree individuals were planted in 8 m × 8 m monospecific cells (size of the cells was based on the canopy properties of full-grown tree individuals), to avoid early outcompeting of less competitive species. Within a cell, tree individuals were planted in rows that were 2 m apart, with the distance between trees within the rows following common planting practice (2 m for the conifers, 1 m for the deciduous species).

3.2.2 Data collection

Spiders were collected by tree beating (white cloth beating sheet of 70 cm diameter) at three time points during the growing season in 2012 (May, June and August). Eight trees per tree species were sampled at each plot by beating three branches each (and tree height was measured at the time of sampling). Samples from individual trees sampled from different periods and different branches were pooled together. Sampled tree individuals were chosen at random and were designated as ‘inner’ or ‘outer’ depending on their position in the monospecific cell. Outer trees were at the edge of monospecific cells and neighbored heterospecific cells, while inner trees were surrounded by tree individuals of the same species. This was done in order to test for neighborhood diversity effects on the community of arboreal spiders.

After beating, the spiders were collected and preserved in 70% ethanol, sorted, and adults were determined to species using the identification key by Nentwig et al. (2021). Nomenclature followed the World Spider Catalog (2021). Tree individual data (72 replicates per tree species) as well as data pooled on the plot level (16 replicates) were used for further analyses. To estimate spider biomass, we measured the body length (tip of prosoma to tip of opisthosoma without spinnerets) of all spider individuals (including juveniles) and calculated their biomass (in mg) based on the body length-biomass equations by Penell et al. (2018). In addition, we retrieved information on the guild classification of spider species by Cardoso et al. (2011) and phenological length in months of the activity period of adults (Nentwig et al., 2021), 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). Furthermore, we distinguished between species associated and those not associated with forests based on data of habitat use provided in Dorrow et al. (2019) and Nentwig et al. (2021).

3.2.3 Statistical analysis

We analyzed the data at two spatial levels, for individual trees and at the plot level, to test the extent to which spatial scale influences spider community patterns. Since plot-level sampling effort varied between the monocultures and different mixtures, rarefied spider species richness (N = 18 spider individuals) was used in the plot-level analyses to calculate abundance-independent species richness. Furthermore, rarefied spider communities were used for the calculation of plot-level functional diversity, while plot-level biomass and abundance data were controlled for sampling effort by standardizing to the same number of sampled tree individuals per plot. Functional diversity was calculated only at the plot level since tree-level spider abundances were too low in some cases (<3 spider individuals) to calculate meaningful functional diversity indices. The functional diversity indices used were functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) (Villéger et al., 2008). Since in some cases spider species were recorded in very low numbers, and might potentially represent accidental occurrences of vagrant species, we focused our analyses of functional diversity patterns on species that were recorded with more than three individuals (see also Schuldt & Scherer-Lorenzen, 2014). The excluded species made up 7% of all adult spider individuals and additional analyses with the full spider data set showed that our results are robust in the case of FRic (Pearson’s $r = 0.93$, $P < 0.001$) and FDiv ($r = 0.83$, $P < 0.001$), while results for FEve were less strongly correlated ($r = 0.43$, $P = 0.1$) but were qualitatively similar (Table B2).

We used abundance (adult and total), biomass (adult and total), community weighted mean (CWM; average biomass of individual adult spiders) biomass and species richness at the tree level, while at the plot-level the functional diversity indices FRic, FEve and FDiv were used in addition to the previously mentioned response variables. Species richness was log(x) transformed at the plot level and log(x + 1) transformed at the tree level, while abundance, biomass and CWM biomass were log (x + 1) transformed to improve modelling assumptions. At the plot level, we used a linear model that included tree species richness, the relative proportion of each tree species as a measure of tree identity effects, as well as their interactions as predictors. At the tree individual level, we used a linear mixed effects model that included tree position (inner/ outer), tree species identity, the interaction between tree position and tree species identity, tree species richness, and the interaction between tree species richness and all previously mentioned variables as predictors. Study plot was included as a random effect. Tree height was not included in the analyses because it was strongly related to tree identity, with higher values for coniferous trees (which, however, did not directly affect our results because spiders were sampled from individual branches independent of tree height). We started from full models and used a stepwise selection procedure based on AICc (Burnham & Anderson, 2010) to acquire models with the fewest number of predictors and the lowest global AICc.

We analyzed the similarity between spider assemblages per tree species at the plot level (36 replicates = four monocultures, six 2-species mixtures, four 3-species mixtures and 2 4-species mixtures) with non-metric multidimensional scaling (NMDS). Similarity was based on the Morisita-Horn index of square root-transformed abundance data (Jost et al., 2011). A stable solution was computed from multiple random starting points on the basis of three reduced dimensions (20 random starts). As in the calculation of functional indices, possible vagrant species (<3 individuals) were not included in the analysis. We additionally analyzed the multivariate homogeneity of group dispersions as a measure of beta diversity (Anderson et al., 2006) with a multidimensional scaling analysis (MDS). Lastly, the indicator values (IndVal) per tree species, species and stand type as well as presence of tree species in the plot, for all spider species were calculated using the IndVal procedure (Dufrêne & Legendre, 1997). We used significant IndVal values > 0.25 as a threshold (Dufrêne & Legendre, 1997). All analyses were performed in R 3.5.1 (http://www.R-project.org).

3.3 Results

We captured a total of 3615 spiders, 775 of which were adults. The families Philodromidae (859), Araneidae (781), Theridiidae (756) and Linyphiidae (744) dominated when taking all spider individuals into account (Table B3). For adult spiders, Linyphiidae and Theridiidae dominated: Linyphiidae accounted for 282 individuals from 17 out of the 57 identified species, with the linyphid species *Entelecara congenera* (219 individuals) being by far the most abundant species, while Theridiidae accounted for 247 individuals from 11 species (Table B4). Of the recorded species, three were in the Red List of German spiders (Blick et al., 2016): *Asianellus festivus* (C. L. Koch, 1834), *Dendryphantes hastatus* (Clerck, 1757) and *Theridion familiare* O. Pickard-Cambridge, 1871 (Table B4). Forty species with 743 individuals were typical forest species. Forest species patterns were highly correlated with the overall catch for all metrics ($r > 0.87$, $P < 0.001$) and thus we only tested patterns in the overall catch.

3.3.1 Plot level effects

At the plot level, tree species richness had a significant positive effect on both rarefied spider species richness and FRic (Fig. 3.1A-B, Table 3.1). The tree proportions of Douglas fir and Norway spruce had significant negative effects on rarefied spider species richness (Fig. 3.2A), and FRic (Fig. 3.2B). Effects of these tree species on spider FEve and FDiv were similar, but not consistently significant (Fig. 3.2C-D, Table 3.1). Likewise, spider total abundance and total biomass significantly decreased (and adult spider biomass tended to decrease) with increasing proportion of Norway spruce in the study plots (Fig. 3.2F-G, Table 3.1). In contrast, the abundance of adult spiders increased with increasing Douglas fir proportion (Fig. 3.2E), but the latter significantly decreased total spider biomass (Fig. 3.2H). Lastly, CWM biomass decreased with an increase in conifer proportion, with the effect being stronger for Douglas fir (Table B5, Fig. B1). Sessile oak proportion also had a negative effect on CWM biomass, but only when including vagrant species (Table B6).

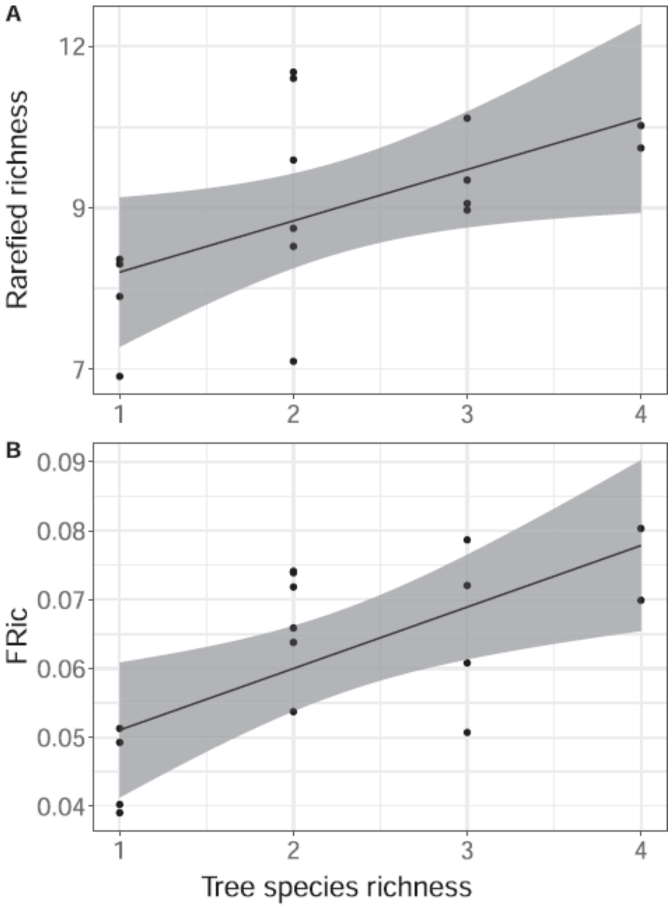

Fig. 3.1. Relationships between tree species richness, and (A) rarefied species richness (log-transformed) and (B) the functional richness (FRic) of arboreal spiders at the plot level. Y-axis values show data adjusted for covariates in the final linear modes.

Table 3.1. Output of the linear models for arboreal spider species richness, functional diversity, adult and total abundance and biomass at the plot level. Significant effects indicated in bold.

	Log(rarefied species richness)			FRic			FEve			FDiv		
	Est. (±SE)	*t*	*P*	Est. (±SE)	*t*	*P*	Est. (±SE)	*t*	*P*	Est. (±SE)	*t*	*P*
Intercept	2.52 (±0.06)	41.6	**<0.001**	0.08 (±0.01)	15.4	**<0.001**	0.72 (±0.01)	66.3	**<0.001**	0.87 (±0.01)	69.3	**<0.001**
Tree species richness	0.08 (±0.03)	2.4	**0.036**	0.01 (±0.00)	3.1	**0.009**						
Douglas fir proportion	-0.60 (±0.13)	-4.8	**<0.001**	-0.04 (±0.01)	-3.8	**0.003**	-0.02 (±0.01)	-2.0	0.067	-0.05 (±0.03)	-1.9	0.08
Spruce proportion	-0.50 (±0.13)	-4.0	**0.002**	-0.03 (±0.01)	-2.6	**0.024**				-0.06 (±0.03)	-2.3	**0.036**
F, DF$_{(n,d)}$, P, Adj.R^2	F=11.6 DF$_{3,12}$ P=**0.001** R^2=0.68			F=8.7 DF$_{3,12}$ P=**0.002** R^2=0.61			F=3.9 DF$_{1,14}$ P=0.067 R^2=0.16			F=3.4 DF$_{2,13}$ P=0.063 R^2=0.25		
	Log(adult abundance+1)			Log(total abundance+1)			Log(adult biomass+1)			Log(total biomass+1)		
	Est. (±SE)	*t*	*P*	Est. (±SE)	*t*	*P*	Est. (±SE)	*t*	*P*	Est. (±SE)	*t*	*P*
Intercept	2.94 (±0.08)	37.4	**<0.001**	4.72 (±0.06)	77.9	**<0.001**	5.15 (±0.13)	40.5	**<0.001**	6.14 (±0.09)	71.7	**<0.001**
Tree species richness												
Douglas fir proportion	0.65 (±0.21)	3.1	**0.008**							-0.58 (±0.18)	-3.3	**0.006**
Spruce proportion				-0.50 (±0.16)	-3.0	**0.009**	-0.67 (±0.34)	-2.0	0.07	-0.74 (±0.18)	-4.1	**0.001**
F, DF$_{(n,d)}$, P, Adj.R^2	F=9.5 DF$_{1,14}$ P=**0.008** R^2=0.36			F=9.3 DF$_{1,14}$ P=**0.009** R^2=0.36			F=3.9 DF$_{1,14}$ P=0.070 R^2=0.16			F=10.6 DF$_{2,13}$ P=**0.002** R^2=0.56		

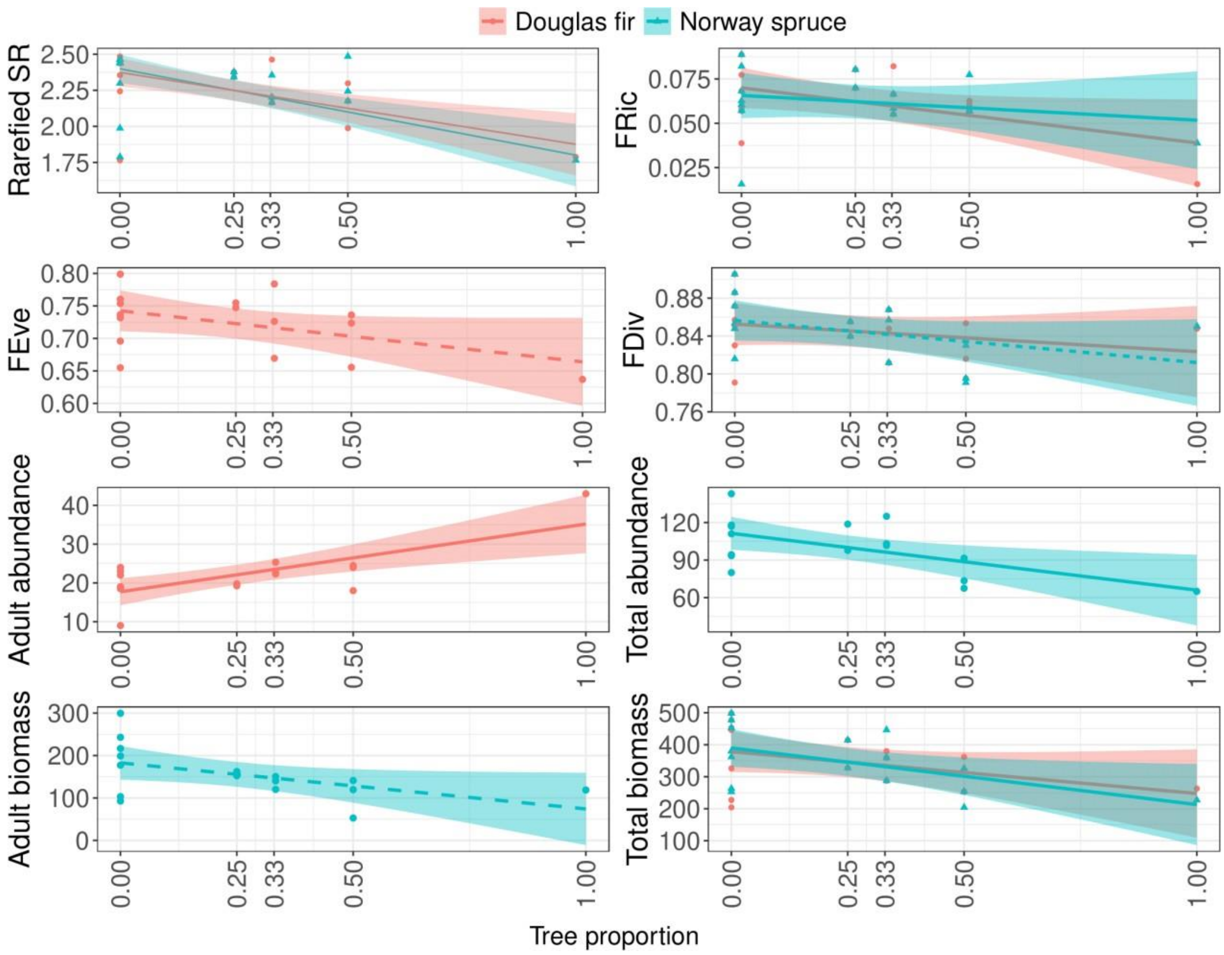

Fig. 3.2. Douglas fir and Norway spruce proportion effects on rarefied species richness (A), FRic (B), FEve (C), FDiv (D), adult abundance (E), total abundance (F), adult biomass (G) and total biomass (H) of arboreal spiders at the plot level. Regression lines show significant ($P \leq 0.05$; full lines) or marginally significant ($P \leq 0.1$; broken lines) relationships. Note that the y-axis in A and E-H is on a logarithmic scale.

3.3.2 Tree level effects

At the level of individual trees, tree species richness had a significant positive effect on the CWM spider biomass, but only for outer trees (Fig. B2, Table B7). However, for most metrics of spider diversity, abundance and biomass, effects of tree species identity were particularly pronounced. As for the CWM of biomass, these effects largely depended on tree position within the plots, with more pronounced differences on the outer than on the inner trees (Fig. 3.3). On the outer trees, total and adult spider abundance (Fig. 3.3A) and species richness (Fig. 3.3E) were significantly higher on conifers than on deciduous trees. Furthermore, adult and total spider biomass (Fig. 3.3C) was significantly higher on Douglas fir than on deciduous trees. European beech had significantly lower CWM biomass than the other tree species (Fig. 3.3G) and values for abundance, biomass and diversity were generally lower than on sessile oak (Fig. 3.3, left column). The inner trees data followed a similar pattern for abundance and species richness, with Douglas fir having significantly higher adult and total spider abundance (Fig. 3.3B) and species richness (Fig. 3.3F) than other trees. On the other hand, Norway spruce had significantly less adult biomass than European beech and significantly less total biomass (Fig. 3.3D), and a lower CWM spider biomass (Fig. 3.3H) than the other tree species. Furthermore, CWM biomass showed a contrast to the inner tree data with European beech having significantly higher values than the coniferous trees (Fig. 3.3H).

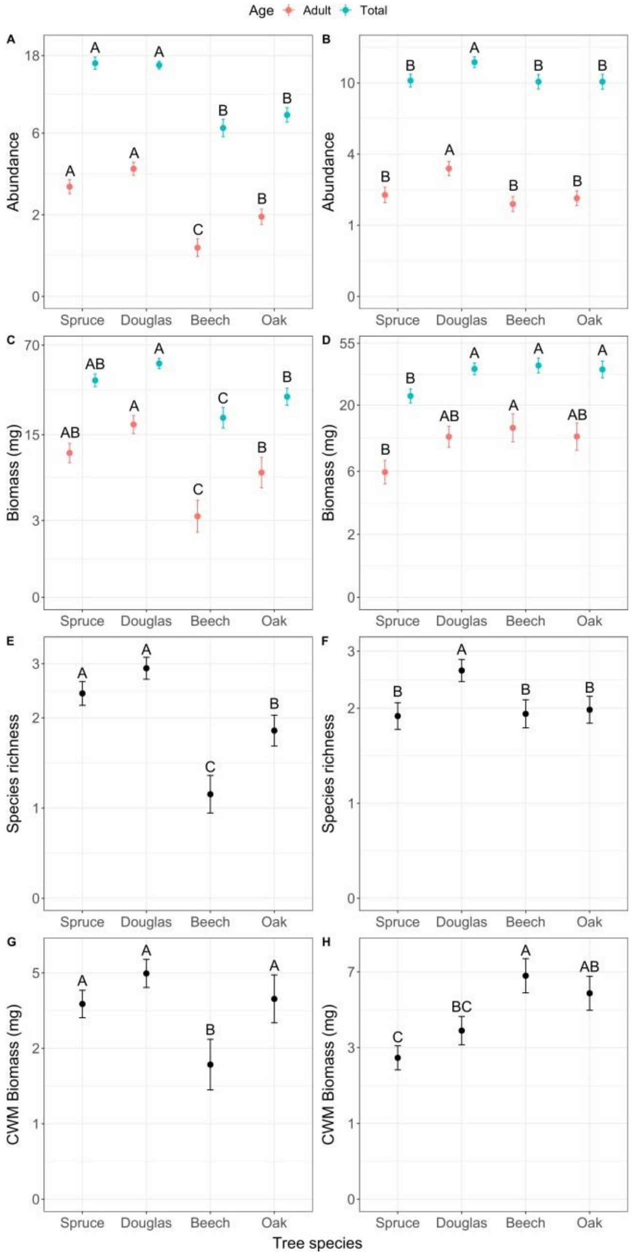

Fig. 3.3. Differences among tree-level (European beech, Douglas fir Norway spruce and sessile oak) patterns of adult and total abundance of arboreal spiders on outer (A) and inner trees (B), biomass on outer (C) and inner trees (D), species richness on outer (E) and inner trees (F) as well as CWM biomass on outer (G) and inner trees. Note that the y-axis in A-D is on a logarithmic scale. Significant differences (linear models; $P \leq 0.05$) in the means indicated by different letters.

The structure of the spider communities inhabiting different tree species showed a clear separation between deciduous and coniferous tree species, with and without possible vagrant species (Fig. 3.4A and B). Centroids (weighted average effects, in blue) of mixtures of coniferous and deciduous trees in the NMDS ordination were located between the monocultures, indicating a larger overlap in community structure.

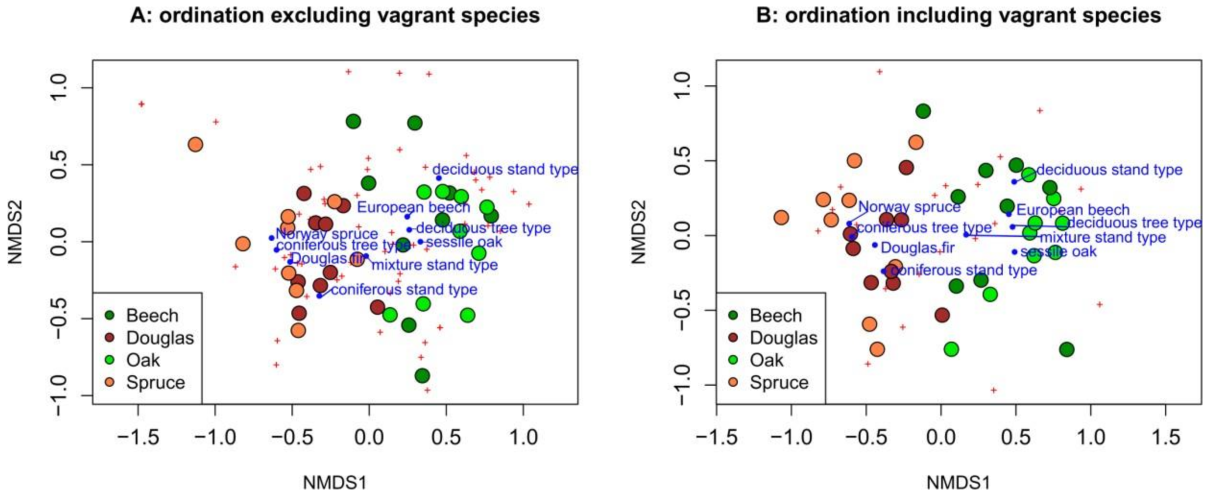

Fig. 3.4. NMDS ordination plot (Morista-Horn index) of arboreal spider communities excluding (A) and including (B) species with ≤ 3 individuals, for each tree species (European beech, Douglas fir Norway spruce and sessile oak) from each of the 16 studied plots. Stress = 0.167 and 0.189 respectively. Red crosses represent spider species. Filled blue circles are centroids of the factor levels of the environmental predictors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The analysis of multivariate homogeneity of group dispersions confirmed this difference in beta diversity between deciduous and coniferous trees. with almost the same dispersion when vagrant species are excluded (Fig. 3.5) and included (Fig. B3). Furthermore, this analysis showed a smaller spread for community structure of coniferous trees when compared to deciduous trees. The IndVal indicator analysis supported this finding, where the most abundant spider, *Entelecara congenera,* had high indval values for coniferous trees and stand types, as well as Douglas fir and Douglas fir presence in the plots, while there were no species that qualified as indicators for deciduous tree species or stand types (Table 3.2).

Table 3.2. Results of the analysis of indicator values (IndVal) of arboreal spider species for different tree species, tree types and stand types, as well as presence of tree species in the plot

Species	Indicator for	IndVal	*P*	Abundance
Entelecara congenera	Coniferous tree type	67.28	0.001	219
Entelecara congenera	Coniferous stand type	44.54	0.001	219
Entelecara congenera	Douglas fir	39.87	0.001	219
Entelecara congenera	Douglas fir presence	27.13	0.027	219
Philodromus collinus	Coniferous trees	26.47	0.001	63

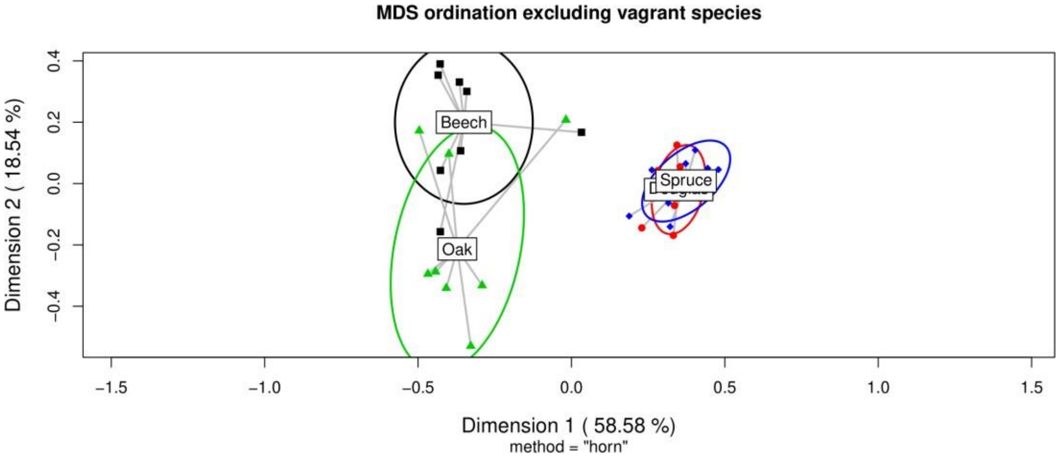

Fig. 3.5. MDS ordination plot (Morista-Horn index) of the multivariate homogeneity of group dispersions (variances) among arboreal spider communities (excluding species with ≤ 3 individuals), for each tree species (European beech, Douglas fir Norway spruce and sessile oak) from each of the 16 studied plots. Ellipses represent the standard deviation around the centroids of each tree species.

3.4 Discussion

In our study, increasing tree species richness promoted arboreal spider species richness and functional richness at the plot level, as well as CWM spider biomass on trees with heterospecific neighborhoods, but did not affect other components of the spider communities. Instead, spiders were more strongly influenced by tree identity and tree composition. Notably, individual Douglas fir trees harbored spider communities with significantly higher abundance and species richness than tree individuals of the deciduous species. On the other hand, the increase in the proportion of coniferous species at the plot level had negative effects on both spider diversity and biomass. The fact that the diversity and abundance of arboreal spiders inhabiting conifers was higher when the conifers were planted in low proportions shows the benefits of planting these highly productive trees in mixtures, both for biodiversity conservation and for promoting biocontrol.

3.4.1 Tree species richness effects

The positive effect of tree species richness on arboreal spider diversity at the plot level is in line with the predictions of the “enemies hypothesis” (Root, 1973), as outlined in the introduction. In contrast, studies in many other tree diversity experiments have shown no evidence for the “enemies hypothesis” for epigeic predators (Moreira et al., 2016; Vehviläinen et al., 2008; Yeeles et al., 2017), including epigeic spiders at our study site (Schuldt and Scherer-Lorenzen, 2014). Our study therefore emphasizes the necessity to include multiple forest strata to better understand tree diversity effects on higher trophic-level diversity and functioning. Other recent research of arboreal predators found positive effects of tree diversity on predator diversity or abundance as well (Ampoorter et al., 2020; Esquivel-G´omez et al., 2017; Setiawan, 2016). The differences in diversity effects on epigeic and arboreal predators may be due to the substantial difference in environmental conditions (e.g., Parker, 1995; Richards, 1996) and structural features (Brokaw & Lent, 1999) along the vertical dimension, making direct associations of tree diversity with arboreal predators more likely than with epigeic predators.

The fact that the diversity effect on spider species richness occurred despite an absence of an accompanying significant effect on spider abundance runs counter to the “more individuals hypothesis” (Srivastava & Lawton, 1998), which predicts an abundance-driven increase of species with increasing resources. In our study, tree diversity could instead have favored an increase in the number of physical refuges or resource types available to arboreal spiders in more diverse forests (Langellotto & Denno, 2004). Arboreal spiders have been indicated to be specific to structures and resources provided by different tree species and stand types (Mupepele et al., 2014). Accordingly, we found that mixtures had a greater number of singletons (see Table B4), suggesting that increased recruitment and turnover of rare, potentially specialized species could have contributed to the observed diversity effect (Esquivel-Gómez et al., 2017). This is also indicated by the lack of tree species richness effects on spider diversity and abundance at the tree level, which means that increased spider diversity is a result of larger-scale turnover of species among trees and tree species.

At the tree level, tree species richness only influenced the CWM spider biomass on outer trees. This finding might be explained by a reduction in the dominance of *Entelecara congenera* at higher diversity levels, possibly as a result of it being outcompeted for habitat space by larger spiders dispersing from surrounding trees. The scale dependence of the effects of tree species richness on spiders can be important because biocontrol might be promoted at larger scales through higher functional richness at the stand level. However, these effects do not necessarily have to cascade down to smaller spatial scales, such as individual trees. Because direct predator–prey interactions take place locally (Muiruri et al., 2016), further research should clarify what the consequences for top-down control of these spatially deviating patterns might be—and how forest management should best develop the diversification of forest stands.

Since most tree diversity experiments, including our study site, currently represent relatively young forest stands, relationships and interactions across trophic levels might differ from more mature forest ecosystems with established predator and herbivore population cycles (Grossman et al., 2018). Nonetheless, observational studies conducted in mature forest stands often revealed a similar pattern where tree diversity had no or even a negative effect on epigeic predator abundance or species richness (e.g. Oxbrough et al., 2012; Schuldt et al., 2008, 2011, 2014; Zou et al., 2013). While comparable data for mature forest canopies is lacking these results indicate that effects of tree species richness on predators might not systematically differ between young and mature forests (see also Staab & Schuldt, 2020).

3.4.2 Tree identity effects

Effects of tree species identity played a key role in structuring spider communities at the tree level, in concordance with research from other forests (Ampoorter et al., 2020; Vehviläinen et al., 2008). In our study, there was a clear difference in spider community structure sampled from coniferous and deciduous trees. Arboreal spiders had higher richness, abundance and biomass per tree on conifers, especially on Douglas fir. Conifers seem to provide more habitat space, as well as more diverse microhabitats (Korenko et al., 2011). In accordance with recent research on tree neighborhood effects on arboreal predators (Setiawan, 2016), tree position strongly mediated this effect, with a stronger difference in arboreal spider communities between tree species on outer trees. This might potentially indicate an effect of mixing tree species that was independent from the actual number of tree species in the mixtures. Heterospecific neighbors might particularly benefit conifer trees if additional, and especially larger, spider species immigrate from these neighbors. Dispersal from conifers to deciduous trees was less likely because many conifer-specific spiders, such as sheet-web builders, require dense needle structures for web attachment (Halaj et al., 2000). In line with these tree identity effects, we also observed a distinction between arboreal spider communities inhabiting purely deciduous and purely coniferous stands and overlapping communities in mixed stands. This is probably due to microclimatic and structural differences in leaf shape, branch and leaf density or bark structure between conifers and deciduous trees (Halaj et al., 2000). This means that tree-level patterns of spider communities will strongly determine plot-level composition. From a conservation point of view, coniferous monocultures apparently cannot act as secondary habitat for many spider species occurring in deciduous forests (see also Finch, 2005). The fact that mixtures of conifers and deciduous tree species showed an intermediate spider species composition (and interestingly, the few red-listed species recorded in our study were all recorded in mixtures, see Table B4) might suggest that mixtures can accommodate the demands for both species conservation and timber production in a better way.

However, arboreal spider communities inhabiting coniferous trees from different plots had lower beta diversity than communities inhabiting deciduous trees. Moreover, our analyses showed that an increasing proportion of Douglas fir and Norway spruce decreased most metrics of spider diversity and biomass at the plot level, probably due to the lower species turnover among coniferous tress. The lower beta diversity on coniferous trees was influenced by the strong dominance of the sheet web weaving hunter *Entelecara congenera*, which had a considerable effect on spider community structure. The dominance of this very small spider on Douglas fir also explains why despite the high spider abundance per tree, biomass decreased at the plot level when proportions of Douglas fir increased.

The presence of effects of tree species richness, but particularly of tree species identity, early in the establishment of forest stands might lead to strong top-down control of herbivores in critical stages of the development of mixtures (Esquivel-Gómez et al., 2017). Tree species selection and the proportion in which these trees are mixed with other species will not only affect the biocontrol potential, but can also be highly relevant for the conservation of predator biodiversity. Our results emphasize the importance of how these trees are spatially distributed within the forest stands. Conifers planted in mixtures with deciduous trees might better promote biodiversity and biocontrol when planted next to heterospecific neighbors (i.e. in single-tree rather than patch-planting patterns). The negative impact of increasing conifer proportions on spiders at the plot level further suggests that establishing tree mixtures of deciduous and coniferous trees that benefit both production and conservation would need to carefully evaluate the maximum proportion of conifers under which conservation goals can still be reached (see also Oxbrough et al., 2012 for epigeic spiders), in addition to the spatial scale at which trees are mixed. In this context, an important finding of our analyses is that potentially negative effects of the non-native Douglas fir on arboreal arthropods (but not on epigeic arthropods, see Schuldt & Scherer-Lorenzen, 2014) were not more severe than effects of native conifers that are planted outside of their natural habitats (which is the case for Norway spruce in most regions of Central Europe; see also Ziesche & Roth, 2008). This is probably mainly due to the phylogenetic closeness of these two species that makes them comparable (Goßner, 2008), especially when it comes to plant structure (Strong et al., 1984).

3.5 Conclusions

Our study shows that the effects of non-native tree species on arboreal predators clearly differ from effects on so far predominantly studied predators on the forest floor, with Douglas fir trees harboring spider communities with significantly higher abundance and species richness than European beech and sessile oak at the local scale of individual trees. Furthermore, small-scale and larger-scale patterns can deviate from each other. Tree diversity promoted spider diversity at the plot level, while a tree-level diversity effect on CWM biomass was recorded only on trees with heterospecific neighborhoods. Both were a result of higher species turnover between heterospecific trees, especially from deciduous to coniferous trees. Furthermore, tree identity effects were dependent on spatial scale, with the positive effect of conifers at the tree level becoming negative at the plot level due to lower species turnover among conifers. These findings highlight that a comprehensive understanding of how tree diversity and non-native tree species affect predator diversity and potential top-down control requires a nuanced approach that incorporates differences in forest strata and spatial scale.

Chapter 4

Non-native Douglas fir (*Pseudotsuga menziesii*) promotes sentinel prey attack rates in Central European forests [1]

Dragan Matevski, Jonas Glatthorn, Peter Kriegel, Andreas Schuldt

Abstract

The increased utilization of non-native tree species in monocultures or tree mixtures has repeatedly been shown to have negative consequences for the abundance and biomass of natural enemies. However, it is often unknown whether these effects translate into lower top-down control, and if so, whether these effects are driven by tree diversity and identity or by factors not strictly attributed to tree identity (e.g. light conditions or vegetation structure). Here, we used model caterpillars to study the effect of non-native Douglas fir (*Pseudotsuga menziesii*) on pest control in Central European forests. Model caterpillars were set at two strata (ground and herb layer) in 40 plots of five forest stand types. Monocultures of European beech (*Fagus sylvatica*), Douglas fir and Norway spruce (*Picea abies*) and two-species mixtures of European beech and each of the conifers were studied. We analyzed plot-level attack rates (total, arthropod, bird, and mammal attack rates) in relation to stand type, stand composition and microhabitat variability. Against expectations, stands with a higher proportion of Douglas fir had higher total and arthropod attack rates. However, this effect was lessened in stands with higher tree species diversity. Indirect effects of Douglas fir were stronger than direct tree identity and proportion effects, with both increased light availability and understory vegetation complexity promoting attack rates. Therefore, promoting vegetation complexity and light availability by thinning, or planting more open Douglas fir stands with a lower stem density could help to promote pest control in forest stands of non-native tree species.

4.1 Introduction

Silviculture is facing multiple challenges given the increasing need to balance social, ecological and economic demands from forests (Albert et al., 2020; Ruckelshaus et al., 2015). One key challenge is dealing with tree damage and mortality due to insect pests (Jactel et al., 2009). This is exacerbated by climate change, where warmer average temperatures and prolonged drought can trigger large-scale outbreaks of insect herbivores, which in turn increases overall tree mortality (Ammer et al., 2018; Jacquet et al., 2012; Netherer et al., 2019). At the same time, climate change requires adaptive forest management to mitigate negative effects of altered environmental conditions on tree growth (Allen et al., 2010). This has resulted in increased utilization of non-native tree species that are well adapted to the expected climatic conditions such as Douglas fir (*Pseudotsuga menziesii*) in Central Europe (Höltermann et al., 2008; Schmid et al., 2014).

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Douglas fir currently accounts for 2–3% of the forest area in several European states (Schmid et al., 2014), but the area is expected to increase making it likely to become the third most important conifer in German forests after Norway spruce and Scots pine (*Pinus sylvestris* L.) (Höltermann et al., 2008). In terms of forest pests, Douglas fir has shown distinct incompatibilities, as even polyphagous herbivores such as black arches (*Lymantria monacha* L., 1758) cannot cope well with a diet of Douglas fir needles (Gruppe & Goßner, 2006). Furthermore, Douglas fir has not been victim to larger pest outbreaks in Europe so far (Roques et al., 2006). However, there are concerns over the negative effects of planting Douglas fir on the abundance and biomass of natural enemies (Finch & Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014), a key force acting on the survival and reproductive success of forest insect populations (Klapwijk et al., 2016; Vidal & Murphy, 2018). The effect of control by natural enemies might become especially important for forest stands containing non-native tree species, as these species can be expected to accumulate introduced herbivores, as well as native herbivores performing a host jump, over time (Roques et al., 2006). Planting Douglas fir in mixtures may alleviate some of these concerns. Enemy to prey ratios may be higher in mixtures than in monocultures due to a higher availability of alternative prey, complementary food resources and microhabitats (Björkman et al., 2015). Moreover, admixing such non-native species with native tree species may have benefits on productivity, climatic stability, and ecological sustainability as well (Tognetti et al., 2010). In this context, the phylogenetic diversity of mixtures is important, with mixtures of more phylogenetically distant tree species being more resistant to herbivores (Castagneyrol et al., 2014), as well as promoting other ecosystem services such as increased wood production (Cadotte et al., 2008).

Forest stands in Central Europe are increasingly transitioning from monocultures to mixed-species forest stands (Pretzsch, 2019), with phylogenetically diverse mixtures of deciduous and coniferous tree species being used to promote both biodiversity and economic utility (Knoke et al., 2008). Recent studies have shown lower arthropod predator abundance and biomass in Douglas fir stands in comparison to native stands, as well as a negative effect of Douglas fir presence in mixtures with native tree species (Finch & Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014, but see Matevski & Schuldt, 2021). However, using predator densities as a measure of pest control intensity is complicated by factors like predator satiation, intraguild predation, and intra- and interspecific competition (Schmitz, 2007). Therefore, there is a need to understand the effects of non-native tree species such as Douglas fir on pest control under field conditions. Moreover, it is important to research the link between predator density and predation pressure to understand the effect of tree species mixing on predators and their efficacy (Staab & Schuldt, 2020). This can be studied by assessing attack rates of multiple generalist predator groups such as arthropods, birds or mammals on artificial clay caterpillars (Howe et al., 2009). Such artificial prey cannot move, defend themselves, or behave as true prey would, and the absence of chemical cues may conceal prey identity, so equating these attack rates as true predation rates is difficult (Lövei & Ferrante, 2017). Nevertheless, the use of artificial sentinel prey has several advantages over using live prey: it is cheaper, does not require prey rearing; producing them can be simple and fast and analyzing attack marks allows distinguishing among attack rates of different generalist predator groups (Lövei & Ferrante, 2017). These generalist predators often have their greatest impact on herbivores with low-density populations and may be responsible for maintaining forest defoliator populations at endemic densities (Elkinton et al., 1996; Gould et al., 1990; Klemola et al., 2002; Nixon & Roland, 2012).

Both abiotic and biotic factors affect the attack rates of these generalist predators. Attack rates were shown to decrease with elevation (Lövei & Ferrante, 2017; Roslin et al., 2017) and, in forested habitats, to increase with latitude (Roslin et al., 2017). Moreover, attack rates may vary with forest stratum from the ground to the canopy, which is important for forest management aimed at promoting control by natural enemies. For example, arthropod attack rates are highest on the ground (Lövei and Ferrante, 2017), while bird attack rates are higher in the canopy than understory (Loiselle & Farji-Brener, 2002). Lastly, predators can show preferences for stands containing certain tree species (Muiruri et al., 2016; Vehviläinen et al., 2008) planted at certain proportions (Matevski & Schuldt, 2021), or promoting particular microhabitat structures (Barton et al., 2009; Kollberg et al., 2014; Pinzon et al., 2018). These effects on predator communities may translate into effects on attack rates, but they remain poorly explored with respect to forest management concepts that include the use of non-native tree species.

Here we utilize a set of forty managed forest stands to assess how stand type, tree species proportions and microhabitat availability influence sentinel prey attack rates at two strata (ground and herb) in stands of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), three of the most economically important tree species in Central Europe. This species pool allows testing for differences in control by natural enemies between native European beech, non-native Douglas fir and its native relative Norway spruce, which can provide important information for future management strategies aimed at optimizing tree species composition. Inclusion of two-species mixtures of European beech with Norway spruce and Douglas fir allows us to assess whether the effects of Douglas fir are modified in mixtures and to what extent these effects deviate from the taxonomically and phytochemically more closely related Norway spruce (Schmid et al., 2014). Moreover, analyzing attack rates on the forest-floor allows us to test a stratum where many herbivores spend a part of their life cycle (Riihimäki et al., 2005), while assessing sentinel prey attack rates in the herb layer can give us insight on predation intensity on seedlings. Lastly, taking into account tree composition and microhabitat variables can reveal whether tree proportions/diversity and/or microhabitat variability are better predictors of attack rates than just stand type. This is important since microhabitat variability can be adapted by forest management to a certain extent without changing the tree species composition of the stand. We hypothesized that (i) sentinel prey attack rates vary with predator type (arthropods, birds, mammals) and forest stratum. Moreover, we expected that (ii) total attack rates are lowest in non-native Douglas fir monocultures and highest in native monocultures, and consequently intermediate in mixtures of native and non-native tree species. Finally, we hypothesized that (iii) these differences in sentinel prey attack rates between stands are better explained by tree proportions and species diversity than just tree identity and (iv) depend on variability in microhabitat features important to predators.

4.2 Materials and methods

4.2.1 Study site

We performed our study in the framework of the research training group (RTG) 2300 - “Enrichment of European beech forests with conifers: impacts of functional traits on ecosystem functioning”. The study sites included 40 0.25 ha mature temperate forest stands (plots), all differing in stand age, tree proportions and site conditions (Table C1). The forest stands comprised three of the most commercially important species in Europe: the broadleaved European beech (*Fagus sylvatica* L.), the coniferous Norway spruce (*Picea abies* (L.) H. Karst.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Plots were organized into eight ‘quintets’, across the federal state of Lower Saxony in Germany, with 4 nutrient rich, higher elevation quintets with higher precipitation in the south and 4 nutrient poor, drier, lower elevation quintets in the north (Figure C1). The quintets were used to avoid bias due to regional clustering of stand types. Each quintet contained one monoculture plot of each tree species and two European beech-conifer (European beech- Norway spruce and European beech-Douglas fir) mixtures. The cutoff point for stands being classified as mixtures was tree proportions of at most 85% of the more dominant target species and at least 15% of the other target species. There were two exceptions to this rule due to the spatial distribution of trees in the stands (Table C1). Classifying the stands in this way is more meaningful from the perspective of forest management (plots were selected together with foresters) since this is how these stand types look like in practice.

4.2.2 Data collection

Clay model caterpillars were used in order to assess attack rates at the study plots (Low et al., 2014; Lövei & Ferrante, 2017). Model caterpillars were 25 mm long and 5 mm wide, made of green non-toxic modeling clay (Staedler Noris Club 8421, leaf green) and were threaded with a 15 cm long wire (diameter 0.4 mm) for attachment. In order to avoid false positive assessments of damage, surfaces of all caterpillars were smoothed before attachment. Model caterpillars were set at eight points (at least 10 m apart) in two linear transects set near the center of each plot. Four caterpillars were set at each point, two at the ground and two at the herb stratum. Ground stratum caterpillars were attached to the bottom of an herbaceous' plant stem by wrapping the threaded wire around the stem, while herb stratum caterpillars were attached on branches and leaves of herbaceous plants at a height of 30 cm by wrapping the threaded wire around the branches/leaves. A total of 1280 clay caterpillars (4 caterpillars × 8 points × 40 plots) were set in the period of 16.–31.05.2019 for 7–8 days. Afterwards, we provided a fresh set of undamaged caterpillars and set them in the period of 24.05–13.06.2019 for 12 days. We pooled data from the two consecutive assessments to represent predator impact over a three week period during an important part of the vegetation period. Due to the discrepancy in exposure time between the periods, as well as small site-specific differences as a result of fieldwork restrictions (1–2 day discrepancy for some sites), all subsequent damage of the caterpillars was assessed on a predation per day basis and expressed in percentage of predated caterpillars per day at the plot level (see Lövei & Ferrante, 2017).

After the exposure period, the model caterpillars were carefully collected from the field, tagged individually with a label, and later analyzed for damage using a stereomicroscope (10–40 × magnification) to avoid missing small damage marks. The presence of any attack marks was noted and all marks were categorized into arthropod, bird and mammal attack marks using the work of Low et al. (2014) as a reference. Only the presence of attack marks of a specific type was noted, since it is impossible to know if multiple attack marks are a result of a single or multiple individuals attacking the model caterpillar.

Multiple predictors were used to explain the variance in sentinel prey attack rates between the plots, including abiotic variables, stand type, stratum (ground, herb stratum), tree proportions, tree diversity, as well as microhabitat variability. The abiotic variables used were latitude and mean annual average temperature (MAAT) from the 1980–2019 period, interpolated from data from the German weather service (Deutscher Wetterdienst, DWD).

Tree proportions were used to describe the stand structure in a more detailed way than the categorical distinction of stand types. As a proxy of tree proportions, we used 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. This way of describing tree proportions is spatially explicit and weighted for tree size, allowing for a more precise description of mixture properties of heterogeneous stands.

Furthermore, we quantified tree species diversity with a novel spatially specific diversity index called neighborhood diversity (NDiv). Using data from the APA maps, this index defines the species diversity of the neighborhood surrounding individual trees by calculating how much of the border area is next to monospecific or heterospecific neighbors. The values range from 0 (all neighbors are monospecific) to 1 (all neighbors are heterospecific), and from these individual tree measurements the diversity is scaled to the plot-level. This allows for a spatially explicit measure of tree diversity with higher values of NDiv in stands with random distribution of trees than patch distribution even if the proportion of tree species is identical.

Microhabitat variability for each study plot was assessed in May/ June 2019 on a grid (20 m × 30 m) of 12 sample points (10 m distance among points) in the center of each plot. Data were measured in a 5 m radius around each sample point and comprised measurements of litter cover and depth, herb vegetation complexity, deadwood volume, as well as leaf area index (LAI) as a measure of light availability. From these measurements data were averaged at the plot level. The percentage of litter cover was visually estimated at each sampling point, while litter depth was measured in four perpendicular 4 m transects from the center of each sampling point, with three measurements per transect (1, 2 and 4 m). Vegetation complexity was assessed by setting up two 60 cm tall metal spikes at a distance of 30 cm from each other in the largest patch of vegetation at each point. 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. Total deadwood volume (m3/ha) of all stumps and logs with a diameter > 5 cm was assessed across the entire sampling grid. Finally, LAI was measured at each of the 12 sample points using a Solariscope (SOL 300).

4.2.3 Statistical analysis

We analyzed sentinel prey attack rates (differentiating between total, arthropod, bird, and mammal attack rates) at plot-level with linear mixed effects models in three successive steps to account for the fact that stand type, stand composition (tree proportions and diversity) and microhabitat variability were not independent from each other. In all models, plot nested in study site (quintet) was included as a random effect on the intercept.

First, we tested for effects of stand type on sentinel prey attack rates. Besides stand type (five levels), the models included MAAT (plot level), latitude (continuous variable at the plot level), stratum (two levels) and the interaction between stand type and stratum as fixed effects to account for potential effects of these site characteristics on sentinel prey attack rates.

Second, we replaced the categorical variable stand type with Douglas fir proportion, Norway spruce proportion, and neighborhood diversity, including all two-way interactions of these variables with stratum. European beech proportion was excluded from the models due to high collinearity with the proportion of conifers (variance inflation factor, VIF > 10). While tree proportions were correlated with stand type (and therefore not entered in the first type of models), they varied among mixtures. Our second model approach therefore aimed at quantifying whether more detailed information on composition can explain sentinel prey attack rates better than the simple distinction among stand types.

Third, we replaced stand type characteristics with microhabitat variables (litter cover, litter depth, herb vegetation complexity, total deadwood volume and LAI) alongside stratum and all two-way interactions between stratum and microhabitat variables. This final modeling approach was aimed at distinguishing key microhabitat variables that might explain observed differences in sentinel prey attack rates among stand types**.**

For all three steps, we started from full models and used a stepwise selection procedure based on AICc (Burnham and Anderson, 2010) to acquire models with the fewest number of predictors and the lowest global AICc. We confirmed that multicollinearity between variables was low in all models using the variance inflation factor (VIF ≤ 5), calculated with the R-package *car* (Fox & Weisberg, 2018). Lastly, we used the Tukey HSD (honest significant difference) post-hoc test and p-values adjusted with the Holm-method using the *multcomp* R-package (Hothorn et al., 2008) to test for significant differences ($P < 0.05$) in sentinel prey attack rates between stands (Table C2). Mixed models were calculated with the *nlme* R-package (Pinheiro et al., 2020). All analyses and figures were done in R 3.6.0 (http://www.R-project.org).

4.3 Results

We set a total of 2560 clay caterpillars, of which twelve (0.47%) went missing. All of the missing clay caterpillars were removed from the dataset prior to analysis. Of the analyzed clay caterpillars, 882 (34.45%) were attacked, resulting in a mean attack rate per day of 3.54%. Arthropods were responsible for most of the attacks with a mean attack rate per day of 1.57%, followed closely by mammals with 1.47% mean attack rate per day. Birds caused the lowest attack rates by far, with a mean of 0.84% per day. Of the attacked models, 12% were attacked by two or three predator groups. However there were no significant differences in the frequency of sentinel prey attacked by multiple groups between the stands.

4.3.1 Stand type effects

Mean attack rates differed significantly among forest stands for total attack rates (both ground and herb stratum; Fig. 4.1A) and for arthropod attack rates at the ground stratum (Fig. 4.1B, Tables C2, C3). In both cases there were significantly higher mean attack rates in coniferous monocultures than in beech monocultures. Moreover, attack rates in Douglas fir monocultures were also significantly higher than attack rates in both mixture types in the case of arthropods (Fig. 4.1B) and higher than in Beech/Spruce mixtures in the case of total attack rates (Fig. 4.1A). For all types of attack types (total, arthropod, bird and mammal), attack rates significantly differed between strata (Table C3). In the case of mean total (Fig. 4.1A), arthropod (Fig. 4.1B) and mammal attack rates (Fig. 4.1C), the attack rates were higher at the ground stratum, while mean bird attack rates were higher at the herb stratum (Fig. C2). Lastly, abiotic factors significantly affected attack rates, with higher temperatures positively affecting total and mammal attack rates, while arthropod attack rates decreased with increasing latitude (i.e. arthropod attack rates were lower in the northern, nutrient poorer sites; Table C3).

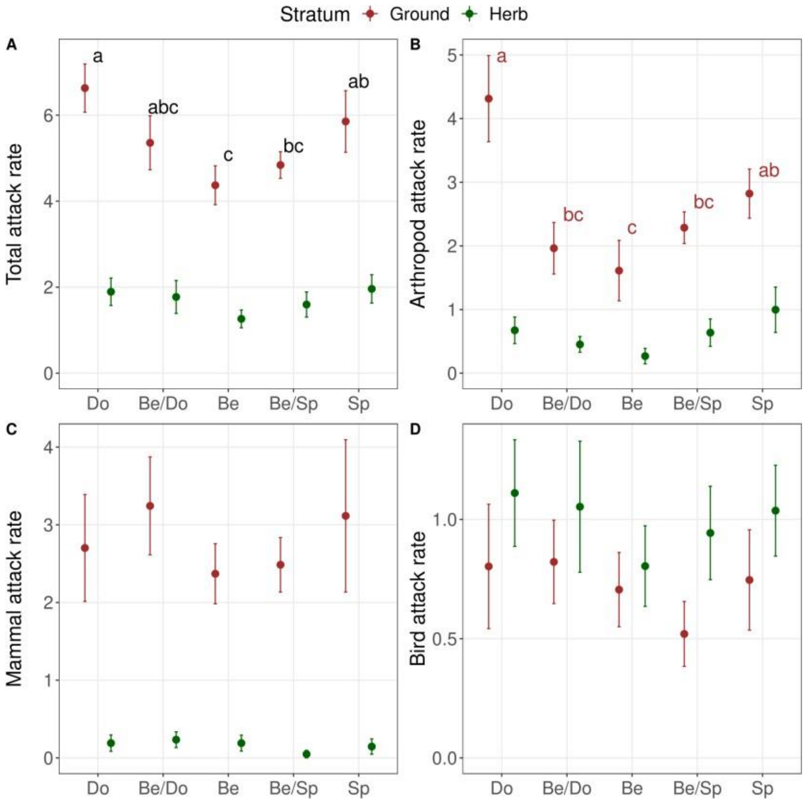

Fig. 4.1. Differences in mean attack rates (% of clay caterpillars attacked per day ± SE) between different strata and stands (Do - Douglas fir monoculture, Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture and Sp – Norway spruce monoculture): mean total (A), arthropod (B), mammal (C) and bird attack rates (D). Significant differences marked with letters.

4.3.2 Tree proportion effects

Models using tree proportions (Table C4) instead of stand type (Table C3) to describe stand conditions explained slightly more variance (between 1 and 2%), but had lower model fit (higher AICc values). Proportions of both conifers (Table C4) positively affected mean total (Fig. 4.2A) and arthropod (Fig. 4.2B) attack rates. However the effect of Douglas fir proportion on arthropod attack rates was stratum dependent, being present only on the ground stratum (Table C4). Furthermore, the interaction of Douglas fir proportion and neighborhood diversity had a significant effect on mean arthropod attack rates (Fig. 4.2C) and a marginally significant effect ($P \leq 0.1$) on total attack rates (Fig. C3). At lower neighborhood diversity levels the increase in Douglas fir proportion had strong positive effects on mean attack rates, with this effect disappearing at stands with higher neighborhood diversity (Fig. 4.2C and C3). Abiotic factors had the same effect on mean attack rates as in the stand type models (Table C4).

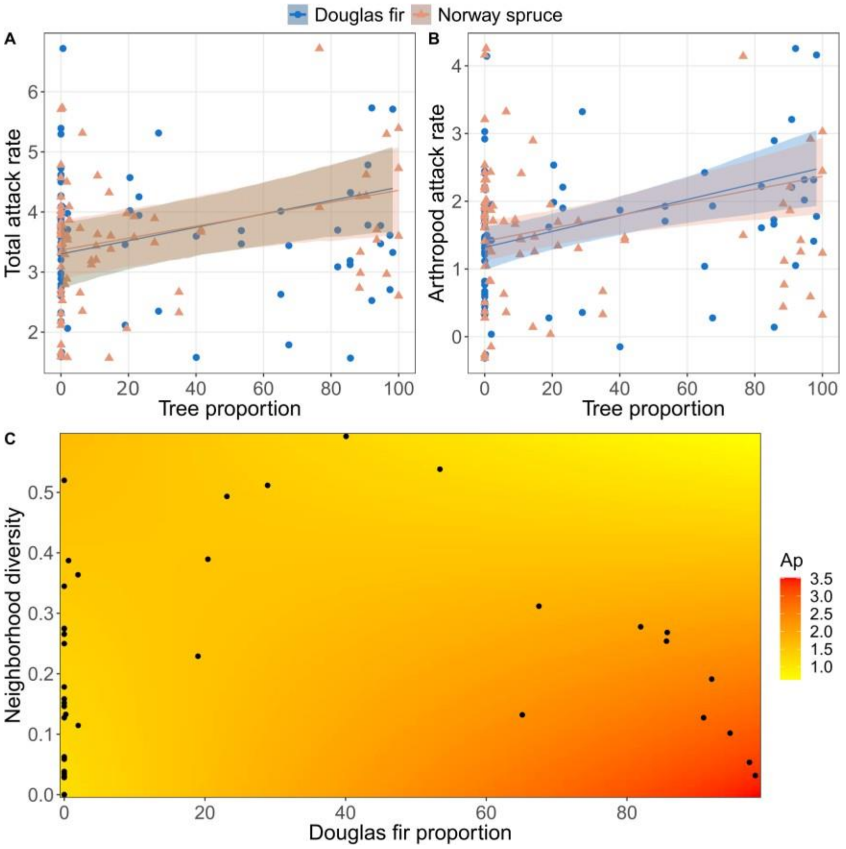

Fig. 4.2. Relationships between tree proportions (in %) of the two conifers on mean attack rates (% of clay caterpillars attacked per day) for total (A) and arthropod (B) predators. Neighborhood diversity (C) modulates the effect of Douglas fir proportion on mean arthropod attack rates. Y-axis values show data adjusted for covariates in the final mixed models. Bands represent 95% confidence intervals. Ap = arthropod attack rate (%) per day.

4.3.3 Microhabitat variability effects

For most cases, models replacing stand characteristics with plot-level microhabitat variability (Table C5) explained more variance and had better fit than stand (Table C3) and tree proportion models (Table C4). The only exception were arthropod attack rate models, where stand models explained more variance and had a better fit. Litter cover had a significant negative effect on mean attack rates (Fig. 4.3A), while litter depth (Fig. 4.3B) negatively affected arthropod attack rates. Moreover, microhabitat variability effects differed significantly depending on the stratum with only ground attack rates being significantly affected by vegetation complexity and light availability (Fig. 4.3C-D). Mammal attack rates tended to increase with increasing vegetation complexity (Fig. 4.3C), while an increase in LAI had a significant negative effect on mean arthropod attack rates (Fig. 4. 3D).

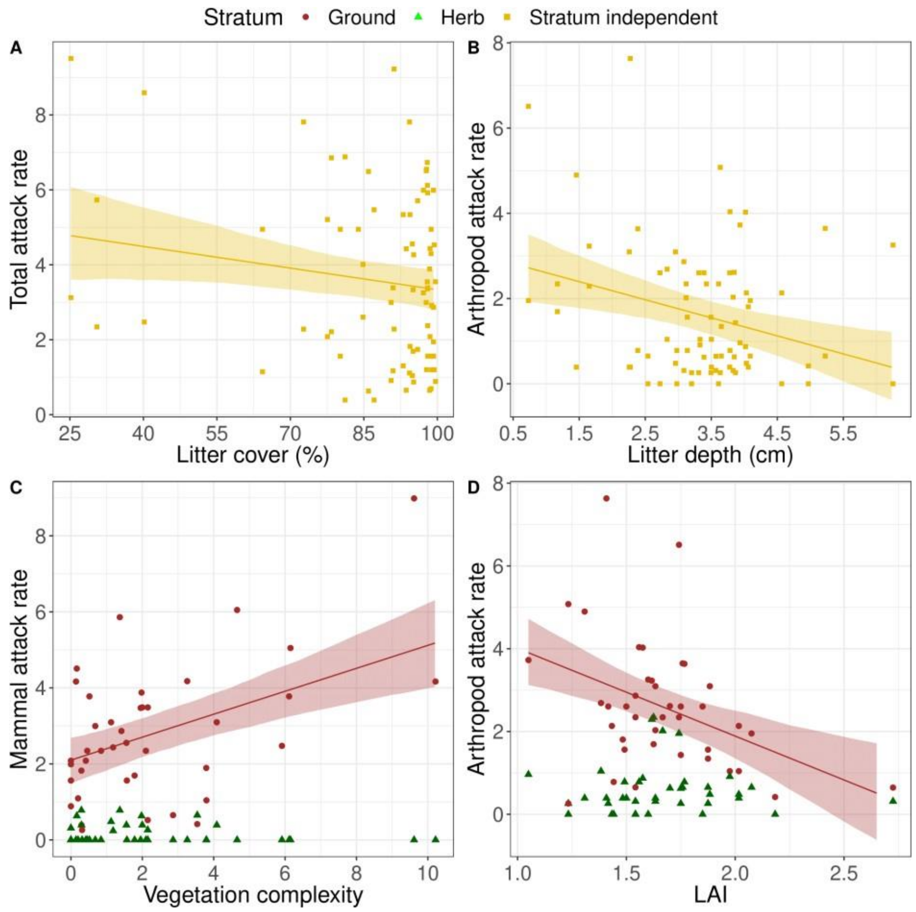

Fig. 4.3. Effects of microhabitat variables, independent (A and B) and dependent (C and D) on stratum, on mean attack rates (% of clay caterpillars attacked per day): litter cover effect on total attack rates (A), litter depth effect on mean arthropod attack rates (B), vegetation complexity effects on mammal attack rates (C), LAI effects on mean arthropod attack rates (D). Regression lines show significant ($P \leq 0.05$) relationships. Y-axis values show data adjusted for covariates in the final mixed models. Bands represent 95% confidence intervals.

4.4 Discussion

Contrary to our expectations, mean attack rates were promoted by non-native Douglas fir at both strata, with Douglas fir monocultures harboring the highest mean arthropod attack rate at the ground stratum. Analyses of tree proportion further confirmed this, showing that total and arthropod attack rates were higher in stands with higher Douglas fir and Norway spruce proportions. The effect on arthropod attack rates was stratum and neighborhood diversity dependent, showing the importance of taking spatial structure into account when analyzing control by natural enemies. Furthermore, microhabitat differences explained more of the variance in attack rates for most models than stand type or tree proportion alone, showing that forest management strategies that promote light availability and vegetation complexity may provide benefits for control by natural enemies. This could be achieved by thinning or with specific management strategies (e.g. promoting structural complexity with continuous cover forestry).

4.4.1 Stand composition effects on pest control

In concordance with other sentinel prey experiments in temperate forests, arthropod attack rates were higher than both mammal and bird attack rates (Lövei & Ferrante, 2017), probably as a result of higher diversity and density of invertebrate predators (Gullan et al., 2014). This highlights the importance of generalist arthropod predators in controlling herbivore populations, especially early instar larvae (Nixon & Roland, 2012). Furthermore, as expected, attack rates of the different taxa were higher in strata where they are more active (ground for ground-active arthropods and small mammals, and herb stratum for birds). On the other hand, the significant differences in attack rates between stand types were unexpected, with Douglas fir monocultures having the highest mean arthropod attack rates, particularly on the ground stratum. Due to large differences in arthropod attack rates between Douglas fir monocultures and other stands, a similar pattern was reflected in the mean total attack rates for both strata, where attack rates in coniferous monocultures were higher than in beech monocultures. This was despite the fact that Douglas fir presence in native Central European forest stands has been shown to negatively affect both the biomass and abundance of generalist arthropod predators (Finch & Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014) – two characteristics that strongly determine control by natural enemies (Saint- Germain et al., 2007). The discrepancy in results could be due to lower prey densities in Douglas fir stands which would trigger increased attack rates on sentinel prey due to the lack of live prey. Further research on prey densities in Douglas fir is necessary to tests this. On the other hand, the difference in results may be due to the more densely shaded subcanopy environment provided by young (Schuldt & Scherer-Lorenzen, 2014) and intermediate-aged Douglas fir stands (Finch & Szumelda, 2007) in comparison to our more mature stands (see section on microhabitats below). This suggests that recommendations for management actions to promote control by natural enemies may depend on the developmental stage of the forest stands – and that more research on the role of Douglas fir in Central European forestry is required to be able to draw general conclusions on its ecological impact (Schmid et al., 2014).

Analysis of tree proportions further supported the positive effect of Douglas fir and its taxonomic relative Norway spruce on control by natural enemies, with plots with higher proportion of both conifers having higher total and arthropod attack rates, particularly at the ground level. The presence of a positive tree proportion effect without an accompanying direct positive neighborhood diversity effect goes against the “enemies hypothesis” which suggests that top-down control is positively correlated with plant diversity (Haddad et al., 2009; Root, 1973). However, recent research has shown that the “enemies hypothesis” is ecosystem dependent, with epigeic forest predator communities being often more strongly affected by tree identity and tree composition than tree diversity (Staab & Schuldt, 2020). Neighborhood diversity had an indirect effect on mean total (marginally significant; $P \leq 0.1$) and arthropod (significant) attack rates, however, with the intensity of the positive effect of Douglas fir proportion on attack rates disappearing in plots with high neighborhood diversity. In other words, considering that neighborhood diversity includes information on tree diversity and spatial structure of a stand, control by ground-active arthropods in mixtures with Douglas fir trees might benefit from planting trees in homospecific patches. Interestingly, these findings contrast with results from a previous study of tree canopies where abundance and biomass of arboreal generalist predators benefited when being planted in heterospecific patches (Matevski & Schuldt, 2021). The contrasting findings highlight the need to consider the effects of forest stratum (ground vs. canopy) and the spatial scale at which trees are mixed, on pest control. Moreover, the latter study was conducted in much younger forest stands, once again indicating that developmental stages during forest management might influence biocontrol in different ways. Our results indicate that besides tree identity and tree diversity, management of mixed-species forests has to consider mixture proportions and the spatial distribution of heterospecific trees in a stand as important moderators of control by natural enemies.

4.4.2 Microhabitat effects on pest control

The positive effect of Douglas fir, and to a lesser extent of Norway spruce, on sentinel prey attack rates could be the result of factors inherent to the tree species, such as tree type (coniferous) and litter type or they could be related to factors that are not strictly attributed to tree species such as vegetation complexity and light availability. The importance of the latter has previously been shown for arthropods, for instance with different stand types featuring a high similarity in spider community structure because of similar ground vegetation cover and canopy closure (Ziesche & Roth, 2008). Furthermore, small mammals' activity can be higher in habitats with higher structural complexity in the understory, benefiting from increased access to shelter (Kollberg et al., 2014). These findings may help explain why in our study, models with microhabitat features and not stand structure as predictors explained more of the variance in attack rates. Specifically, increases in litter cover and litter depth led to lower total and arthropod attack rates, respectively, as a result of litter properties having a significant effect on arthropod communities (Barton et al., 2009; Pinzon et al., 2018). Furthermore, mammal ground stratum attack rates were higher in stands with higher vegetation complexity, probably as a result of small mammals benefiting from the increase in shelter (Kollberg et al., 2014). Lastly, the increase in irradiation in sites with lower LAI (i.e. lower canopy closure) led to higher arthropod attack rates, probably as a result of arthropod predators such as spiders displaying higher activity in less dense forest stands (Košulič et al., 2016). Considering that previous studies showing negative effects of Douglas fir on epigeic arthropod predators were conducted in young (Schuldt & Scherer-Lorenzen, 2014) and intermediate-aged stands (Finch & Szumelda, 2007) with lower light availability, it is possible that the perceived negative Douglas fir effect is in part an effect of canopy closure. This is supported by our finding of a positive effect of Douglas fir proportion in monocultures as a result of the more open canopies of mature Douglas fir stands, contributing to a more diversified stand structure and higher microhabitat diversity (Finch & Szumelda, 2007). Such management strategies have been recommended for Douglas fir plantations in its native range in North America (Yi & Moldenke, 2005), and our study suggests that similar measures may also help in promoting the ecological compatibility of Douglas fir in forest stands outside its native range.

4.4.3 Future prospects

Model caterpillars are a suitable method to quantify predation beyond just predator density, but they can only provide relative comparisons as attack rates on sentinel prey are lower than predation on live prey and can depend on the size of the model prey (Lövei & Ferrante, 2017). Furthermore, it is difficult to assess whether the attack marks on a model caterpillar belong to attacks from one or multiple individuals. Our results capture attack rates at only two strata in the forest, and model caterpillar attack rates (Loiselle & Farji-Brener, 2002) as well as predator density (Matevski & Schuldt, 2021) can strongly differ between strata. However, knowledge from the ground stratum can provide insight on predation on herbivores in a stratum where they spend a part of their life cycle (Riihimäki et al., 2005), while sentinel prey attack rates in the herb layer can give us insight on predation intensity on seedlings in critical early stages of their development. Lastly, since forests are often expected to balance multiple ecosystem demands, and often promoting specific ecosystem services leads to trade-offs (Manning et al., 2018), the possible negative consequences of planting Douglas fir monocultures on other ecosystem services needs to be kept in mind. One such service is the provision of high biodiversity, which plays a critical role for many ecosystem processes (Cardinale et al., 2012; Grossman et al., 2018). Negative consequences on biodiversity are not specific to Douglas fir (Gossner & Utschick, 2015; Roques et al., 2006), but concern many non-native plants in general (Mack et al., 2000; Vilà et al., 2011).

Keeping these limitations in mind, our study shows that control by natural enemies, like other ecosystem services, is driven by multiple forest attributes (Felipe-Lucia et al., 2018) such as tree identity, tree diversity, tree proportion, light availability and understory vegetation complexity. This means that the spatial distribution of tree species and their proportions in forest stands can be important in determining how tree species mixtures influence control by natural enemies. Contrary to previous studies in younger stands (Finch & Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014), our study shows that Douglas fir may promote pest control, at least in lower strata, in mature stands, especially when planted next to conspecific trees, probably as a result of the higher light availability in mature versus young Douglas fir stands. Age dependent effects of Douglas fir are important to consider in this respect. The latter is especially crucial since it has been shown that identical stand types vary in the community structure of predators when key environmental factors differ (Ziesche & Roth, 2008). Management practices independent of tree identity may therefore be implemented to promote biocontrol. For Douglas fir as a non-native tree species planted in production forests to maximize economic benefits, thinning of dense intermediate-aged stands, or generally more open stands with a lower stem density could have indirect positive effects on pest control by increasing light availability and understory vegetation complexity.

Chapter 5

Introduction of non-native Douglas fir reduces leaf damage on both saplings and mature trees in European beech forests

Dragan Matevski, Estela Foltran, Norbert Lamensdorf, Andreas Schuldt

Abstract

Recent ecological research suggests that, in general, mixtures are more resistant to leaf damage than monocultures. However, we know little about mixtures with non-native trees, where enemy release could lead to patterns that differ from commonly observed relationships among native species. This becomes particularly relevant when considering that adaptation strategies to climate change increasingly promote a larger share of non-native tree species, such as North-American Douglas fir in Central Europe. We studied leaf damage on saplings and mature European beech (*Fagus sylvatica*) trees across a wide range of site conditions in monocultures and mixtures with phylogenetically distant conifers – native Norway spruce (*Picea abies*) and non-native Douglas fir (*Pseudotsuga menziesii*). We analyzed leaf herbivory (sucking, chewing, mining, skeletonizing, galling) and pathogen damage in relation to tree diversity and identity effects, as well as effects of plot characteristics. We observed lower sapling herbivory and tree sucking damage on beech in non-native Douglas fir mixtures than in European beech monocultures probably due to lower herbivore diversity on Douglas fir trees, and higher pathogen damage on beech saplings in mixtures with Norway spruce than with Douglas fir likely as a result of higher canopy openness. Our findings suggest that even for low diversity gradients, tree diversity effects on herbivory can depend on the identity of the admixed tree species, in addition to modifications caused by feeding guild and tree ontogeny, with effects of identity, diversity and plot characteristics being different in sites with low or high nutrient capacity. The presence of contrasting identity effects of the two conifers provides important information on our understanding of the relationships between tree diversity and trophic interactions in the light of non-native tree species introductions. Especially with recent Norway spruce die-off, the planting of Douglas fir as replacement is likely to strongly increase in Central Europe. Our findings suggest that mixtures with Douglas fir could benefit survival or growth rates of beech saplings and mature trees due to lower leaf damage, emphasizing that a more explicit consideration of non-native species may be crucial to understand biodiversity-ecosystem function relationships under ongoing environmental change.

5.1 Introduction

Forests provide a wide array of ecosystem goods and services (Bateman et al., 2013), the provisioning of which can be compromised by disturbances caused by abiotic and biotic hazards (Trumbore et al., 2015). Anthropogenic stressors are increasing the frequency, extent and severity of these disturbances (Millar & Stephenson, 2015), including the activity of forest pathogens and foliar insect pests as key moderators of ecosystem functioning (Jactel et al., 2012).

Recent ecological research suggests that, in general, tree species mixtures are more resistant than monocultures to natural disturbances such as herbivore and pathogen attack (Jactel et al., 2017; Jactel et al., 2021). However, this effect of tree diversity on resistance to herbivores and pathogens is strongly dependent on tree identity and consumer specialization (Castagneyrol et al., 2014) as well as on resource allocation patterns during tree ontogeny (Boege & Marquis, 2005). Decreasing herbivory with increasing tree diversity has been found to be most pronounced at larger phylogenetic distance of neighboring trees (Jactel et al., 2021). This associational resistance is particularly common for damage caused by specialists (Jactel et al., 2021), because heterospecific neighbors lower the chance of host detection by reducing host abundance or frequency (resource concentration hypothesis; Root, 1973), mixing of cues (host apparency hypothesis; Castagneyrol et al., 2013), preference of non-host trees (decoy hypothesis; Ruttan & Lortie, 2015), or promotion of top-down control by natural enemies (enemies hypothesis; Root, 1973, but see Staab & Schuldt 2020). However, not all specialists cause less damage in mixtures (Plath et al., 2012), and for generalist herbivores, the opposite pattern of associational susceptibility has frequently been observed (Jactel & Brockerhoff, 2007; Schuldt et al. 2010). Generalists can benefit from the broader diet range (Unsicker et al., 2008) and spill-over from highly preferred to less-preferred hosts (White & Whitham, 2000) in mixtures. However, a general understanding of the influence of tree diversity on herbivores and pathogens is complicated by the effects of tree identity, phylogenetic composition and environmental context (Castagneyrol et al., 2014; Jactel et al., 2021; Kambach et al., 2016).

The effects of tree identity and composition and the need for a better understanding of their modifying role on herbivory and pathogen damage are particularly relevant when it comes to non-native tree species. Non-native species are playing an increasingly important role in forests worldwide, in some cases as invasive species (Dickie et al., 2014), but particularly as new floral elements that either track changing climatic conditions or are actively promoted as options for climate adaptation of future forests (Remeš et al., 2020). Non-native trees often harbor less diverse herbivore communities (Burghardt & Tallamy, 2015), but at the same time pose a potential risk of introducing pests or pathogens which perform a host jump to native trees (Slippers et al., 2005). Because individual herbivore groups respond in distinct ways to tree species identity and changes in tree diversity (Castagneyrol et al. 2014; van Schrojenstein-Lantman et al., 2018,), the presence and proportion of non-native trees in forests may lead to pronounced changes and impacts on native trees when planted in mixtures with non-natives. However, research so far has mainly focused on how increasing the diversity of native tree species leads to associational resistance (Haase et al., 2015) or associational susceptibility (Pearse & Hipp, 2014) on non-native trees, leaving a gap in our knowledge of how non-native trees might affect leaf damage on native trees. This lack of knowledge is particularly relevant in the context of climate change, as adaptation strategies increasingly promote new mixture types and a larger share of non-native tree species, such as the North-American Douglas fir in Central Europe (Schmid et al., 2014).

For such mixture types, an important research issue is the need to understand the spatial scales at which impacts of tree diversity and tree identity are effective (Chase et al., 2018). While community-level tree species composition and tree species proportions may be important drivers of tree mixture effects on leaf damage (e.g. Hantsch et al., 2014; Muiruri et al., 2018), local tree neighborhoods might strongly influence diversity effects via modification of host apparency and environmental conditions (Castagneyrol et al., 2013; Grossman et al., 2018). The resulting heterogeneity at local spatial scales can be expected to cause spatial variation in community composition of herbivores and pathogens (Crist et al., 2006; Tack & Laine, 2013), which should lead to higher variation in damage in more heterogeneous mixtures. This local variability in damage rates has received relatively little attention in the context of tree diversity effects so far, although it might be a potentially important moderator of diversity-stability relationships (Xu et al., 2020) especially when considering the higher propensity of herbivore or pathogen outbreaks with ongoing environmental change (Logan et al., 2003). In general, environmental variation can be considered an important moderator of tree diversity and tree identity effects, e.g. via modifications of (micro)climate and resource availability for tree growth and ontogenetic development (Bale et al., 2002; Basset et al., 2001; Nigel & Hughes, 2005; Orians & Fritz, 1996; Zvereva et al., 2020). This makes it important to consider potential diversity and identity effects in relation to effects of other environmental drivers on herbivory and pathogen damage, especially when it comes to evaluating the potential impact of non-native tree species.

Here we performed a high-resolution analysis (exact damage rates in % instead of commonly used categories of damage) of both herbivory and pathogen damage on European beech (*Fagus sylvatica* L.), the dominant deciduous tree species in Central Europe (Brunet et al., 2010), in monocultures and mixtures with phylogenetically distant coniferous tree species across a gradient in soil quality from texture-poor to texture-rich forest sites (Foltran et al., 2021). Specifically, we compared leaf damage and damage variability in pure beech forests and in two-species mixtures of European beech with either non-native Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) or native Norway spruce (*Picea abies* (L.) H. Karst.). We considered both saplings and mature trees to test whether tree diversity and identity effects vary with tree ontogeny. Comparing non-native Douglas fir and native Norway spruce is especially important as tree species composition in European forests will change due to climate change (Buras & Menzel, 2019) and increased utilization of European beech-Douglas fir mixtures is likely due to its beneficial economic effects (Thurm & Pretzsch, 2016).

While we expected (i) reduced leaf damage in mixtures as a result of associational resistance (Jactel et al., 2021), as well as larger spatial variation in leaf damage as a result of larger spatial heterogeneity in mixtures, we hypothesized that mixture effects will be modified in the presence of non-native Douglas fir. Specifically, we expected that (ii) mixtures with non-native Douglas fir have the lowest herbivory damage due to Douglas fir hosting a low diversity of phytophagous arthropods (Roques et al., 2006). Moreover, we expected (iii) that diversity effects are modified by consumer feeding guild (Jactel et al., 2021), and host developmental stage (Zvereva et al., 2020). Lastly, we expected (iv) that the differences in herbivory and pathogen damage between tree communities are better explained by tree diversity than just stand type identity, and that plot and plant characteristics contribute to explaining leaf damage.

5.2 Materials and methods

5.2.1 Study site

This study was performed on 18 forest plots, covering an area of 0.25 ha each. The plots were spatially arranged into six triplets in the federal state of Lower Saxony, Germany (Table D1) to cover the range of environmental conditions under which the three tree species are growing in Central Europe. Three of the triplets were situated on higher altitudes in the southern half of the state, comprising loamy soils (i.e., loess-influenced Dystric Cambisols, developed over Triassic sandstone), while three were in the drier northern half with sandy soils (Göhrde I: Spodic Arenosol; Nienburg and Göhrde II: Haplic Podzol; both developed from dystrophic sand deposits during glacial periods; Figure D1). Each triplet contained three forest types: one European beech (*Fagus sylvatica*) monoculture and two mixtures of European beech and highly productive conifer tree species growing outside of their native range, one with native Norway spruce (*Picea abies*), and another with non-native Douglas fir (*Pseudotsuga menziesii*).

5.2.2 Data collection

We assessed standing levels of leaf damage on mature European beech trees and on beech saplings in August 2019, i.e. at a time of the growing season where most of the damage before leaf-fall has accumulated. In each plot, we collected 20 leaves per tree from 20 saplings and 50 leaves per tree from eight mature trees for a total of 400 leaves of saplings and mature trees, respectively, per plot. No beech saplings were found at site 5 and the pure beech plot at site 4 and therefore only mature trees were sampled there. We sampled leaves of each sapling randomly from different plant heights (up to 2.5 m), while mature trees were sampled from branches in the lower canopy of the tree (5-8 m). After digitally scanning all leaves, we used ImageJ to quantify mean leaf damage (in %) of photosynthetically active tissue (top of leaves) of each sampled seedling and mature tree. To do this, we first approximated the total leaf area of leaves that were defoliated at the margins and then we used the color threshold feature in ImageJ to calculate mean leaf damage of different damage types after manually coloring them. We differentiated between galling, skeletonizing, mining, sucking, chewing, as well as overall herbivory damage, pathogen damage and total damage (herbivory + pathogen damage).

We used several predictors to explain the differences in mean damage and damage variation within and between the plots, including forest type, tree diversity, as well as plot and plant characteristics including mixture proportions, soil quality, nutrient capacity, canopy openness and plant height. We used proportions of the three target species, to describe the tree community composition in a more detailed way than the categorical distinction of the three forest types. For this purpose, we used proportions calculated from maps of the area potentially available (APA; Gspaltl et al. 2012) to each of the three target tree species (in m^2). 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 the identity effects of the target conifers (Douglas fir and Norway spruce) 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 and from these measurements diversity is scaled up to the plot-level. This allows for a spatially specific measure of tree diversity with higher values of NDiv in stands with random distribution of tree species than patch distribution, even if the proportion of tree species is identical.

Data on factors not strictly attributed to tree identity, including canopy openness and plant height, were also collected. The height (in cm) of each sapling sampled was measured at the time of collection, while the heights of the sampled mature trees (in cm) were extrapolated from diameter at breast height measurements with the use of tree height curves based on already measured trees. Canopy openness was measured using a Solariscope (SOL 300) at each plot in July 2019 at 12 sample points (10 m distance between points) on a 20 m x 30 m grid at the center of each plot. The mean plot-level values for each plot were used for further analyses.

In terms of abiotic variables, we included soil variables such as soil quality (pH(KCl), carbon and nitrogen stocks and C:N ratio), and cation exchange capacity (CEC) as a proxy for fertility and soil nutrient retention capacity (nutrient capacity). Soil samples were taken from four randomly selected points at each plot in November/December 2017. Carbon and nitrogen stocks were calculated from the soil bulk density, concentrations of nutrient and depth of the soil layer (all samples considered here/in the given context were taken from the most upper 0-5 cm mineral soil layer soil depth), pH was measured with a glass electrode, while CEC was analyzed by ICP-OES (Spectro Genesis, Spectro, Kleve, Germany; Foltran et al., 2021). Measurements at the European beech/Douglas fir mixtures in sites 3 and 4 as well as the

European beech/Norway spruce mixture in site 4 were done at nearby sites, which had to be replaced after storm damage prior to the leaf damage assessment. However, differences in soil parameters between the abandoned and replacement sites can be assumed to be marginal due to geographic closeness. We performed dimension reduction by PCA on the soil variables and we used the first two principal components (PCs) for further analysis. PC1 (55.87 % of variance explained) was negatively correlated with C and N stocks, while positively correlated with C/N ratio (Table D2). PC2 (34.64 % of variance explained) was negatively correlated with pH and positively correlated with C stocks (Table D2).

5.2.3 Statistical analysis

We analyzed mean values of leaf damage per European beech individual (saplings and mature trees), differentiating between individual damage types (total, herbivory, chewing, sucking, mining, skeletonizing and galling damage), using linear mixed effects models with study plot nested in study site triplet as a random effect. Furthermore, we assessed the variability of different damage types at the plot-level using study site triplets as a random effect. We calculated variation in damage using the coefficient of variation (CV) with the *sjstats* R-package (Lüdecke, 2018). The linear modeling was done in three successive steps to account for the fact that forest types, tree diversity, as well as plot and plant characteristics were not completely independent from each other. Response variables were log+1 transformed when this improved model fit.

Firstly, we tested for effects of forest type on leaf damage and their CVs. Besides forest type, the models included nutrient capacity and the interaction between nutrient capacity and forest type. When effects of forest type turned out to be non-significant, we simplified this predictor to a contrast between monoculture and mixtures.

Secondly, we replaced the categorical variable forest type with plot-level NDiv and added the two principal components of the PCA of soil variables. We did this to test whether tree diversity had an effect of associational susceptibility or resistance and whether soil quality and nutrient capacity influence this effect.

Lastly, we replaced forest type with plot and plant characteristics to see if looking at plots at a greater detail than just forest type/diversity yields models with better fit. This model included plot-level Douglas fir and Norway spruce APA as measures of tree proportions, since even though tree proportions were correlated with forest type (and therefore not entered in the first type of models), they varied among mixtures. Furthermore, we added canopy openness and sapling/or mature tree height as factors not strictly attributed to forest type, and checked for influence of nutrient capacity, and whether nutrient capacity affects tree proportion and plant height effects. Lastly we added the two principal components of the PCA of soil variables. Due to a lack of replicates for the sapling data (some sites lacked European beech saplings) we had to exclude one of the predictors in the sapling damage and variation models. We chose the canopy openness-nutrient capacity interaction since we were more interested in how nutrient capacity modulates sapling height effects, and whether it modulates the two conifer proportion effects differently.

We estimated all models with the *nlme* R-package (Pinheiro et al., 2020) and subsequently performed a stepwise selection procedure based on AICc (Burnham & Anderson, 2010) in order to acquire models with the fewest number of predictors and the lowest global AICc. Afterwards, we confirmed that multicollinearity between variables was low using VIF (≤ 5), calculated with the R-Package *car* (Fox & Weisberg, 2018). Lastly, we used the Tukey HSD (honest significant difference) post-hoc test and p-values adjusted with the Holm-method using the *multcomp* R-package (Hothorn et al., 2008) to test for significant differences ($p < 0.05$) in leaf damage and leaf damage variation among stand types (Table S2). All analyses and figures were made in R 4.0.2 (http://www.R-project.org).

5.3 Results

Both mean herbivory and pathogen damage were higher in saplings, with 6% (±0.17 SE) and 2.3% (±0.14 SE) mean leaf damage respectively, compared to mature trees with 4.2% (±0.23 SE) mean herbivory and 1.6% (±0.31 SE) mean pathogen damage. Herbivory damage was primarily caused by suckers, which were responsible for the main damage on 57.9% of saplings and 83.4% of mature trees. Chewing damage was dominant on 17.5% of saplings and 5.5% of mature trees while mining damage dominated on 2.1% of saplings and 1.4% of mature trees. Gallers and skeletonizers were responsible for only a minute amount of leaf damage (1.7% ± 0.01 SE) and were not dominant on a single sapling or mature tree. Only pathogen, sucking and chewing damage are therefore considered separately in the following analyses, as they represent 91.3% of the total damage.

5.3.1 Community effects

Significant differences in mean leaf damage and leaf damage variation between forest types were registered for several damage types on European beech saplings and mature trees (Fig. 5.1A-F, Table D3-5). Saplings suffered higher sucking damage rates in monocultures than mixtures (Fig. 5.1A), and saplings in European beech/Douglas fir mixtures suffered less herbivory damage than European beech monocultures (Fig. 5.1B), less pathogen damage than European beech/Norway spruce mixtures (Fig. 5.1C), and higher CV of herbivory damage than European beech monocultures (Fig. 5.1D). Similarly, mature European beech trees suffered more herbivory damage in monocultures than mixtures (Fig. 5.1E), while sucking damage was lower in European beech/Douglas fir mixtures than European beech monocultures (Fig. 5.1F). Furthermore, nutrient capacity significantly increased mature tree herbivory and sucking damage (Table D4). Lastly, nutrient capacity modulated the effect of forest type on leaf damage, with a significant difference in European beech/Douglas fir mixture response to nutrient capacity for sapling chewing damage (Fig. 5.1G) and in European beech/Norway spruce mixture for mature tree sucking damage (Fig. 5.1H).

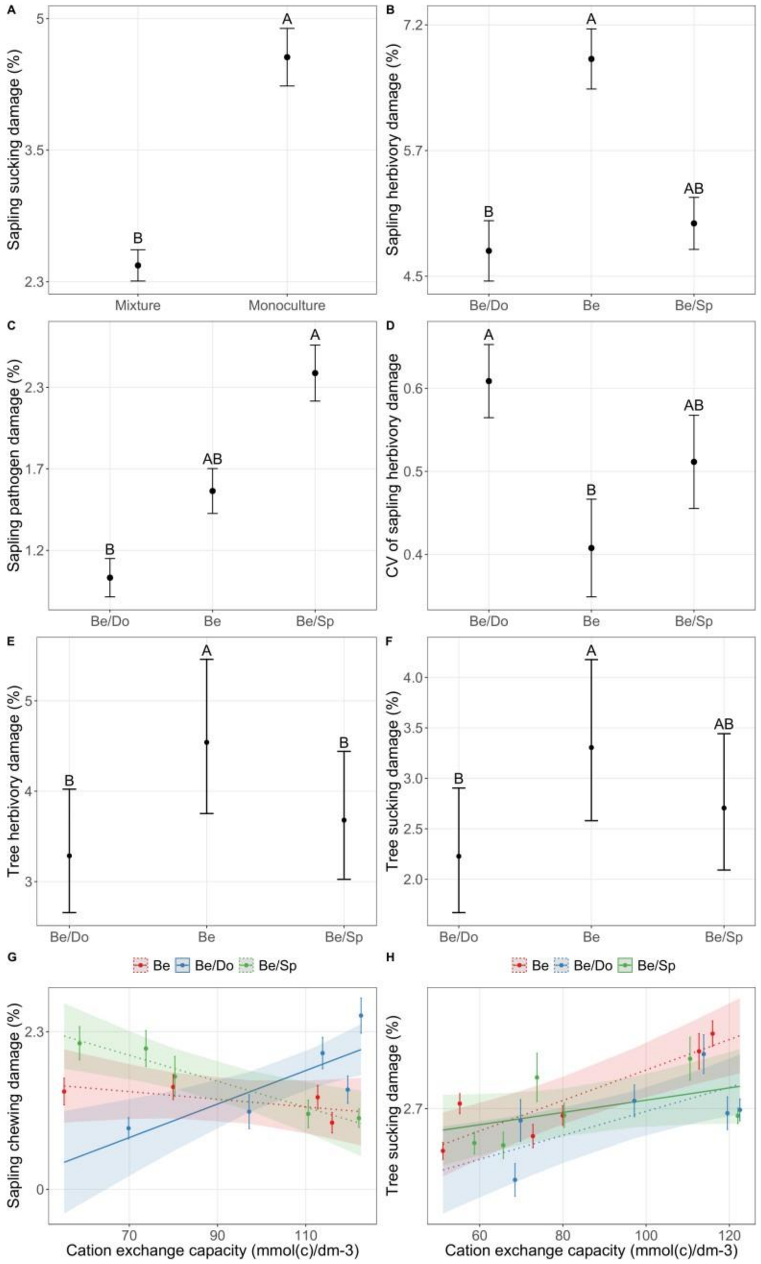

Fig. 5.1 Effects of forest type (Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture) on sapling and mature tree leaf damage and their respective coefficients of variation (CV). Differences in mean ± SE of sapling sucking damage (A), sapling herbivory (B), sapling pathogen (C), and CV of sapling herbivory damage (D). Differences in predicted values from linear models ±95% confidence intervals of mature tree herbivory (E) and sucking damage (F). Significant differences in nutrient capacity effects on plot-level ± SE sapling chewing (G) and mature tree sucking damage (H) dependent on forest type. Significant differences calculated with Tukey HSD post-hoc with p-values adjusted with the Holm-method (A-D) or their respective linear models (E,F), marked with different letters. Solid lines in interaction plots represent the forest type with a significantly different response to nutrient capacity. Note that the response variables for panels A-C and E-H were log+1 transformed to improve model fit, and the Y-axes show back-transformed values.

5.3.2 Effects of neighborhood diversity

Models using NDiv (Tables D6-7) instead of forest type (Tables D4-5) to describe stand conditions explained similar variation and had a similar fit for leaf damage models, while explaining more variation (between 1-24%) and having a similar model fit for CV of leaf damage models.

European beech sapling sucking damage decreased with increasing plot-level NDiv (Fig. 5.2A, Table D6) and sapling chewing damage increased (Fig. 5.2B, Table D6). Furthermore, the CV of sapling herbivory damage increased with increasing NDiv (Fig. 5.2C, Table D7). This effect was stronger in plots with higher nutrient capacity (Fig. 5.2D, Table D7) and absent in plots with low nutrient capacity (CEC<75). Lastly, nutrient capacity had similar effects as in the forest type model, with an additional negative effect on sapling pathogen damage and CV of sapling sucking damage, while PC1 decreased mature tree chewing damage (Table D6-7).

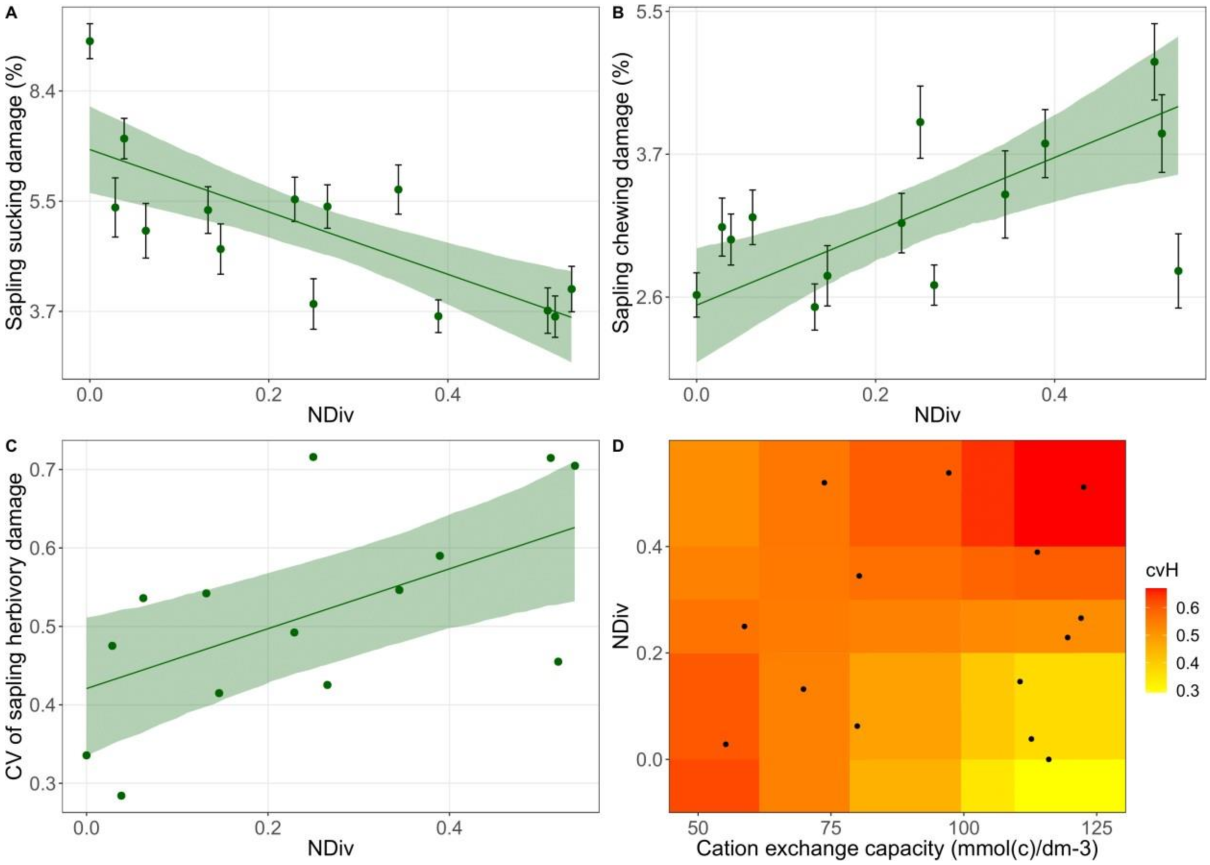

Fig. 5.2 Effect of plot-level NDiv on sapling and mature tree leaf damage and their respective CVs. Differences in plot-level ± SE sapling sucking (A), sapling chewing (B) as well as CV of sapling herbivory damage (C) in study plots with different plot-level neighborhood diversity. Heat map displaying the interaction between the effect of plot-level NDiv and nutrient capacity on CV of sapling herbivory damage (D). Colors in heatmap show predicted values of the mixed-effects model of tree herbivore damage. Bands represent 95% confidence intervals. Note that the response variables in panels A and B were log+1 transformed in order to improve model fit. Y-axes show back-transformed values.

5.3.3 Effects of plot and plot characteristics

Models using plot and plant characteristics (Tables D8-9) instead of forest type (Tables D4-5) to describe stand conditions explained the most variation (up to 75%), but had the lowest model fit (mean ΔAICc of 7.7).

Total sapling (Fig. 5.3A) and tree herbivory damage (Fig. 5.3B) damage was lower in plots with higher Douglas fir proportion, while the CV of sapling chewing damage was higher in plots with higher proportion of both conifers (Fig. 5.3C; Tables D8-9). The effect of Douglas fir proportion on sapling chewing damage was modulated by soil nutrient capacity, with a positive effect registered for plots with high soil nutrient capacity (CEC>100;Fig. 5.3D, Table D8). Additionally, the CV of total tree damage was higher in plots with higher canopy openness (Fig. 5.3E, Table D9). Nutrient capacity of soil modified the effect of canopy openness on tree pathogen damage, with a negative effect being clear for plots with high nutrient capacity (CEC>100), that becomes less clear the lower the nutrient capacity is (Fig. 5.3F, Table D8). Sapling height had a negative effect on total sapling damage (Fig. 5.3G, Table D8), but only in stands with low nutrient capacity (CEC<100; Fig. 5.3H, Table D8).

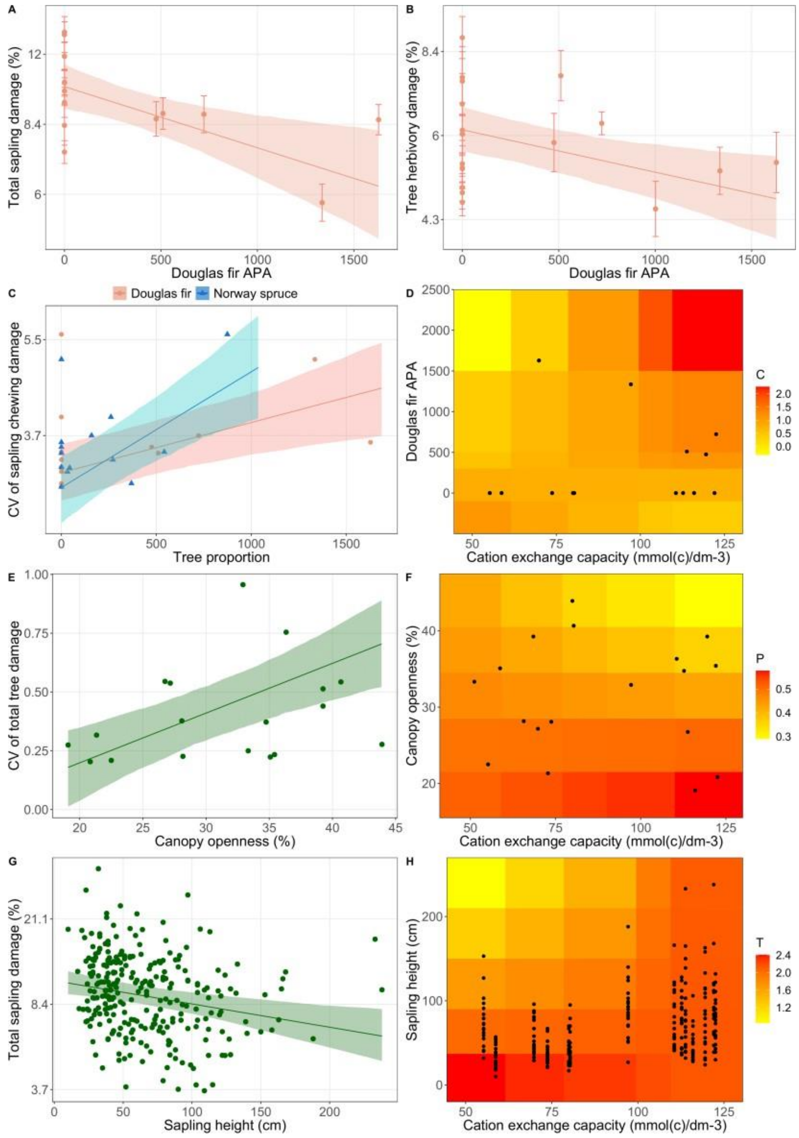

Fig. 5.3 Effects of plot and plant characteristics on sapling and mature tree damage. Differences in plot-level ± SE total sapling (A) and tree herbivory damage (B) in stands with different Douglas fir proportions. Differences in CV of sapling chewing damage in stands with different

proportions of both conifers (C). Heat map displaying the interaction between the effect of nutrient capacity and Douglas fir proportions on sapling chewing damage (D). Differences CV of total tree damage in stands with different canopy openness (E). Heat map displaying the interaction between the effect of nutrient capacity and canopy openness on tree pathogen damage (F). Differences total sapling damage on saplings of a different height (G). Heat map displaying the interaction between the effect of nutrient capacity and sapling height on total sapling damage (H). Colors in heat maps show predicted values of the mixed-effect models. Bands in linear regressions represent 95% confidence intervals. Note that response variables of panels A, B and G were log+1 transformed. Y-axes show back-transformed values.

5.4 Discussion

Our analyses showed that European beech saplings and mature trees suffer less leaf damage in mixtures, especially when admixed with Douglas fir. This suggests that although higher tree diversity generally led to associational resistance to leaf herbivory, this effect was modulated by several factors that might require more attention in biodiversity-ecosystem functioning research in forests. Tree identity modified diversity effects on saplings with lower sapling herbivory and tree sucking damage in European beech/Douglas fir mixtures in comparison to European beech monocultures, and sapling pathogen damage was lower in European beech/Douglas fir mixtures than European beech/Norway spruce mixtures. Notably, both diversity and identity effects strongly depended on ontogeny and soil nutrient capacity, with stronger impacts on saplings. Lastly, diversity effects were modified by feeding guild, with higher sapling chewing damage but lower sucking damage in stands with higher neighborhood diversity.

5.4.1 Tree diversity effects on leaf damage are modulated by tree identity and canopy openness

We observed an effect of associational resistance for sapling sucking damage and mature tree herbivory in mixtures, possibly as a result of lowered effectiveness of the relatively low diet breadth of the dominant suckers and chewers (Forister et al., 2015) when non-host tree species are introduced, especially when they are phylogenetically distant (see also Jactel et al., 2021 and references therein).

Diversity effects were strongly dependent on tree identity, with higher sapling herbivory and tree sucking damage in European beech monocultures in comparison to Douglas fir mixtures. While a possible explanation for this pattern could be higher predation pressure in Douglas fir mixtures due to a potentially lower prey availability (Goßner & Ammer, 2006), a previous study at the same sites found no significant difference in ground and herb layer clay caterpillar attack rates between European beech/Douglas fir mixtures and European beech monocultures (Matevski et al., 2021). Therefore, a more likely explanation could have to do with the fact that Douglas fir hosts a low diversity of arthropods in general (i.e. herbivores, predators and others; Roques et al., 2006) and that the resulting altered trophic interaction networks may also affect beech-associated arthropods (Neff et al., 2021). This effect of Douglas fir could also be the reason why we registered a significant negative effect of Douglas fir proportion on total sapling and tree herbivory damage. However, we currently lack data on overall arthropod species composition in our study plots, and future work should therefore directly link arthropod data and damage data in such systems to test this hypothesis.

On the other hand, beech saplings suffered higher pathogen damage in mixtures with Norway spruce than mixtures with Douglas fir. This pattern is likely a result of significant differences in plot characteristics (particularly canopy openness) between European beech/Norway spruce mixtures and European beech/Douglas fir mixtures. Canopy openness has been connected to higher pathogen damage on shade trees before (Gagliardi et al., 2021), which could be a result of increased light levels reducing physiological resistance (Eskes, 1982).

The presence of different identity effects of Douglas fir and Norway spruce, despite their phylogenetic closeness, is important to consider also in the context of forest management and for a better understanding of biodiversity-ecosystem functioning relationships under realistic scenarios, since Douglas fir is likely to be grown more in Central Europe at the expense of Norway spruce under a changing climate (Schmid et al., 2014; Krejza et al., 2021). From an ecological perspective, our research findings and the expected increase of non-native trees in forest ecosystems in many parts of the world (Castro-Díez et al., 2019) suggest that more attention toward the potentially modifying role of such species for biodiversity effects may be an important avenue for future research.

5.4.2 Modification of diversity effects by feeding guild identity, tree ontogeny and soil nutrient capacity

Our results highlight the context-dependency of tree diversity effects on trophic interactions, which were modified by herbivore identity, tree development and environmental context.

The dominant feeding guilds (suckers and chewers) had different responses to tree diversity, with sucking damage being lower in plots with higher neighborhood diversity, while chewing damage was higher. Such a contrasting response of herbivores with a small diet breadth to tree diversity has been observed before (Plath et al., 2012). In our study it could be the case that leaf suckers are mobile enough to take advantage of the higher resource quantity in monocultures and can access higher quality food by “intraspecific dietary mixing” (Mody et al., 2007). On the other hand, the less mobile lepidopteran caterpillars, which can be assumed to cause a large share of the leaf chewing damage, might benefit less from the increased quantity of resources. Furthermore, these herbivores can show a tendency to oviposit their eggs at a higher rate on trees surrounded by heterospecific neighbors because they represent a “competitor free space” (Bonebrake, 2010).

Ontogeny affected diversity effects on leaf damage, with saplings suffering higher damage rates than mature trees and being more responsive to tree diversity and identity effects. The lower damage rates on mature trees could be explained by an increasing resource allocation to defense at the expense of growth as trees age (Stiegel et al., 2017). This also could be the reason behind lower total sapling damage for taller saplings. Our finding stresses the importance of taking into account multiple life history stages of tree development to develop a fuller understanding of diversity effects in forest ecosystems (Boege & Marquis, 2005; Zvereva et al., 2020).

Moreover, our results stress that environmental context is very important in the assessment of tree identity effects and the possible role of non-native tree species. In our study, soil nutrient capacity had a positive effect on mature tree herbivory and sucking damage, which conforms to the compensatory continuum hypothesis which suggests that plants are more tolerant to herbivory in low-stress, benign environments and may invest less in defenses (Hawkes & Sullivan, 2001). However, the effect of soil nutrient capacity was modulated by non-native tree presence for sapling chewing damage, tending towards a positive response to nutrient capacity in European beech/Douglas fir mixtures compared to a negative response in the two other forest types. On the other hand, soil nutrient capacity modulated the effects of Douglas fir proportion, canopy openness and sapling height on leaf damage with a distinct difference between plots with high and low nutrient capacity. Plots with higher nutrient capacity were the only ones where Douglas fir proportion had a negative effect on sapling chewing damage and canopy openness a negative effect on tree pathogen damage, while in these plots sapling height had no effect on total sapling damage. These results show that soil nutrient capacity can influence tree identity effects, as well as effects of plot and plant characteristics. In the context of environmental variation it is also interesting to note that mixtures and plots with higher neighborhood diversity/conifer proportion had higher variation in different leaf damage types, probably as a result of higher spatial variation in environmental conditions (Crist et al., 2006). This higher variation in damage did not lead to consistent increases or decreases in mean leaf damage, with lower sapling sucking but higher chewing damage in the more spatially heterogenous mixtures. Thus, further examination on the implications of leaf damage variation on mean leaf damage is required to better understand how spatial variation in damage may affect ecosystem stability.

5.5 Conclusions

Our findings suggest that associational resistance is not the only response to leaf damage when mixing phylogenetically distant tree species. Even at a low diversity gradient we observed different responses to tree diversity dependent on the feeding guild and more importantly, the identity of the admixed tree species. The different identity effects of native Norway spruce and non-native Douglas fir on European beech leaf damage shed light on what the ecological consequences can be for enriching European beech with these two conifers. Our findings are not only important in the specific case of Douglas fir introduction in Central Europe, but highlight more broadly that our understanding of the relationships between tree diversity and trophic interactions will benefit from closer inspection of the role of non-native tree species introductions in this context.

Chapter 6

General discussion

This thesis confirms that, for generalist arthropod predators in low diversity Central European forests, tree diversity effects are less important than tree identity effects. Positive effects of tree diversity were registered only on arboreal spider taxonomic and functional diversity (**Chapter 3**) in study sites with the highest diversity gradient (1-4 in comparison to 1-2 tree species). Furthermore, increasing tree diversity resulted in both associational resistance and associational susceptibility effects on leaf herbivory depending on the feeding guild studied (**Chapter 5**). In terms of tree identity effects, enriching European beech forests with non-native Douglas fir generally benefitted generalist arthropod diversity, density (**Chapters 2 & 3**) and top-down control (**Chapter 4**) and led to lower leaf herbivory on European beech saplings and mature trees (**Chapter 5**). Norway spruce effects on arthropod diversity and arthropod-mediated ecosystem functions were generally similar to non-native Douglas fir effects, implying that increased utilization of Douglas fir at the expense of Norway spruce will not lead to drastic changes, at least in this aspect of biodiversity and ecosystem functioning. Lastly, this thesis highlights the importance of taking into account the environmental context of tree diversity and identity effects, by registering strong modulating effects of regional differences in environmental variables, as well as significant effects of local microhabitat variables that are not strictly attributed to tree identity.

6.1 Monocultures vs low tree diversity mixtures

Considerable research has been done into teasing out the relationship between biodiversity and ecosystem functioning (Naeem & Wright, 2003). Meta-analyses of hundreds of biodiversity-ecosystem functioning (BEF) experiments have shown consistent linkages between biodiversity and ecosystem functioning across different ecosystem types and functions (Cardinale et al., 2011; O'Connor et al., 2017). However, effects of diversity on ecosystem functioning strongly depend on the length of the diversity gradient with longer diversity gradients being more likely to affect ecosystem functioning (Balvanera et al., 2006).

This thesis confirms that the length of the diversity gradient could play a role, with no significant effect of tree diversity on epigeal spiders (two species gradient; **Chapter 2**), while tree diversity significantly affected arboreal spider (four species gradient; **Chapter 3**). Arboreal spider taxonomic and functional diversity was promoted by tree diversity at the plot level, while the mean spider size was promoted by tree diversity at the tree level, only when trees were planted in heterospecific patches, emphasizing the importance of both spatial scale and neighborhood tree diversity for arboreal predators (Setiawan, 2016). Additionally, neighborhood tree diversity had a significant effect on arboreal spider community structure with a stronger difference in arboreal spider communities between tree species on trees planted in heterospecific patches. This might potentially indicate an effect of mixing tree species that is independent from the number of tree species in the forest stand. Heterospecific neighbors particularly benefited conifer trees as additional, and especially larger, spider species immigrated from heterospecific neighbors, especially from deciduous trees. Dispersal from conifers to deciduous trees was less likely because many conifer-specific spiders, such as sheet-web weavers, require dense needle structures for web attachment (Halaj et al., 2000).

In terms of tree diversity effects on arthropod-mediated ecosystem functions, ground clay caterpillar attack rates were not directly influenced by tree diversity (**Chapter 4**). However, the effect of non-native Douglas fir was modified by spatially explicit neighborhood tree diversity (NDiv) with Douglas fir having a stronger impact in less diverse stands, i.e. when planted in monospecific patches. Even though top-down control wasn't higher in mixtures, leaf damage on European beech trees was lower (**Chapter 5**). This effect of associational resistance (Jactel et al., 2017; Jactel et al., 2021) was consistent for both saplings and mature trees, with the exception of chewing damage which was higher in stands with higher NDiv, showing that different feeding guilds can respond differently to tree diversity (Plath et al., 2012).

This shows that herbivory is more strongly affected by tree diversity than top-down control, which has shown ambiguous responses to tree diversity (Staab & Schuldt, 2020). This is especially true for the relatively short tree diversity gradients in Central European temperate forest ecosystems (Oxborough et al., 2012; Oxborough et al., 2016), where tree identity effects are more important as the relative contribution of each tree species in the species pool is large (Nadrowski et al., 2010).

6.2 Non-native Douglas fir effects

In the context of tree identity effects, our knowledge of how native/non-native identity affects generalist arthropod predators (spiders) is limited (Ingle et al., 2020; Oxborough et al., 2016). However it has been generally shown that replacing native forests with non-native plantations leads to a loss in arthropod biodiversity (Brockerhoff et al., 2008), possibly as a consequence of structural changes in understory vegetation and loss of associated species directly dependent upon the native tree for their existence (Ennos et al., 2019). Contrary to our expectations non-native Douglas fir promoted the diversity and density of epigeal and arboreal spiders, with this effect being dependent on the stratum and spatial scale studied (**Chapters 2 & 3**).

At the plot-level, epigeal spider communities inhabiting Douglas fir monocultures had higher functional richness than those inhabiting European beech monocultures as a result of higher canopy openness which can result in changes to habitat structure, influencing biodiversity characteristics (Perry et al., 2018). On the other hand, increasing plot-level Douglas fir proportion lead to decreases in arboreal spider species richness as well as several measures of functional diversity probably due to the lower species turnover among coniferous tress. Furthermore, increasing plot-level Douglas fir proportion led to increases in plot-level arboreal spider abundance as the dense needle structure seems to provide more habitat space, as well as more diverse microhabitats (Korenko et al., 2011). However, the increase in arboreal spider abundance didn't lead to an increase in arboreal spider biomass. The opposite was true, as lower beta diversity on Douglas fir trees, influenced by the strong dominance of the small sheet web weaving hunter *Entelecara congenera*, lead to decreased arboreal spider biomass. Results at the local scale were different, with stands with higher local (10 m radius around each trap) Douglas fir proportion harboring an epigeal spider community with higher abundance, biomass and functional richness, but lower functional divergence due to Douglas fir's effects as an ecosystem engineer (Schmid et al, 2014). Moreover at the local scale for arboreal spiders, Douglas fir trees harbored the highest spider species richness, abundance and biomass due to the dense needle structure. (Korenko et al., 2011).

These effects on generalist arthropod predators were accompanied by effects on top-down control and herbivory with higher clay caterpillar attack rates and lower European beech leaf damage in stands with higher plot-level Douglas fir proportion (**Chapters 4 & 5**). Nonetheless, it is important to note that European beech saplings and mature trees in European beech/Douglas fir mixtures harbored less leaf damage than in European beech monocultures without an accompanying difference in arthropod predation rates and generalist predator abundance and biomass (Kriegel et al., 2021; Matevski et al., 2021; Matevski & Schuldt, 2021). The only registered difference was in Rao's Q of carabids where Douglas fir monocultures had higher values than European beech/Douglas fir mixtures (Kriegel et al., 2021).

Native Norway spruce effects on generalist arthropod predator diversity and functioning were similar to Douglas fir effects. Stands with higher share of Norway spruce promoted epigeal spider taxonomic and functional richness as a result of canopy openness. For arboreal spiders, similar to Douglas fir effects, Norway spruce promoted spider diversity and density at the tree level as a result of needles providing more habitat space (Korenko et al., 2011). On the other hand, increasing plot-level Norway spruce proportion decreased arboreal spider diversity and biomass as a result of a spider community structure that is very similar to the one inhabiting Douglas fir. These effects on generalist predator communities were accompanied with a positive effect of plot-level Norway spruce proportion on arthropod clay caterpillar attack rates. All of this shows that non-native Douglas fir effects are not more severe than effects of native conifers that are planted outside of their natural habitats (which is the case for Norway spruce in most regions of Central Europe). On the contrary, both conifers can have beneficial effects on generalist arthropod predator diversity and top-down control. Results for herbivory were different however, with a less consistent conifer effect, and more of a distinction between the native and non-native conifer. In fact, planting Douglas fir in mixtures with European beech appears to be a better choice for lessening leaf damage, as outside of mixture effects, only increasing Douglas fir proportion led to decreasing leaf herbivory. Additionally, European beech sapling pathogen damage was lower in mixtures with Douglas fir than mixtures with Norway spruce, highlighting that enriching European beech forests with non-native Douglas fir could reduce foliar fungi damage as well. On the other hand, the lower European beech herbivory damage in mixtures with Douglas fir may have a negative consequence on biodiversity conservation, as Douglas fir seems to be a less suitable habitat for some herbivores at least (Gruppe & Goßner, 2006).

All this shows that increasing the utilization of Douglas fir in Central Europe may not be as detrimental to the diversity of generalist arthropod predators (spiders) as previously thought, and could have benefits to ecosystem functioning by increasing top-down control and benefiting growth and survival rates of European beech. Such results contrast recent research that has shown that non-native Douglas fir effects on arthropod diversity and functioning are non-significant (Ziesche & Roth, 2008) or negative (Finch & Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014). This discrepancy in results is likely due to studies being limited to a few sites (Ziesche & Roth, 2008) or due to differences in stand age (Finch & Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014). Differences in stand age are accompanied by differences in the environmental context with young (Schuldt & Scherer-Lorenzen, 2014) and intermediate age (Finch & Szumelda, 2007) Douglas fir stands having higher canopy closure than mature stands which could be the main difference for the negative effect of Douglas fir on arthropod diversity and ecosystem functioning. As such it is important to take into account the impacts of the environmental context when assessing tree identity effects.

6.3 Importance of environmental context

At large spatial scales, climatic conditions have been shown to influence diversity and identity effects (Ampoorter et al., 2020), while 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).

This thesis shows that large scale differences in environmental conditions between the northern and southern region were responsible for most of the variance in abundance, biomass and mean biomass of epigeal spiders, with higher values in the warmer southern sites (**Chapter**

2). Regional environmental differences were also responsible for structuring epigeal spider assemblages with no significant difference in assemblage structure between different stand types. Furthermore, regional differences in environmental conditions modulated tree identity effects with Norway spruce effects being stronger in the northern region, possibly as a result of higher canopy openness differences among stands there, or as a result of stronger tree identity effects on the soil (Foltran et al., 2021). Additionally, regional differences in community structure modulated microhabitat effects, as they were influenced by which spider guild was dominant.

Moreover, regional differences in soil nutrient capacity significantly impacted European beech leaf damage, and modulated effects of tree identity and canopy openness (**Chapter 5**). Increasing soil nutrient capacity had a positive effect on increased mature tree herbivory damage, conforming to the compensatory continuum hypothesis which suggests that plants are more tolerant to herbivory in low-stress, benign environments and may invest less in defenses (Hawkes & Sullivan, 2001). Additionally, soil nutrient capacity modulated the effects of Douglas fir proportion and canopy openness on leaf damage with a distinct difference between plots with high and low nutrient capacity. Plots with higher nutrient capacity were the only ones where Douglas fir proportion had a negative effect on sapling chewing damage and canopy openness a negative effect on mature tree pathogen damage. These results show that soil nutrient capacity can influence tree identity effects, as well as effects of plot and plant characteristics.

Local scale differences in factors not strictly attributed to tree identity also influenced arthropod diversity and functioning. For instance, between stand differences in epigeal spider assemblages were mainly due to differences in canopy openness and litter cover (**Chapter 2**). Furthermore, promoting forest associated microhabitat variables such as canopy closure, litter cover and fine deadwood cover led to a tradeoff between epigeal spider diversity and density. Promoting local canopy closure and litter cover benefited spider abundance and biomass, as increasing litter cover benefits the activity density of both large sheet web weavers and cursorial hunters, which were numerically dominant in our study sites. However, promoting plot-level forest associated microhabitat variables such as litter depth and canopy closure led to a decrease in arthropod predation rates, emphasizing once more the importance of scale when looking at effects of the environmental context (**Chapter 4**). On the other hand, promoting canopy openness consistently promoted epigeal spider taxonomic and functional diversity, while increasing local fine deadwood cover had a negative effect on spider species richness, when taking into account the most abundant species.

Understanding the multitude of factors that encompass the environmental context of research on non-native effects on arthropod diversity and functioning is important to try and disentangle tree identity effects from effects not strictly attributed to tree identity. Moreover, analyzing the effects of factors not strictly attributed to tree identity and their spatial scale dependence may also provide foresters with ways to promote biodiversity and top-down control without changing tree species composition. However, as the findings presented in this thesis suggest, there is no management practice that would benefit biodiversity and top-down control, with further research being necessary to better balance both demands.

6.4 General conclusions and future prospects

As climate change is altering ecosystems worldwide (Scheffers et al., 2016), Central European forestry faces challenges in balancing ecological and economic demands (Albert et al., 2020; Ruckelshaus et al., 2015). One key challenge is dealing with tree damage and mortality due to insect pests (Jactel et al., 2009). With temperature maxima increasing and extreme drought events becoming more frequent, more and more large-scale outbreaks of insect herbivores will be triggered, which in turn will increases overall tree mortality (Ammer et al., 2018; Jacquet et al., 2012; Netherer et al., 2019). Recent ecological research suggests that, generally, tree mixtures are more resistant to natural disturbances such as herbivore outbreaks, especially mixtures with phylogenetically distant tree species (Jactel et al., 2021). This would mean that enriching Central European beech forests with Norway spruce planted beyond its natural range would benefit pest control. However, recent Norway spruce dieback in Central Europe as a result of extreme weather and bark beetle outbreaks (Krejza et al., 2021; Mezei et al., 2021) has led foresters to look for an alternative tree species with lower risk and higher yield. During this search foresters have turned towards non-native tree species, the most utilized of which is Douglas fir, which was introduced from North America almost two centuries ago (Essl, 2005; Knoerzer & Reif, 2002). High growth rates, good wood properties, and a low number of pests and diseases are factors that have contributed to the large present-day distribution of Douglas fir in European forests (Busler & Blaschke, 2004). Although, recent research has shown that forest ecosystems in Central Europe can deal with the introduction of non-native Douglas fir relatively well, the full extent of ecological consequences of its increased utilization are not fully known (Schmid et al., 2014).

In this thesis I tried to answer what would be the consequences of enriching Central European forests with conifers, especially with Douglas fir, on generalist arthropod predator communities and arthropod-mediated ecosystem function. Tree diversity effects were less important than tree identity effects with only arboreal spiders and European beech saplings and mature trees benefiting from mixture planting. Contrary to recent results showing negative effects of non-native Douglas fir on generalist arthropod predator diversity and density (Finch & Szumelda, 2007; Schuldt & Scherer-Lorenzen, 2014), my results show that increasing Douglas fir utilization could benefit generalist arthropod predator diversity, density and top-down control, as well as lower European beech leaf damage. Douglas fir effects were usually stronger in monocultures and stands with higher Douglas fir proportion, with only arboreal spider communities benefiting when Douglas fir trees were planted n heterospecific patches. The discrepancy in results with previous research is mostly due to differences in the environmental context studied, emphasizing the importance of taking into account regional differences in environmental variables, and local microhabitat variables that can be altered by forest management. It is also important to note that Norway spruce effects were similar to Douglas fir effects, showing that replacing Norway spruce with Douglas fir would not lead to drastic changes in arthropod diversity and arthropod-mediated ecosystem functions.

In the frame of RTG2300, similar results have been found for other forest associated groups (other arthropods, small mammals, fungi and vascular plants), with non-native Douglas fir monocultures having equal or higher multi-taxon diversity and abundance than European beech and Norway spruce monocultures. Such results make Douglas fir a promising alternative to Norway spruce, but further research is necessary to understand the totality of ecological consequences of increased Douglas fir utilization in Central European forests. In the context of arthropod diversity and functioning, further research is being conducted in the canopy as well as on trophic niches, by the second cohort of Subproject 6. This will be able to answer a multitude of research questions including:

- Are the beneficial effects of Douglas fir on arboreal spiders detected in young forest stands present in mature stands and to what extent are they dependent on canopy structure?
- Does the increased utilization of Douglas fir only benefit arboreal spiders, or does this effect extend to other canopy arthropod groups?

- Are clay caterpillar attack rates higher in Douglas fir canopies or is the positive effect of Douglas fir on top-down control limited to the ground layer?
- How would the increased utilization of Douglas fir affect the trophic niche structure of generalist arthropod predators?

In addition to answering these questions, further research is necessary to understand temporal dynamics in Douglas fir stands, especially considering that it has been shown that it has a negative effect on canopy arthropods during winter (Gossner & Utschick, 2015). Furthermore, by collecting epigeal arthropods with litter sifting, it can be seen if Douglas fir effects on the most active generalist arthropod predators collected by pitfall traps apply to the whole community. All of this will helps us understand the full extent of the consequences of increased Douglas fir utilization on arthropod diversity and ecosystem functioning.

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Appendix A

Supplementary materials for Chapter 2

Tree identity effects on spider diversity and density are influenced by large and small spatial scale differences in the environmental context

Table A1. Data on soil type, stand age (provided by the local forest management authority), proportion of tree species based on area potentially available (Do - Douglas fir, Sp – Norway spruce, Be – European beech), total basal area, and climatic variables such as mean annual average temperature (MAAT) and mean annual precipitation (MAP) calculated since 1980 from interpolated data from the German weather service (Deutscher Wetterdienst, DWD), as well as data on latitude, longitude (ETRS89/UTM32N; EPSG:25832) and elevation of all sites.

Quintet	Stand	Soil	Age	Do %	Be %	Sp %	Basal Area ($m^2 .ha^{-1}$)	MAAT °C	MAP mm/yr	Latitude	Longitude	elevation m.a.s.l
1. Harz	Do	Brown earth / podsol brown earth from hard clay and slit slates with shares of greywacke, sandstone, quartzite and phyllite	52	95	5	-	43.10	7.63	1029.24	5736340	596152	520.00
	Do/Be		102	67	33	-	51.62	7.63	1029.24	5736435	596606	492.00
	Be		102		100		31.85	7.63	1029.24	5736534	596543	524.00
	Sp/Be		97		59	41	43.19	7.63	1029.24	5736279	596272	507.00
	Sp*		92		11	89	56.25	7.63	1029.24	5736419	596457	511.00
2. Dassel	Do	Podsol brown earth from low-base quartz sandstones and conglomerates	43	97	3		36.46	8.75	814.87	5732580	547776	362.00
	Do/Be		90	22	78		38.31	8.56	822.89	5730316	549045	442.00
	Be		89		100		24.85	8.56	822.89	5730430	548875	442.00
	Sp/Be*		89		90	10	22.70	8.56	822.89	5730338	548791	442.00
	Sp		69			100	49.43	8.56	822.89	5730305	548652	442.85
3. Winnefeld	Do	Podsol brown earth from low-base quartz isandstones and conglomerates	46	98	2		31.75	8.83	839.26	5725299	538367	336.99
	Do/Be		91	19	81		30.42	8.92	818.22	5723181	540118	339.66
	Be		91		100		27.81	8.92	818.22	5723255	540025	379.00
	Sp/Be		96		85	15	26.33	8.92	818.22	5723033	540382	345.00
	Sp*		60		11	89	42.39	9.02	820.02	5724683	538958	344.67
4. Nienover	Do	Podsol brown earth from low-base quartz sandstones and conglomerates	46	86		14	34.34	8.82	895.36	5728206	536392	405.00
	Do/Be		74	29	55	16	38.51	9.06	869.87	5726824	536587	282.31
	Be		88		98	2	28.28	9.06	869.87	5727251	536091	320.00
	Sp/Be		86		66	34	37.45	9.06	869.87	5727849	537565	310.05
	Sp		56			100	52.02	8.82	895.36	5728113	536446	299.47
5. Nienburg	Do	Podsol brown earth from low-base quartz sandstones and conglomerates	62	100			36.27	9.70	733.34	5828569	517938	88.00
	Do/Be		108	53	47		39.31	9.70	733.34	5828882	518483	89.00
	Be		79		100		28.57	9.70	733.34	5832537	520245	101.00
	Sp/Be*		79		89	11	31.15	9.70	733.34	5832258	520183	98.00
	Sp		62	1		99	29.92	9.70	733.34	5828387	518344	84.00
7. Ghörde II	Do	Podsol, brown earth from dry, nutrient- poor sands	54	1	90	9	35.24	9.19	681.68	5888449	620170	128.00
	Do/Be		67	49	48	3	35.35	9.19	681.68	5888393	620255	126.00
	Be		97	94		6	34.52	9.19	681.68	5888973	620345	117.00
	Sp/Be		118		72	28	37.83	9.19	681.68	5886878	622986	138.00

	Sp		57		4	96	34.78	9.19	681.68	5886722	622981	140.00
8. Ghörde I	Do	Podsol, brown earth from dry, nutrient- poor sands	54	91	9		37.70	9.20	672.63	5896091	620170	126.00
	Do/Be		75	65	35		39.72	9.20	672.63	5896024	620099	125.00
	Be		131		99	1	24.26	9.20	672.63	5896425	620270	115.00
	Sp/Be		81		76	24	32.67	9.20	672.63	5896221	620524	113.00
	Sp		62	2	1	97	44.76	9.20	672.63	5896085	620384	121.00

* Two monocultures (1.5 and 3.5) and two mixtures (2.4 and 5.4) have similar proportions (89/11 and 90/10) but are classified as different stand types. This is due to the fact that the proportions in the monocultures were strongly influenced by individual individual large trees (1.5) or a few non-target trees in close proximity to each other (3.5), making the stands fit the monoculture stand type better. Furthermore in the case of both mixtures (2.4 and 5.4) due to the spatial distribution of the mixed tree species, there was a large enough area where the species would interact despite the lacking proportions.

Table A2. Abundance of different spider guilds inhabiting different stand types (Be-European beech monoculture, Do-Douglas fir monoculture, Sp-Norway spruce monoculture, Be/Do-European Beech/Douglas fir mixture Be/Sp- European Beech/Norway spruce mixture) and regions (North-South), as well as total abundance and number of species

Spider guild	Do	Be/Do	Be	Be/Sp	Sp	North	South	Abundance	N of species
Ambush hunters	133	18	14	24	83	261	11	272	8
Ground hunters	344	815	574	447	549	1580	1149	2729	19
Orb web weavers	6	0	0	0	2	6	2	8	3
Other hunters	570	558	649	482	391	1152	1498	2650	44
Sensing web weavers	12	1	1	2	4	16	4	20	1
Sheet web weavers	2055	2304	1631	1859	2047	3228	6668	9896	44
Space web weavers	18	15	20	8	22	46	37	83	7
Specialists	102	72	63	84	232	189	364	553	4

Table A3. Abundance of different spider species inhabiting different stand types (Be-European beech monoculture, Do-Douglas fir monoculture, Sp-Norway spruce monoculture, Be/Do- European Beech/Douglas fir mixture Be/Sp- European Beech/Norway spruce mixture) and regions (North-South), as well as total species abundance. G- Species with endangerment of unknown extent, 3- Endangered species

Spider species	Do	Be/Do	Be	Be/Sp	Sp	North	South	Abundance
Agelenidae	1074	1298	947	1011	1009	780	4559	5339
1. *Coelotes terrestris* (Wider, 1834)	754	949	635	712	801	636	3215	3851
2. *Histopona torpida* (C. L. Koch, 1837)	50	68	66	66	62	9	303	312
3. *Inermocoelotes inermis* (L. Koch, 1855)	270	280	245	232	143	136	1034	1170
4. *Tegenaria silvestris* (L. Koch, 1872)	3	1	1	1	3	2	7	9
Amaurobiidae	201	182	172	197	137	33	856	889
5. *Amaurobius fenestralis* (Ström, 1768)	81	122	90	59	52	33	371	404
6. *Callobius claustrarius* (Hahn, 1833)	120	60	82	138	85	0	485	485
Anyphaenidae	1	0	0	1	0	2	0	2
7. *Anyphaena accentuata* (Walckenaer, 1802)	1	0	0	1	0	2	0	2
Araneidae	1	0	0	0	1	1	1	2
8. *Araneus sturmi* (Hahn, 1831)	1	0	0	0	1	1	1	2
Clubionidae	20	19	31	22	12	28	76	104

9. *Clubiona comta* C. L. Koch, 1839	2	0	1	3	1	4	3	7
10. *Clubiona subsultans* (Thorell, 1875)	0	0	0	1	0	1	0	1
11. *Clubiona terrestris* Westring, 1851	18	19	30	18	11	23	73	96
Cybaeidae	6	11	0	0	15	1	31	32
12. *Cryphoeca silvicola* (C. L. Koch, 1834)	1	3	0	0	14	1	17	18
13. *Cybaeus angustiarum* L. Koch, 1868	5	8	0	0	1	0	14	14
Dictynidae	0	1	1	1	4	4	3	7
14. *Lathys humilis* (Blackwall, 1855)	0	1	1	1	4	4	3	7
Dysderidae	96	71	62	83	232	182	362	543
15. *Dysdera erythrina* (Walckenaer, 1802)	51	36	25	21	52	181	4	185
16. *Harpactea hombergi* (Scopoli, 1763)	0	0	0	0	1	1	0	1
17. *Harpactea lepida* (C. L. Koch, 1838)	45	35	37	62	179	0	358	358
Gnaphosidae	23	47	45	50	129	270	24	294
18. *Drassyllus lutetianus* (L. Koch, 1866)	0	0	0	0	1	1	0	1
19. *Haplodrassus signifer* (C. L. Koch, 1839)	1	0	0	0	1	2	0	2
20. *Haplodrassus silvestris* (Blackwall, 1833)	1	19	41	41	4	105	1	106
21. *Haplodrassus soerenseni* (Strand, 1900)	12	10	2	7	49	80	0	80
22. *Scotophaeus quadripunctatus* (Linnaeus, 1758)	0	1	0	0	0	1	0	1
23. *Zelotes clivicola* (L. Koch, 1870)	4	8	0	1	67	68	12	80
24. *Zelotes subterraneus* (C. L. Koch, 1833)	5	9	2	1	7	13	11	24

Hahniidae	73	69	46	57	65	255	55	310
25. *Cicurina cicur* (Fabricius, 1793)	3	1	9	2	3	3	15	18
26. *Hahnia helveola* Simon, 1875	16	30	8	11	9	73	1	74
27. *Hahnia pusilla* C. L. Koch, 1841	54	38	29	44	53	179	39	218
Linyphiidae	1230	1270	1068	1044	1167	3230	2549	5779
28. *Abacoproeces saltuum* (L. Koch, 1872)	0	0	0	0	2	2	0	2
29. *Agyneta conigera* (O. P.-Cambridge, 1863)	7	0	0	0	2	4	5	9
30. *Araneoncus humilis* (Blackwall, 1841)	1	0	0	0	0	1	0	1
31. *Asthenargus paganus* (Simon, 1884)	0	0	0	0	1	1	0	1
32. *Bathyphantes gracilis* (Blackwall, 1841)	0	0	0	1	0	1	0	1
33. *Bathyphantes parvulus* (Westring, 1851)	1	0	0	0	0	1	0	1
34. *Centromerita bicolor* (Blackwall, 1833)	0	0	0	0	1	1	0	1
35. *Centromerus brevipalpus* (Menge, 1866)	1	0	0	1	7	9	0	9
36. *Centromerus cavernarum* (L. Koch, 1872)	0	0	0	0	1	0	1	1
37. *Centromerus dilutus* (O. P.-Cambridge, 1875)	14	5	3	14	13	44	5	49
38. *Centromerus pabulator* (O. P.-Cambridge, 1875)	4	1	0	1	2	2	6	8
39. *Centromerus serratus* (O. P.-Cambridge, 1875)	0	10	5	11	13	39	0	39
40. *Centromerus sylvaticus* (Blackwall, 1841)	1	4	1	1	1	3	5	8
41. *Ceratinella brevis* (Wider, 1834)	130	166	98	121	134	146	503	649
42. *Dicymbium nigrum* (Blackwall, 1834)	3	3	1	0	1	1	7	8

43. *Dicymbium tibiale* (Blackwall, 1836)	3	3	3	2	5	3	13	16
44. *Diplocephalus cristatus* (Blackwall, 1833)	0	0	14	0	2	0	16	16
45. *Diplocephalus latifrons* (O. P.-Cambridge, 1863)	194	25	11	1	46	13	264	277
46. *Diplocephalus picinus* (Blackwall, 1841)	8	58	148	93	26	39	294	333
47. *Diplostyla concolor* (Wider, 1834)	1	0	7	2	15	24	1	25
48. *Drapetisca socialis* (Sundevall, 1833)	0	0	0	1	1	0	2	2
49. *Entelecara erythropus* (Westring, 1851)	0	0	0	1	0	0	1	1
50. *Erigone atra* Blackwall, 1833	2	0	1	2	1	4	2	6
51. *Erigonella hiemalis* (Blackwall, 1841)	11	0	0	0	2	0	13	13
52. *Gonatium rubellum* (Blackwall, 1841)	2	33	32	23	6	8	88	96
53. *Linyphia hortensis* Sundevall, 1830	1	1	1	2	0	4	1	5
54. *Macrargus rufus* (Wider, 1834)	11	10	14	25	19	34	45	79
55. *Maso sundevalli* (Westring, 1851)	1	0	0	0	0	0	1	1
56. *Metopobactrus prominulus* (O. P.-Cambridge, 1873)	0	0	8	0	1	0	9	9
57. *Micrargus herbigradus* (Blackwall, 1854)	14	5	3	4	0	4	22	26
58. *Microneta viaria* (Blackwall, 1841)	6	40	56	19	6	93	34	127
59. *Minyriolus pusillus* (Wider, 1834)	6	2	1	3	11	10	13	23
60. *Mioxena blanda* (Simon, 1884)	0	0	0	0	1	1	0	1
61. *Monocephalus castaneipes* (Simon, 1884)	1	0	0	0	0	0	1	1
62. *Neriene clathrata* (Sundevall, 1830)	0	0	2	2	0	2	2	4

63. *Neriene emphana* (Walckenaer, 1841)	0	2	0	0	0	2	0	2
64. *Neriene peltata* (Wider, 1834)	1	0	0	0	0	0	1	1
65. *Nusoncus nasutus* (Schenkel, 1925)	0	0	0	0	1	0	1	1
66. *Palliduphantes pallidus* (O. P.-Cambridge, 1871)	1	4	2	3	2	3	9	12
67. *Panamomops mengei* Simon, 1926	0	0	0	7	0	7	0	7
68. *Pelecopsis radicicola* (L. Koch, 1872)	24	2	1	1	120	148	0	148
69. *Porrhomma microphthalmum* (O. P.-Cambridge, 1871)	0	1	0	0	0	0	1	1
70. *Saaristoa abnormis* (Blackwall, 1841)	0	1	0	0	0	1	0	1
71. *Saloca diceros* (O. P.-Cambridge, 1871)	0	7	0	2	0	0	9	9
72. *Silometopus elegans* (O. P.-Cambridge, 1873)	0	0	0	0	1	0	1	1
73. *Stemonyphantes lineatus* (Linnaeus, 1758)	0	1	0	0	1	1	1	2
74. *Tapinocyba insecta* (L. Koch, 1869)	68	21	23	24	51	186	1	187
75. *Tapinocyba pallens* (O. P.-Cambridge, 1873)	12	10	11	13	29	0	75	75
76. *Tapinocyba praecox* (O. P.-Cambridge, 1873)	4	0	0	0	0	1	3	4
77. *Tapinopa longidens* (Wider, 1834)	5	2	0	5	6	11	7	18
78. *Tenuiphantes alacris* (Blackwall, 1853)	15	1	0	1	4	5	16	21
79. *Tenuiphantes cristatus* (Menge, 1866)	0	3	0	2	2	0	7	7
80. *Tenuiphantes flavipes* (Blackwall, 1854)	333	377	259	323	352	1538	106	1644
81. *Tenuiphantes tenebricola* (Wider, 1834)	129	88	3	44	96	9	351	360
82. *Tenuiphantes tenuis* (Blackwall, 1852)	11	23	10	8	18	25	45	70

83. *Tenuiphantes zimmermanni* (Bertkau, 1890)	2	1	3	5	0	2	9	11
84. *Thyreosthenius parasiticus* (Westring, 1851)	0	0	0	1	0	1	0	1
85. *Walckenaeria acuminata* Blackwall, 1833	0	1	0	0	1	1	1	2
86. *Walckenaeria atrotibialis* (O. P.-Cambridge, 1878)	86	16	5	6	24	60	77	137
87. *Walckenaeria capito* (Westring, 1861)	0	0	1	0	0	1	0	1
88. *Walckenaeria corniculans* (O. P.-Cambridge, 1875)	74	219	219	172	99	551	232	783
89. *Walckenaeria cucullata* (C. L. Koch, 1836)	27	38	59	60	8	122	70	192
90. *Walckenaeria cuspidata* Blackwall, 1833	2	37	33	22	17	1	110	111
91. *Walckenaeria dysderoides* (Wider, 1834)	5	20	11	6	14	34	22	56
92. *Walckenaeria furcillata* (Menge, 1869)	0	11	0	0	0	11	0	11
93. *Walckenaeria mitrata*[G](Menge, 1868)	0	1	2	3	0	6	0	6
94. *Walckenaeria obtusa* Blackwall, 1836	8	17	17	6	1	9	40	49
Liocranidae	66	96	91	31	32	277	39	316
95. *Agroeca brunnea* (Blackwall, 1833)	65	96	87	30	29	268	39	307
96. *Apostenus fuscus* Westring, 1851	1	0	4	1	3	9	0	9
Lycosidae	254	669	438	365	381	1023	1084	2107
97. *Alopecosa pulverulenta* (Clerck, 1757)	1	1	0	2	13	12	5	17
98. *Pardosa amentata* (Clerck, 1757)	1	0	0	0	0	0	1	1
99. *Pardosa lugubris* (Walckenaer, 1802)	4	9	6	11	13	10	33	43
100. *Pardosa saltans* Töpfer-Hofmann, 2000	35	536	378	267	130	502	844	1346

101. *Piratula hygrophila* (Thorell, 1872)	25	12	0	1	83	118	3	121
102. *Trochosa terricola* Thorell, 1856	188	111	54	84	142	381	198	579
Mimetidae	6	1	1	1	0	7	2	9
103. *Ero furcata* (Villers, 1789)	6	1	1	1	0	7	2	9
Miturgidae	0	2	0	1	1	2	2	4
104. *Zora spinimana* (Sundevall, 1833)	0	2	0	1	1	2	2	4
Philodromidae	5	2	0	3	18	14	14	28
105. *Philodromus albidus* (Kulczyński, 1911)	0	0	0	0	1	0	1	1
106. *Philodromus aureolus* (Clerck, 1757)	1	0	0	0	0	1	0	1
107. *Philodromus collinus* C. L. Koch, 1835	4	2	0	3	17	13	13	26
Phrurolithidae	0	1	0	0	5	6	0	6
108. *Phrurolithus festivus* (C. L. Koch, 1835)	0	1	0	0	5	6	0	6
Salticidae	13	10	15	5	12	32	23	55
109. *Ballus chalybeius* (Walckenaer, 1802)	0	1	3	1	0	4	1	5
110. *Euophrys frontalis* (Walckenaer, 1802)	0	0	0	0	2	2	0	2
111. *Neon reticulatus* (Blackwall, 1853)	10	9	11	4	9	21	22	43
112. *Pseudeuophrys erratica* (Walckenaer, 1826)	3	0	1	0	1	5	0	5
Segestriidae	12	1	1	2	4	16	4	20
113. *Segestria senoculata* (Linnaeus, 1758)	12	1	1	2	4	16	4	20
Tetragnathidae	5	0	0	0	1	5	1	6

114. *Metellina mengei* (Blackwall, 1869)	1	0	0	0	0	1	0	1
115. *Tetragnatha obtusa* C. L. Koch, 1837	4	0	0	0	1	4	1	5
Theridiidae	18	15	20	8	22	46	37	83
116. *Anelosimus vittatus* (C. L. Koch, 1836)	0	1	0	0	0	1	0	1
117. *Enoplognatha ovata* (Clerck, 1757)	2	1	0	1	1	5	0	5
118. *Euryopis flavomaculata* (C. L. Koch, 1836)	2	2	8	0	14	26	0	26
119. *Paidiscura pallens* (Blackwall, 1834)	2	2	2	0	2	3	5	8
120. *Platnickina tincta* (Walckenaer, 1802)	1	1	0	0	0	2	0	2
121. *Robertus lividus* (Blackwall, 1836)	10	8	10	7	3	9	29	38
122. *Robertus scoticus* Jackson, 1914	1	0	0	0	2	0	3	3
Thomisidae	133	18	14	24	83	261	11	172
123. *Diaea dorsata* (Fabricius, 1777)	0	1	0	0	0	0	1	1
124. *Ozyptila praticola* (C. L. Koch, 1837)	60	13	11	17	39	137	3	140
125. *Ozyptila trux* (Blackwall, 1846)	72	2	1	0	39	113	1	114
126. *Xysticus audax* (Schrank, 1803)	0	0	0	1	1	2	0	2
127. *Xysticus cristatus* (Clerck, 1757)	0	0	1	0	0	0	1	1
128. *Xysticus lanio* C. L. Koch, 1835	0	1	1	6	4	8	4	12
129. *Xysticus luctuosus*[3](Blackwall, 1836)	1	0	0	0	0	1	0	1
130. *Xysticus ulmi* (Hahn, 1831)	0	1	0	0	0	0	1	1

Table A4. Differences in microhabitat characteristics between stand types (Be-European beech monoculture, Do-Douglas fir monoculture, Sp-Norway spruce monoculture, Be/Do- European Beech/Douglas fir mixture Be/Sp-European Beech/Norway spruce mixture) supported by a post-hoc Tukey test adjusted by Holm test.

Stand type	Canopy openness			Log(Deadwood cover+1)		
	Est. (±SE)	z	*P*	Est. (±SE)	z	*P*
Be/Do-Be	-2.13 (±5.80)	-0.4	1.000	-0.21 (±0.22)	-0.9	1.000
Be/Sp-Be	8.96 (±5.80)	1.5	0.956	0.04 (±0.22)	0.1	1.000
Do-Be	-10.46 (±5.80)	-1.8	**<0.001**	0.32 (±0.22)	1.4	0.905
Sp-Be	-23.60 (±5.80)	-4.1	**<0.001**	0.44 (±0.22)	2.0	0.388
Be/Sp-Be/Do	11.09 (±5.80)	1.9	0.956	0.24 (±0.22)	1.1	1.000
Do-Be/Do	-8.33 (±5.80)	-1.4	**<0.001**	0.53 (±0.22)	2.4	0.167
Sp-Be/Do	-21.47 (±5.80)	-3.7	**0.001**	0.65 (±0.22)	2.9	**0.038**
Do-Be/Sp	-19.42 (±5.80)	-3.3	**0.021**	0.29 (±0.22)	1.3	1.000
Sp-Be/Sp	-32.56 (±5.80)	-5.6	**0.021**	0.41 (±0.22)	1.8	0.490
Sp-Do	-13.14 (±5.80)	-2.3	1.000	0.12 (±0.22)	0.5	1.000

Table A5. Differences in spider abundances, biomass and diversity metrics between stand types (Be-European beech monoculture, Do-Douglas fir monoculture, Sp-Norway spruce monoculture, Be/Do- European Beech/Douglas fir mixture Be/Sp- European Beech/Norway spruce mixture) and regions (North and South) supported by a post-hoc Tukey test adjusted by Holm test

Stand type	Spider abundance per trap/day			Spider biomass per trap/day			Hill number q=0			CWM biomass			Functional richness		
	Est. (±SE)	Z	*P*	Est. (±SE)	Z	*P*	Est. (±SE)	z	*P*	Est. (±SE)	z	*P*	Est. (±SE)	z	*P*
Be/Do-Do													-0.00 (±0.00)	-0.5	1.000
Be-Do													-0.00 (±0.00)	-3.1	**0.017**
Be/Sp-Do													-0.00 (±0.00)	-2.3	0.141
Sp-Do													-0.00 (±0.00)	-0.1	1.000
Be-Be/Do													-0.00 (±0.00)	-2.6	0.075
Be/Sp-Be/Do													-0.00 (±0.00)	-1.8	0.369
Sp-Be/Do													0.00 (±0.00)	0.4	1.000
Be/Sp-Be													0.00 (±0.00)	0.8	1.000
Sp-Be													0.00 (±0.00)	3.0	**0.023**
Sp-Be/Sp													0.00 (±0.00)	2.2	0.165
Be/Do-Be (Only northern sites)							0.05 (±0.16)	0.3	1.00						
Be/Sp-Be (Only northern sites)							0.18 (±0.16)	1.1	1.00						
Do-Be (Only northern sites)							0.26 (±0.16)	1.7	0.667						

Sp-Be (Only northern sites)							0.47 (±0.16)	3.0	**0.028**						
Be/Sp-Be/Do (Only northern sites)							0.12 (±0.16)	0.8	1.000						
Do-Be/Do (Only northern sites)							0.21 (±0.16)	1.3	1.000						
Sp-Be/Do (Only northern sites)							0.42 (±0.16)	2.7	0.072						
Do-Be/Sp (Only northern sites)							0.09 (±0.16)	0.6	1.000						
Sp-Be/Sp (Only northern sites)							0.30 (±0.16)	1.9	0.491						
Sp-Do (Only northern sites)							0.21 (±0.16)	1.3	1.000						
Northern- Southern sites	0.02 (±0.01)	4.4	**<0.001**	0.73 (±0.13)	5.7	**<0.001**				0.79 (±0.14)	5.6	**<0.001**			

Table A6. Output of the linear models for stand type (Be-European beech monoculture, Do-Douglas fir monoculture, Sp-Norway spruce monoculture, Be/Do-European Beech/Douglas fir mixture Be/Sp- European Beech/Norway spruce mixture) effects and North/South effects on abundance, biomass and diversity of spiders with AICc and conditional R squared values (cR)2. Data leveled for European beech/northern sites. Significant effects indicated in bold.

	Log(spider abundance per trap/day+1)				Log(spider biomass per trap/day+1)				Log(Hill number0+1)				Log(Hill number1+1)				Log(Hill number2+1)			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*				
Intercept	0.09 (±0.00)	245	35.5	**<0.001**	1.41 (±0.06)	245	22.4	**<0.001**	2.92 (±0.09)	245	34.2	**<0.001**	2.30 (±0.08)	245	27.9	**<0.001**	1.89 (±0.09)	245	20.9	**<0.001**
Be/Do									0.03 (±0.09)	20	0.3	0.736								
Be/Sp									0.08 (±0.09)	20	0.8	0.412								
Do									0.16 (±0.09)	20	1.8	0.095								
Sp									0.19 (±0.09)	20	2.1	**0.044**								
Southern sites	0.01 (±0.00)	5	4.4	**0.007**	0.36 (±0.06)	5	5.7	**0.002**	-0.01 (±0.09)	5	-0.1	0.911	-0.15 (±0.08)	5	-1.8	0.134	-0.14 (±0.09)	5	-1.6	0.177
Be/Do: Southern sites									-0.02 (±0.09)	20	-0.2	0.834								
Be: Southern sites									-0.09 (±0.09)	20	-1.0	0.339								
Be/Sp: Southern sites									-0.09 (±0.09)	20	-1.0	0.316								
Sp: Southern sites									-0.24 (±0.09)	20	-2.7	**0.014**								
cR^2 / AICc	0.403/-1367.14				0.762/55.035				0.190/362.937				0.463/172.074				0.460/179.707			
	Log(CWM biomass+1)				FRic				FDis				FEve				FDiv			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	3.60 (±0.07)	245	51.5	**<0.001**	0.01 (±0.00)	245	9.2	**<0.001**	0.26 (±0.01)	245	24.6	**<0.001**	0.58 (±0.01)	245	59.0	**<0.001**	0.81 (±0.02)	245	52.7	**<0.001**
Be/Do					-0.00 (±0.00)	24	-0.5	0.597												
Be/Sp					-0.00	24	-3.1	**0.005**												

					(±0.00)															
Do					-0.00 (±0.00)	24	-2.3	**0.029**												
Sp					-0.00 (±0.00)	24	-0.1	0.906												
Southern sites	0.39 (±0.07)	5	5.6	**0.003**													-0.02 (±0.02)	5	-1.5	0.188
cR^2 / AICc	0.777/83.505				0.274/-2295.285				0.524/-1048.763				0.196/-674.493				0.424/-611.440			

Table A7. Output of the linear models for tree proportions, neighborhood diversity and microhabitat effects on abundance, biomass and diversity of spiders with AICc and conditional R squared values (cR)2. Significant effects indicated in bold.

	Log(spider abundance per trap/day+1)				Log(spider biomass per trap/day +1)				Log(Hill number0+1)				Log(Hill number1+1)				Log(Hill number2+1)			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	0.09 (±0.00)	235	41.4	**<0.001**	1.40 (±0.05)	239	26.3	**<0.001**	3.02 (±0.06)	241	51.0	**<0.001**	2.30 (±0.07)	241	30.7	**<0.001**	1.90 (±0.08)	241	22.5	**<0.001**
Do proportion	0.00 (±0.00)	235	2.3	**0.024**	0.06 (±0.03)	239	2.1	**0.037**												
Sp proportion									0.04 (±0.03)	241	1.3	0.200								
Oak proportion	0.00 (±0.00)	235	0.7	0.489					-0.04 (±0.03)	241	-1.7	0.098								
NDiv					-0.00 (±0.02)	239	-0.2	0.863					0.02 (±0.03)	241	0.6	0.558	0.00 (±0.03)	241	0.2	0.828
Log(Vegetation complexity+1	-0.00 (±0.00)	235	-0.8	0.419																
Canopy openness	-0.00 (±0.00)	235	2.7	**0.007**	-0.04 (±0.02)	239	-2.4	**0.020**	0.05 (±0.03)	241	2.0	**0.043**	0.06 (±0.02)	241	3.2	**0.001**	0.05 (±0.02)	241	2.3	**0.013**
Log(Litter cover)	0.01 (±0.00)	235	2.3	**0.020**	0.08 (±0.04)	239	2.3	**0.024**												
Log(Deadwood cover+1)	0.00 (±0.00)	235	1.7	0.099									-0.04 (±0.02)	241	-1.8	0.078	-0.05 (±0.02)	241	-2.5	**0.006**
Southern sites	0.01 (±0.00)	5	4.9	**0.005**	0.36 (±0.05)	5	6.6	**0.001**	-0.09 (±0.06)	5	-1.6	0.173	-0.15 (±0.08)	5	-1.9	0.109	-0.14 (±0.08)	5	-1.7	0.141
Sp proportion: Southern sites									-0.09 (±0.03)	241	-3.3	**0.001**								
Oak proportion: Southern sites	-0.00 (±0.00)	234	-1.5	0.144																
NDiv: Southern siters					-0.04 (±0.02)	239	-1.5	0.125					0.04 (±0.03)	241	1.6	0.115	0.04 (±0.02)	241	1.8	0.103

Log(Vegetation complexity+1): Southern sites	-0.00 (±0.00)	235	-1.7	0.086																
Log(Litter cover): Southern sites	0.00 (±0.00)	235	2.1	**0.040**	0.05 (±0.03)	239	1.7	0.084												
Log(Deadwood cover+1): Southern sites	-0.00 (±0.00)	235	-1.9	0.065																
cR^2 / AICc	0.473/-1264.152				0.778/86.245				0.231/346.187				0.498/188.644				0.503/195.392			
	Log(CWM biomass+1)				FRic				FDis				FEve				FDiv			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	3.60 (±0.07)	245	51.5	**<0.001**	0.01 (±0.00)	237	10.8	**<0.001**	0.26 (±0.01)	243	26.2	**<0.001**	0.58 (±0.01)	240	54.9	**<0.001**	0.81 (±0.01)	242	59.0	**<0.001**
Do proportion					0.00 (±0.00)	237	4.8	**<0.001**									-0.02 (±0.01)	242	-2.0	**0.049**
Sp proportion					0.00 (±0.00)	237	4.3	**<0.001**									-0.03 (±0.01)	242	-2.9	**0.004**
Log(Vegetation complexity+1)					0.00 (±0.00)	237	0.9	0.372												
Canopy openness					0.00 (±0.00)	237	1.8	0.073	0.00 (±0.00)	243	2.0	**0.042**	0.01 (±0.00)	240	1.9	0.058				
Log(Litter cover)					0.00 (±0.00)	237	1.7	0.094	-0.01 (±0.00)	243	-1.9	0.054	-0.02 (±0.01)	240	-2.9	**0.004**	-0.01 (±0.01)	242	-1.7	0.082
Log(Deadwood cover+1)					-0.00 (±0.00)	237	-1.5	0.143					-0.00 (±0.00)	240	-0.1	0.925				
Southern sites	0.39 (±0.07)	5	5.6	**0.003**	-0.00 (±0.00)	5	-0.6	0.578					0.00 (±0.01)	5	0.1	0.933	-0.02 (±0.01)	5	-1.6	0.168
Sp proportion: Southern sites					-0.00 (±0.00)	237	-3.0	**0.003**												
Log(Vegetation complexity+1): Southern sites					0.00 (±0.00)	237	1.8	0.080												
Log(Litter cover): Southern sites													-0.02 (±0.01)	240	-2.4	**0.016**				

Log(Deadwood cover+1): Southern sites													-0.01 (±0.00)	240	-1.9	0.062				
cR^2 / AICc	0.785/83.504				0.316/-2224.271				0.542/-1033.153				0.263/-628.033				0.445/-591.442			

Table A8. Results of the analysis of indicator values (IndVal) of spider species and functional guilds for different regions, sites, stand types (Be-European beech monoculture, Do-Douglas fir monoculture, Sp-Norway spruce monoculture, Be/Do- European Beech/Douglas fir mixture Be/Sp- European Beech/Norway spruce mixture) and tree species presence/absence

		Region			Site			Stand			Tree sp. presence/absence		
Species/guilds	Abundance	Group	IndvaL	*P*	Group	IndvaL	*P*	Group	IndvaL	*P*	Presence/ Absence	IndvaL	*P*
Agroeca brunnea	307	North	0.649	0.001	Gohrde I	0.252	0.001				Do Presence/ Sp Absence	0.319/ 0.381	0.002/ 0.001
Amaurobius fenestralis	404	South	0.622	0.001	Dassel	0.393	0.001				Sp Absence	0.322	0.036
Ambush hunters	272	North	0.589	0.001							Be Absence	0.350	0.001
Callobius claustrarius	485	South	0.306	0.001	Harz	0.886	0.001						
Ceratinella brevis	649	South	0.589	0.001									
Coelotes terrestris	3851	South	0.794	0.001	Dassel	0.306	0.001						
Diplocephalus latifrons	277	South	0.353	0.001				Do	0.386	0.001	Do Presence/ Be Absence	0.311/ 0.412	0.001
Diplocephalus picinus	333	South	0.4	0.001	Harz	0.272	0.001				Do Absence/ Be Presence	0.289/ 0.424	0.005/ 0.001
Dysdera erythrina	185	North	0.517	0.001	Gohrde II	0.554	0.001						
Gonatium rubellum	96	South	0.301	0.001	Harz	0.264	0.001				Be Presence	0.289	0.001
Hahnia helveola	74	North	0.313	0.001									
Hahnia pusilla	218	North	0.501	0.001	Gohrde I	0.418	0.001						
Haplodrassus silvestris	106	North	0.43	0.001							Be Presence	0.267	0.001
Haplodrassus soerenseni	80				Gohrde I	0.428	0.001						
Harpactea lepida	358	South	0.513	0.001	Winnefeld	0.605	0.001						

Histopona torpida	312	South	0.678	0.001	Winnefeld	0.314	0.001						
Inermocoelotes inermis	1170	South	0.674	0.001	Harz	0.513	0.001						
Microneta viaria	127	North	0.279	0.001	Gohrde II	0.328	0.001				Be Presence	0.309	0.001
Ozyptila praticola	140	North	0.509	0.001							Be Absence	0.266	0.001
Ozyptila trux	114	North	0.273	0.001							Be Absence	0.272	0.001
Pardosa_saltans	1346				Winnefeld	0.263	0.003	Be/Do	0.26	0.041	Be Presence	0.588	0.001
Pelecopsis_radicicola	148				Nienburg	0.389	0.001						
Piratula_hygrophila	121				Nienburg	0.489	0.001						
Tapinocyba insecta	187	North	0.606	0.001	Gohrde II	0.446	0.001						
Tapinocyba pallens	75	South	0.331	0.001									
Tenuiphantes flavipes	1644	North	0.949	0.001	Gohrde II	0.459	0.001						
Tenuiphantes tenebricola	360	South	0.465	0.001	Harz	0.443	0.001				Do Presence/ Be Absence	0.259/ 0.338	0.003/ 0.001
Trochosa terricola	579	North	0.590	0.001	Gohrde I	0.322	0.001				Do Presence/ Be Absence	0.414/ 0.462	0.025/ 0.001
Walckenaeria atrotibialis	137							Do	0.416	0.001	Do Presence/ Be Absence	0.357/ 0.415	0.001
Walckenaeria corniculans	783	North	0.667	0.001	Nienburg	0.256	0.001				Be Presence	0.542	0.001
Walckenaeria cucullata	192	North	0.339	0.001							Be Presence	0.377	0.001
Walckenaeria cuspidata	111	South	0.303	0.001									

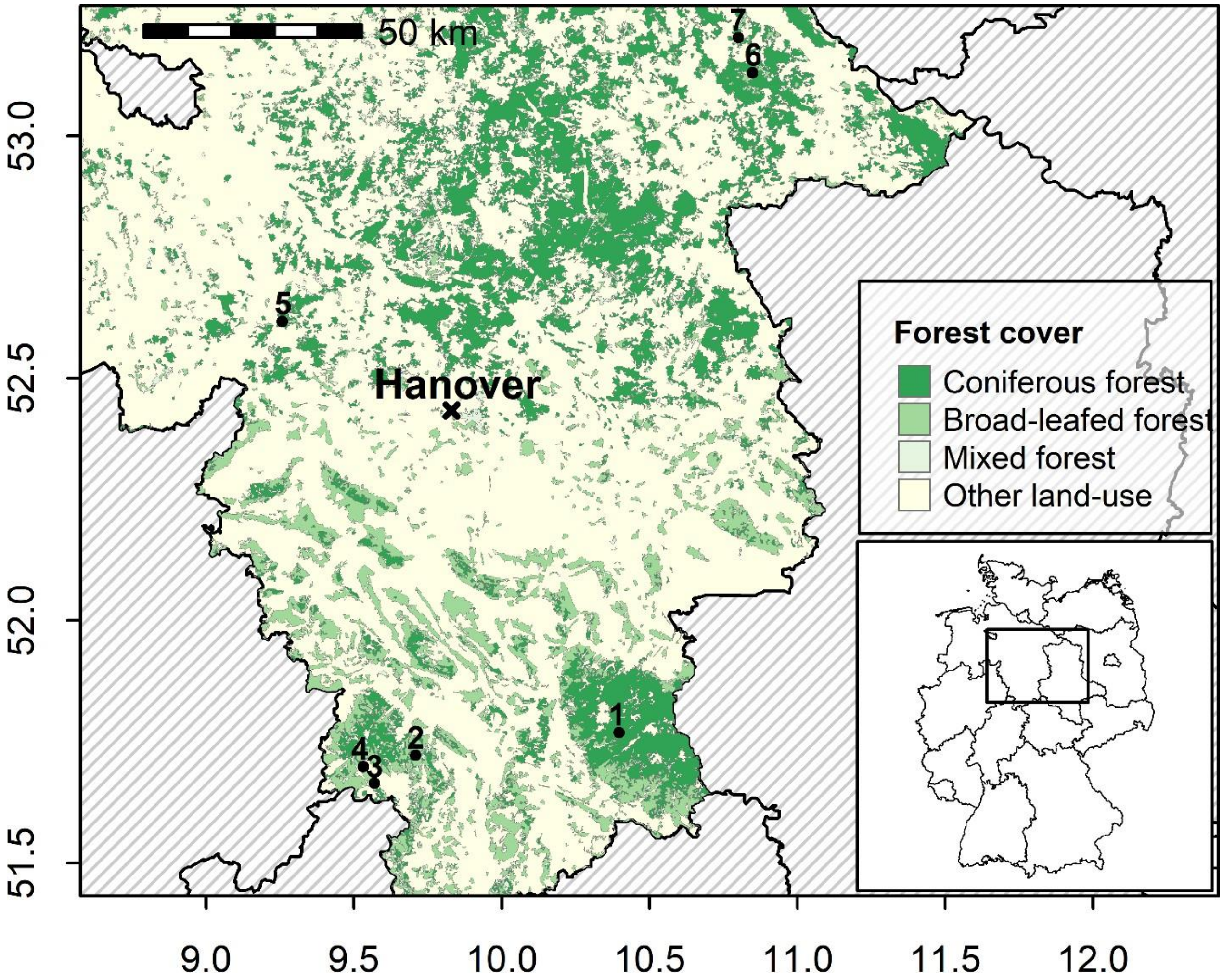

Fig. A1 Map with locations for all 7 of the quintets studied

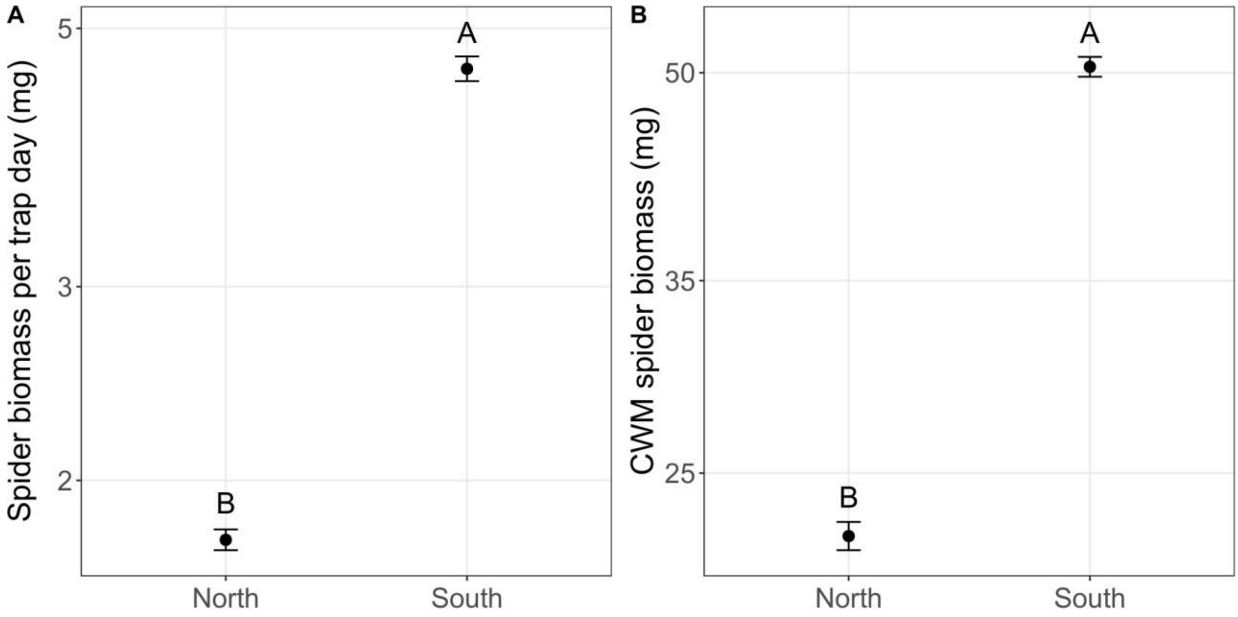

Fig. A2 Differences in mean ± SE biomass per trap day (a; note that traps were open for up to 183 days in total), as well as CWM biomass (B). Significant differences calculated with Tukey HSD post-hoc with p-values adjusted with the Holm-method marked with different letters. Note that the response variables for all panels were log+1 transformed to improve model fit, and the Y-axes show back-transformed values.

Appendix B

Supplementary material for Chapter 3

Tree species richness, tree identity and non-native tree proportion affect arboreal spider diversity, abundance and biomass[1]

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[1] Published in *Forest Ecology and Management* https://doi.org/10.1016/j.foreco.2020.118775

Table B1. Site conditions (taken from http://www.treedivnet.ugent.be/ExpBIOTREE.html)

Former land use	cropland till 1975, then grassland
Coordinates	50°47´ N, 10°13
Elevation	325 m a.s.l.
Soil type	Orthoeutric arenosols with loamy sand on a sandstone bedrock
Mean annual temperature	7.8 °C
Mean annual precipitation	650 mm
Area	23 ha
N of plots	16
Plot size	48 m x 124 m
N of trees sampled	288
Planting date	spring 2004
Diversity gradient	1, 2, 3, 4 species
Species pool	*Fagus sylvatica*, *Picea abies*, *Pseudotsuga menziessii*, *Quercus petraea*

Table B2. Output of the plot level linear model for FEve including vagrant species

Identity effect	FEve		
	Est. (±SE)	*t*	*P*
Intercept	0.67 (±0.01)	79.2	<0.001
Douglas proportion	-0.03 (±0.01)	-3.8	<0.002
F, $DF_{(n,d)}$, P, Adj.R^2	F=14.4 $DF_{1,14}$ P=0.002 R^2=0.51		

Table B3. Total abundance of different spider families inhabiting different tree species and diversity levels (DLs)

Species	Beech	Oak	Douglas fir	Norway spruce	DL1	DL2	DL3	DL4
Anyphaenidae	40	41	11	7	8	36	39	16
Araneidae	156	187	200	238	117	201	261	202
Clubionidae	6	7	1	4	2	7	3	6
Dictynidae	3	2	6	8	2	2	6	9
Linyphiidae	89	63	323	269	72	237	250	185
Lycosidae				1		1		
Mimetidae		1		2		2	1	
Oxyopidae	2		2	1			3	2
Philodromidae	222	179	219	239	103	248	293	215
Pisauridae				1				1
Salticidae	6	3	18	4	3	8	13	7
Sparassidae	1						1	
Tetragnathidae	10	27	45	46	20	43	44	21
Theridiidae	164	200	220	172	104	190	280	182
Thomisidae	26	62	44	37	12	59	78	20

Table B4. Abundance of different spider species inhabiting different tree species and diversity levels (DLs). Forest species marked with an asterisk (*) and Red List species with a plus (+)

Species	Beech	Oak	Douglas fir	Norway spruce	DL1	DL2	DL3	DL4
1. *Agyneta affinis* (Kulczyński, 1898)				1		1		
2. *Agyneta rurestris* (Kulczyński, 1898)		3				1	1	1
3. *Anyphaena accentuata* (Walckenaer, 1802)*	2	1	1			2	1	1
4. *Araneus diadematus* Clerck, 1757*	1		1				2	
5. *Araneus sturmi* (Hahn, 1831)*	1	2	1		2	1		1
6. *Araneus triguttatus* (Fabricius, 1775)*	3	6			3	3	1	2
7. *Araniella cucurbitina* (Clerck, 1757)*	6	7	12	10	3	10	13	9
8. *Araniella opistographa* (Kulczyński, 1905)*	9	17	1		5	7	9	6
9. *Asianellus festivus* (C. L. Koch, 1834)$^{+}$	1							1
10. *Aulonia albimana* (Walckenaer, 1805)				1		1		
11. *Bathyphantes gracilis* (Blackwall, 1841)*	1						1	
12. *Clubiona diversa* O. Pickard-Cambridge, 1862	1						1	
13. *Dendryphantes hastatus* (Clerck, 1757)$^{*,+}$			1			1		
14. *Dendryphantes rudis* (Sundevall, 1833)*			3			1	2	
15. *Diaea dorsata* (Fabricius, 1777)*	2	1	1	1		2	3	
16. *Dictyna arundinacea* (Linnaeus, 1758)		1		2	1	1		1
17. *Diplocephalus latifrons* (O. Pickard-Cambridge, 1863) *			1	1		1		1
18. *Dipoena melanogaster* (C. L. Koch, 1837)*		1	1			1		1
19. *Dismodicus bifrons* (Blackwall, 1841) *	2	2	4	2	1	1	5	3
20. *Dismodicus elevates* (C. L. Koch, 1838)*		2	3	8		4	8	1
21. *Enoplognatha latimana* Hippa & Oksala, 1982	1				1			
22. *Enoplognatha ovata* (Clerck, 1757)*	5	3	3	2	2	4	4	3
23. *Entelecara congenera* (O. Pickard-Cambridge, 1879)*	3	4	123	89	33	75	77	34
24. *Entelecara erythropus* (Westring, 1851)*			2			2		
25. *Erigone atra* Blackwall, 1833	1	1	1			1	2	
26. *Ero aphana* (Walckenaer, 1802)*		1					1	
27. *Ero furcata* (Villers, 1789)*				1		1		
28. *Evarcha arcuata* (Clerck, 1757)	2					1	1	
29. *Gongylidiellum vivum* (O. Pickard-Cambridge, 1875)*	1			1		1	1	
30. *Heliophanus dubius* C. L. Koch, 1835*		1					1	
31. *Linyphia triangularis* (Clerck, 1757)*	7	1	4	4	1	9	2	4
32. *Mangora acalypha* (Walckenaer, 1802)*	1		1	2		1	1	2

33. *Maso sundevalli* (Westring, 1851)*	1					1		
34. *Micrommata virescens* (Clerck, 1757)*	1						1	
35. *Misumena vatia* (Clerck, 1757)	1			1		1	1	
36. *Neottiura bimaculata* (Linnaeus, 1767)*	15	2	4	10	7	5	13	6
37. *Neriene peltata* (Wider, 1834)*			1	1	1		1	
38. *Oedothorax fuscus* (Blackwall, 1834)		1						1
39. *Paidiscura pallens* (Blackwall, 1834)*	5	38	15	9	10	20	24	13
40. *Philodromus aureolus* (Clerck, 1757)*	4	12	3		3	6	6	4
41. *Philodromus cespitum* (Walckenaer, 1802)*	15	16	5	1	1	10	10	16
42. *Philodromus collinus* C. L. Koch, 1835*	5	1	26	31	11	17	23	12
43. *Phylloneta impressa* (L. Koch, 1881)	2	2			2	1	1	
44. *Phylloneta sisyphia* (Clerck, 1757)*	10	10	15	8	1	10	20	12
45. *Platnickinia tincta* (Walckenaer, 1802)*	2	6	25	15	10	10	21	7
46. *Simitidion simile* (C. L. Koch, 1836)*			6			1	4	1
47. *Synageles venator* (Lucas, 1836)		1		1	1			1
48. *Tenuiphantes mengei* (Kulczyński, 1887)*				1			1	
49. *Tenuiphantes tenuis* (Blackwall, 1852)*			1					1
50. *Tetragnatha extensa* (Linnaeus, 1758)		1				1		
51. *Tetragnatha montana* Simon, 1874*	1	1				1	1	
52. *Tetragnatha obtusa* C. L. Koch, 1837*		2	7		1	4	3	1
53. *Theridion familiare* O. Pickard-Cambridge, 1871^{+}		1		1			2	
54. *Theridion varians* Hahn, 1833*	8	11	8	4	2	8	11	10
55. *Trematocephalus cristatus* Hahn, 1833*	1	3				4		
56. *Xysticus cristatus* (Clerck, 1757)	1					1		
57. *Xysticus ulmi* (Hahn, 1831)	2	1			1	2		

Table B5. Output of plot level linear models for the response variables log(CWM biomass+1).

Identity effect	Log(CWM Biomass+1)		
	Est. (±SE)	*t*	*P*
Intercept	2.46 (±0.12)	20.6	<0.001
Douglas proportion	-0.96 (±0.25)	-3.9	0.002
Spruce proportion	-0.60 (±0.25)	-2.4	0.031
F, $DF_{(n,d)}$, P, Adj.R^2	F=8.24 $DF_{2,13}$ P<0.005 R^2=0.56		

Table B6. Output of the linear models for arboreal spider species richness, functional diversity, adult and total abundance and biomass at the tree level (leveled for Douglas fir and outer trees. Significant effects in bold

	Log(adult abundance+1)				Log(total abundance+1)				Log(adult biomass+1)			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	1.57 (±0.10)	265	15.8	**0.000**	2.86 (±0.10)	264	28.2	**0.000**	2.88 (±0.23)	264	12.5	**0.000**
Beech	-0.98 (±0.13)	265	-7.5	**0.000**	-0.86 (±0.13)	264	-7.9	**0.000**	-1.60 (±0.31)	264	-5.2	**0.000**
Oak	-0.61 (±0.13)	265	-4.6	**0.000**	-0.70 (±0.11)	264	-6.5	**0.000**	-0.86 (±0.31)	264	-2.8	**0.006**
Norway spruce	-0.20 (±0.13)	265	-1.5	0.134	-0.03 (±0.11)	264	0.3	0.776	-0.46 (±0.31)	264	-1.5	0.143
Inner trees	-0.15 (±0.12)	265	-1.2	0.220	-0.19 (±0.10)	264	-1.8	0.072	-0.32 (±0.29)	264	-1.1	0.282
Tree species richness					0.13 (±0.08)	14	1.6	0.133	0.27 (±0.15)	14	1.7	0.109
Inner Beech	0.59 (±0.18)	265	3.4	**0.001**	0.53 (±0.15)	264	3.7	**0.000**	1.70 (±0.41)	264	4.1	**0.000**
Inner Oak	0.28 (±0.18)	265	1.6	0.117	0.33 (±0.15)	264	2.3	**0.025**	0.83 (±0.41)	264	2.0	**0.047**
Inner Norway Spruce	-0.05 (±0.18)	265	-0.3	0.779	-0.16 (±0.15)	264	-1.1	0.260	-0.09 (±0.41)	264	-0.2	0.831
Inner: Tree species richness					-0.15 (±0.06)	264	-2.5	**0.015**	-0.25 (±0.17)		-1.5	0.138

	log(Total biomass+1)				log(CWM biomass+1)				log (SR)			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	3.95 (±0.14)	264	28.9	**0.000**	1.74 (±0.16)	264	10.9	**0.000**	1.27 (±0.08)	265	15.4	**0.000**
Beech	-0.98 (±0.22)	264	-5.4	**0.000**	-0.73 (±0.22)	264	-3.3	**0.001**	-0.71 (±0.11)	265	-6.5	**0.000**
Oak	-0.62 (±0.20)	264	-5.4	**0.001**	-0.21 (±0.22)	264	-1	0.335	-0.35 (±0.11)	265	-3.2	**0.002**
Norway spruce	-0.30 (±0.18)	264	-1.6	0.103	-0.24 (±0.22)	264	-1.1	0.287	-0.12 (±0.11)	265	-1.1	0.268
Inner trees	-0.29 (±0.17)	264	-1.7	0.098	-0.17 (±0.21)	264	-0.8	0.419	-0.08 (±0.10)	265	-0.8	0.427
Tree species richness	0.18 (±0.09)	14	2	0.068	0.25 (±0.10)	14	2.4	**0.029**				
Inner Beech	0.96 (±0.24)	264	4	**0.000**	1.23 (±0.30)	264	4.1	**0.000**	0.48 (±0.15)	265	3.3	**0.001**
Inner Oak	0.53 (±0.24)	264	2.2	**0.030**	0.55 (±0.30)	264	1.9	0.066	0.15 (±0.15)	265	1.0	0.326
Inner Norway Spruce	-0.14 (±0.24)	264	-0.59	0.557	-0.02 (±0.30)	264	-0.1	0.953	-0.09 (±0.15)	265	-0.6	0.524
Inner: Tree species richness	-0.19 (±0.10)	264	-2	0.052	-0.19 (±0.12)	264	-1.6	0.102				

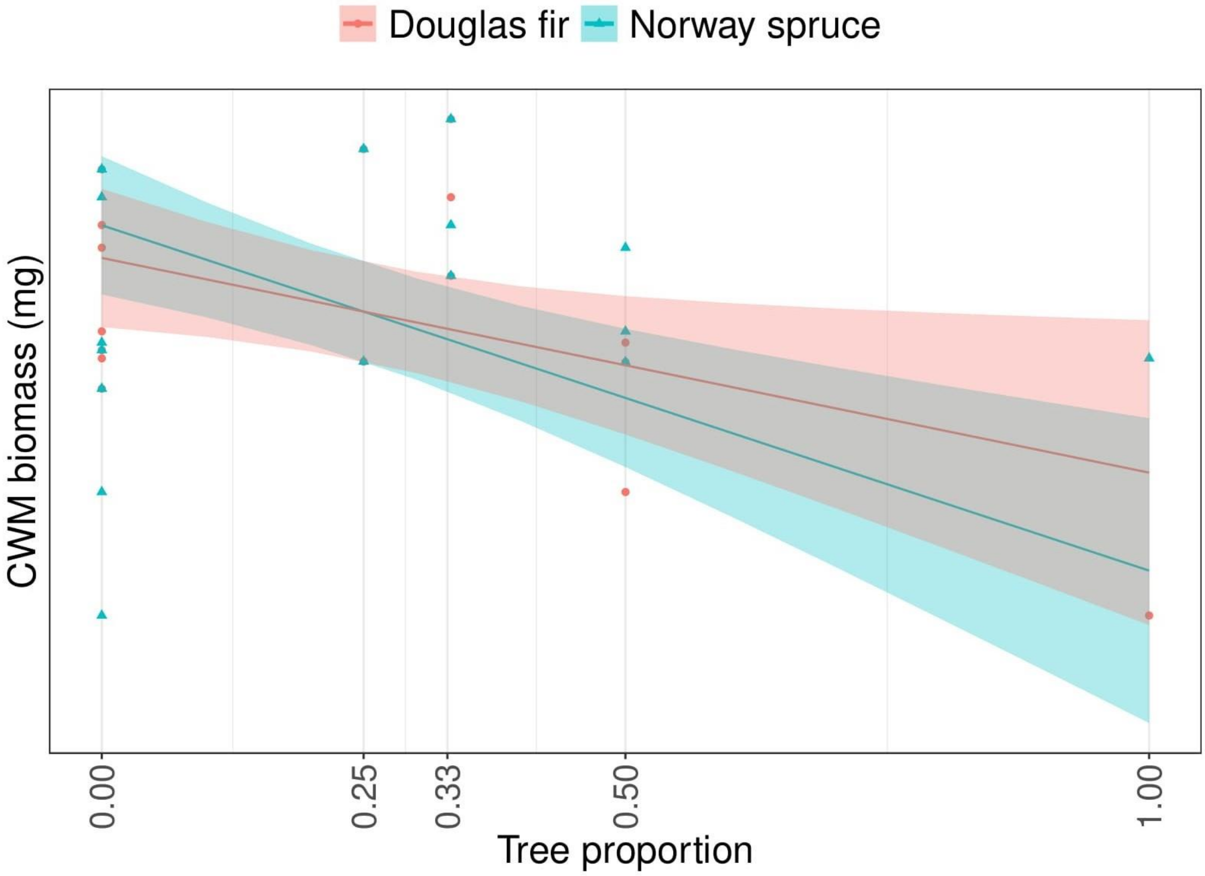

Fig B1. Douglas fir and Norway spruce proportion effects on log(CWM of biomass +1) at the plot level

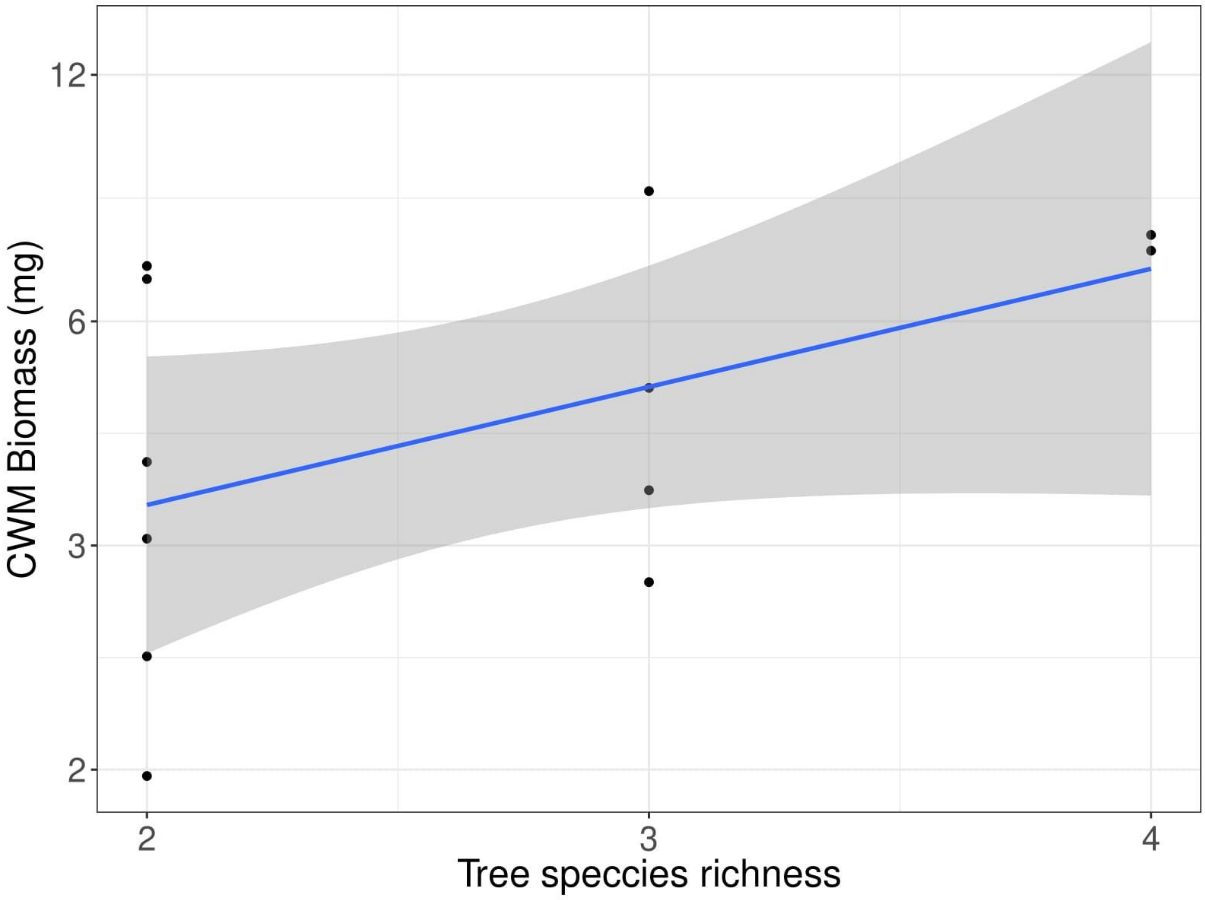

Fig B2. Relationships between tree species richness and CWM spider biomass for outer trees

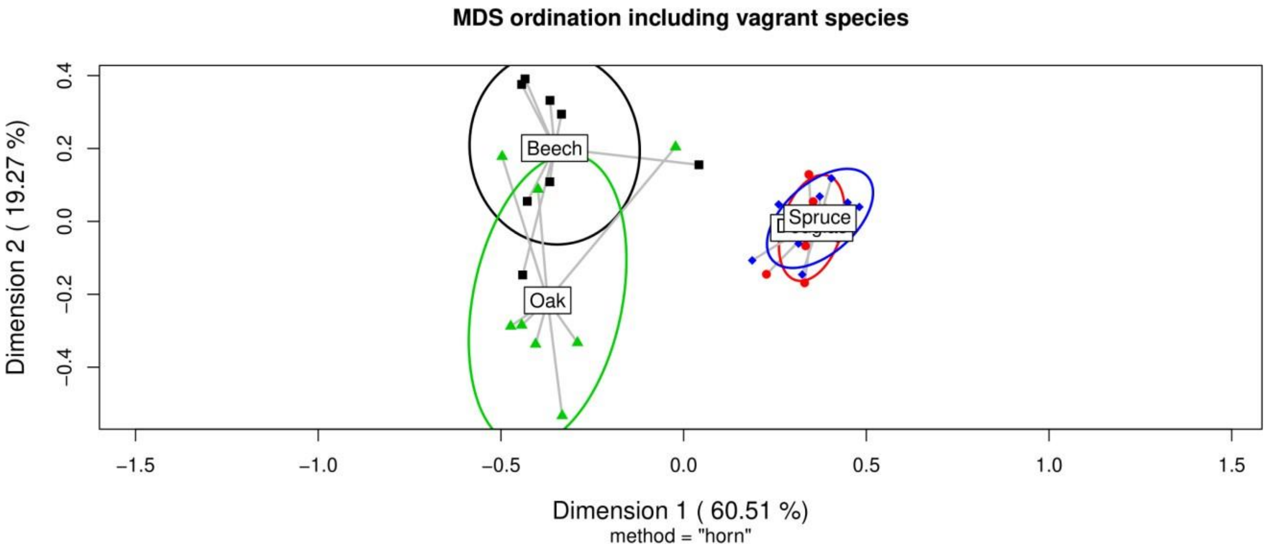

Fig B3. MDS ordination plot (Morista-Horn index) of the multivariate homogeneity of group dispersions (variances) among arboreal spider communities (including species with ≤ 3 individuals), for each tree species (European beech, Douglas fir Norway spruce and sessile oak) from each of the 16 studied plots.

Appendix C

Supplementary material for Chapter 4[1]

Non-native Douglas fir (Pseudotsuga menziesii) promotes sentinel prey attack rates in Central European forest[1]

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[1] Published in *Forest Ecology and Management* https://doi.org/10.1016/j.foreco.2021.119099

Table C1. Data on soil type, stand age (provided by the local forest management authority), proportion of tree species based on area potentially available (Do - Douglas fir, Sp – Norway spruce, Be – European beech), total basal area, and climatic variables such as mean annual average temperature (MAAT) and mean annual precipitation (MAP) calculated since 1980 from interpolated data from the German weather service (Deutscher Wetterdienst, DWD), as well as data on latitude, longitude (ETRS89/UTM32N; EPSG:25832) and elevation of all sites.

Quintet	Stand	Soil	Age	Do %	Be %	Sp %	Basal Area ($m^2 .ha^{-1}$)	MAAT °C	MAP mm/yr	Latitude	Longitude	elevation m.a.s.l
1. Harz	Do	Brown earth / podsol brown earth from hard clay and slit slates with shares of greywacke, sandstone, quartzite and phyllite	52	95	5	-	43.10	7.63	1029.24	5736340	596152	520.00
	Do/Be		102	67	33	-	51.62	7.63	1029.24	5736435	596606	492.00
	Be		102		100		31.85	7.63	1029.24	5736534	596543	524.00
	Sp/Be		97		59	41	43.19	7.63	1029.24	5736279	596272	507.00
	Sp*		92		11	89	56.25	7.63	1029.24	5736419	596457	511.00
2. Dassel	Do	Podsol brown earth from low-base quartz sandstones and conglomerates	43	97	3		36.46	8.75	814.87	5732580	547776	362.00
	Do/Be		90	22	78		38.31	8.56	822.89	5730316	549045	442.00
	Be		89		100		24.85	8.56	822.89	5730430	548875	442.00
	Sp/Be*		89		90	10	22.70	8.56	822.89	5730338	548791	442.00
	Sp		69			100	49.43	8.56	822.89	5730305	548652	442.85
3. Winnefeld	Do	Podsol brown earth from low-base quartz isandstones and conglomerates	46	98	2		31.75	8.83	839.26	5725299	538367	336.99
	Do/Be		91	19	81		30.42	8.92	818.22	5723181	540118	339.66
	Be		91		100		27.81	8.92	818.22	5723255	540025	379.00
	Sp/Be		96		85	15	26.33	8.92	818.22	5723033	540382	345.00
	Sp*		60		11	89	42.39	9.02	820.02	5724683	538958	344.67
4. Nienover	Do	Podsol brown earth from low-base quartz sandstones and conglomerates	46	86		14	34.34	8.82	895.36	5728206	536392	405.00
	Do/Be		74	29	55	16	38.51	9.06	869.87	5726824	536587	282.31
	Be		88		98	2	28.28	9.06	869.87	5727251	536091	320.00
	Sp/Be		86		66	34	37.45	9.06	869.87	5727849	537565	310.05
	Sp		56			100	52.02	8.82	895.36	5728113	536446	299.47
5. Nienburg	Do	Podsol brown earth from low-base quartz sandstones and conglomerates	62	100			36.27	9.70	733.34	5828569	517938	88.00
	Do/Be		108	53	47		39.31	9.70	733.34	5828882	518483	89.00
	Be		79		100		28.57	9.70	733.34	5832537	520245	101.00
	Sp/Be*		79		89	11	31.15	9.70	733.34	5832258	520183	98.00
	Sp		62	1		99	29.92	9.70	733.34	5828387	518344	84.00
6. Unterlüß	Do	Podsol-Regosol from dry, nutrient-poor sands	71	100			50.22	9.03	746.56	5854644	590701	167.00
	Do/Be		86	26	74		36.17	9.03	746.56	5854938	590332	166.00
	Be		86		100		27.18	9.03	746.56	5854926	590408	162.00
	Sp/Be		123		79	21	34.63	9.03	746.56	5854080	588669	162.00
	Sp		112			100	30.05	9.03	746.56	5856116	588161	149.00
7. Ghörde II	Do	Podsol, brown earth from dry, nutrient-poor sands	54	1	90	9	35.24	9.19	681.68	5888449	620170	128.00
	Do/Be		67	49	48	3	35.35	9.19	681.68	5888393	620255	126.00
	Be		97	94		6	34.52	9.19	681.68	5888973	620345	117.00
	Sp/Be		118		72	28	37.83	9.19	681.68	5886878	622986	138.00
	Sp		57		4	96	34.78	9.19	681.68	5886722	622981	140.00

8. Ghörde I	Do	Podsol, brown earth from dry, nutrient-poor sands	54	91	9		37.70	9.20	672.63	5896091	620170	126.00
	Do/Be		75	65	35		39.72	9.20	672.63	5896024	620099	125.00
	Be		131		99	1	24.26	9.20	672.63	5896425	620270	115.00
	Sp/Be		81		76	24	32.67	9.20	672.63	5896221	620524	113.00
	Sp		62	2	1	97	44.76	9.20	672.63	5896085	620384	121.00

* Two monocultures (1.5 and 3.5) and two mixtures (2.4 and 5.4) have similar proportions (89/11 and 90/10) but are classified as different stand types. This is due to the fact that the proportions in the monocultures were strongly influenced by individual individual large trees (1.5) or a few non-target trees in close proximity to each other (3.5), making the stands fit the monoculture stand type better. Furthermore in the case of both mixtures (2.4 and 5.4) due to the spatial distribution of the mixed tree species, there was a large enough area where the species would interact despite the lacking proportions.

Table C2. Differences in total and arthropod attack rates (only at ground level) between stand types supported by a post-hoc Tukey test adjusted by Holm test

	Total attack rates			Arthropod attack rates		
	Est. (±SE)	z	*P*	Est. (±SE)	z	*P*
Beech - Douglas	-1.46 (±0.37)	-3.9	**0.001**	-1.55 (±0.34)	-4.6	**<0.001**
Beech/Douglas - Douglas	-0.72 (±0.37)	-1.9	0.326	-1.29 (±0.34)	-3.8	**0.001**
Beech/Spruce - Douglas	-1.06 (±0.37)	-2.8	**0.040**	-1.03 (±0.34)	-3.0	**0.019**
Spruce - Douglas	-0.42 (±0.37)	-1.1	1.000	-0.62 (±0.34)	-1.8	0.334
Beech/Douglas - Beech	0.74 (±0.37)	2.0	0.326	0.26 (±0.34)	0.8	0.874
Beech/Spruce - Beech	0.40 (±0.37)	1.1	1.000	0.52 (±0.34)	1.5	0.508
Spruce - Beech	1.05 (±0.37)	2.8	**0.040**	0.93 (±0.34)	2.7	**0.045**
Beech/Spruce – Beech/Douglas	-0.34 (±0.37)	-0.9	1.000	0.25 (±0.34)	0.7	0.874
Spruce – Beech/Douglas	0.30 (±0.37)	0.8	1.000	0.66 (±0.34)	2.0	0.307
Spruce – Beech/Spruce	0.65 (±0.37)	1.7	0.413	0.41 (±0.34)	1.2	0.687

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Table C3. Output of the linear mixed effect models for stand type effects on mean attack rates (% of clay caterpillars attacked per day) leveled for Douglas fir and ground stratum. Significant effects indicated in bold

	Total attack rates				Bird attack rates				Arthropod attack rates				Mammal attack rates			
	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*
Intercept	40.83 (±20.18)	1/39	2.0	0.061	0.85 (±0.11)	1/39	7.4	**<0.001**	29.45 (±9.59)	1/35	2.9	**0.007**	26.80 (±18.09)	1/39	1.5	0.147
Beech	-1.46 (±0.37)	1/26	-3.9	**0.001**					-1.55 (±0.34)	1/27	-4.6	**<0.001**				
Beech / Douglas	-0.72 (±0.37)	1/26	-1.9	0.065					-1.29 (±0.34)	1/27	-3.8	**0.001**				
Beech / Spruce	-1.06 (±0.37)	1/26	-2.8	**0.009**					-1.03 (±0.34)	1/27	-3.0	**0.005**				
Spruce	-0.42 (±0.37)	1/26	-1.1	0.276					-0.62 (±0.34)	1/27	-1.8	0.078				
Herb stratum	-3.74 (±0.24)	1/39	-15.8	**<0.001**	0.13 (±0.05)	1/39	2.4	**0.022**	-3.64 (±0.47)	1/35	-7.7	**<0.001**	-1.32 (±0.12)	1/39	-10.5	**<0.001**
Latitude	-0.08 (±0.04)	1/26	-2.0	0.0575					-0.04 (±0.02)	1/27	-2.6	**0.014**	-0.06 (±0.03)	1/30	-1.7	0.096
MAAT	1.06 (±0.48)	1/26	2.2	**0.034**									1.01 (±0.43)	1/30	2.4	**0.025**
Beech : Herb stratum									1.16 (±0.34)	1/35	3.4	**0.002**				
Beech / Douglas : Herb stratum									1.07 (±0.17)	1/35	3.2	**0.003**				
Beeech / Spruce : Herb stratum									1.00 (±0.34)	1/35	3.0	**0.005**				
Spruce : Herb stratum									0.88 (±0.34)	35	2.6	**0.013**				
R^2 /AICc	0.797 / 278.708				0.313 / 137.405				0.647 / 247.430				0.640 / 270.272			

Table C4. Output of the linear models for tree proportion effects on mean attack rates (% of clay caterpillars attacked per day) leveled at ground stratum. Significant effects indicated in bold.

	Total attack rates				Bird attack rates				Arthropod attack rates				Mammal attack rates			
	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*
Intercept	41.18 (±21.66)	1/38	1.9	0.065	0.85 (±0.11)	1/39	7.4	**<0.001**	26.75 (±11.19)	1/37	2.4	**0.022**	26.80 (±18.09)	1/39	1.5	0.147
Proportion of spruce	0.34 (±0.13)	1/26	2.6	**0.017**					0.34 (±0.12)	1/27	2.8	**0.009**				
Proportion of Douglas	0.41 (±0.14)	1/26	3.0	**0.007**					0.43 (±0.12)	1/27	3.5	**0.002**				
Neighborhood diversity	0.10 (±0.12)	1/26	0.8	0.408					-0.10 (±0.11)	1/27	-0.9	0.351				
Proportion of Douglas: Neighborhood diversity	-0.33 (±0.17)	1/26	-2.0	0.059					-0.36 (±0.15)	1/27	-2.4	**0.022**				
Herb stratum	-1.88 (±0.12)	1/38	-16.3	**<0.001**	0.13 (±0.05)	1/39	2.4	**0.022**	-1.01 (±0.10)	1/37	-9.7	**<0.001**	-1.32 (±0.12)	1/39	-10.6	**<0.001**
Latitude	-0.08 (±0.04)	1/26	-2.0	0.059					-0.04 (±0.02)	1/27	-2.2	**0.033**	-0.06 (±0.03)	1/30	-1.7	0.096
MAAT	1.06 (±0.51)	1/26	2.1	**0.049**									1.01 (±0.43)	1/30	2.4	**0.025**
Proportion of Douglas : Herb stratum	-0.19 0.12	1/38	-1.6	0.108					-0.36 (±0.11)	1/37	-3.4	**0.002**				
Herb stratum: Neighborhood diversity									0.19 (±0.11)	1/37	1.8	0.087				
R^2 / AICc	0.810 / 277.563				0.313 / 137.405				0.659 / 260.419				0.640 / 288.692			

Table C5. Output of the linear models for microhabitat variability effects on mean attack rates (% of clay caterpillars attacked per day) leveled at ground stratum. Significant effects in bold.

	Total attack rates				Bird attack rates				Arthropod attack rates				Mammal attack rates			
	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*	Est. (±SE)	numDF/denDF	*t*	*P*
Intercept	3.54 (±0.25)	1/37	14.3	**<0.001**	0.85 (±0.11)	1/39	7.4	**<0.001**	1.59 (±0.19)	1/37	8.2	**<0.001**	1.47 (±0.23)	1/35	6.4	**<0.001**
Litter depth	-0.30 (±0.16)	1/29	-1.9	0.074					-0.44 (±0.13)	1/29	-3.5	**0.002**	-0.13 (±0.12)	1/28	-1.1	0.288
Litter cover	-0.34 (±0.17)	1/29	-2.0	**0.050**												
Vegetation complexity	0.03 (±0.16)	1/29	0.2	0.846									0.34 (±0.12)	1/28	2.8	**0.010**
Leaf area index									-0.28 (±0.13)	1/29	-2.2	**0.035**	0.22 (±0.12)	1/28	1.8	0.088
Total deadwood volume									0.05 (±0.13)	1/29	0.4	0.709	-0.07 (±0.13)	1/28	-0.5	0.606
Herb stratum	-1.88 (±0.10)	1/37	-19.0	**<0.001**	0.13 (±0.05)	1/39	2.4	**0.022**	-1.01 (±0.11)	1/37	-9.3	**<0.001**	-1.32 (±0.10)	1/35	-13.0	**<0.001**
Herb stratum: Litter depth	0.26 (±0.10)	1/37	2.5	**0.016**									0.24 (±0.11)	1/35	2.2	**0.032**
Herb stratum: Vegetation complexity	-0.30 (±0.10)	1/37	-2.9	**0.006**									-0.41 (±0.11)	1/35	-3.9	**<0.001**
Herb stratum: Leaf area index									0.34 (±0.11)	1/37	3	**0.004**	-0.21 (±0.11)	1/35	-2.0	0.056
Herb stratum: Total deadwood volume									-0.24 (±0.11)	1/37	-2.1	**0.042**	0.20 (±0.11)	1/35	1.9	0.069
R^2 / AICc	0.856 / 260.184				0.313 / 137.405				0.641 / 260.486				0.761 / 264.084			

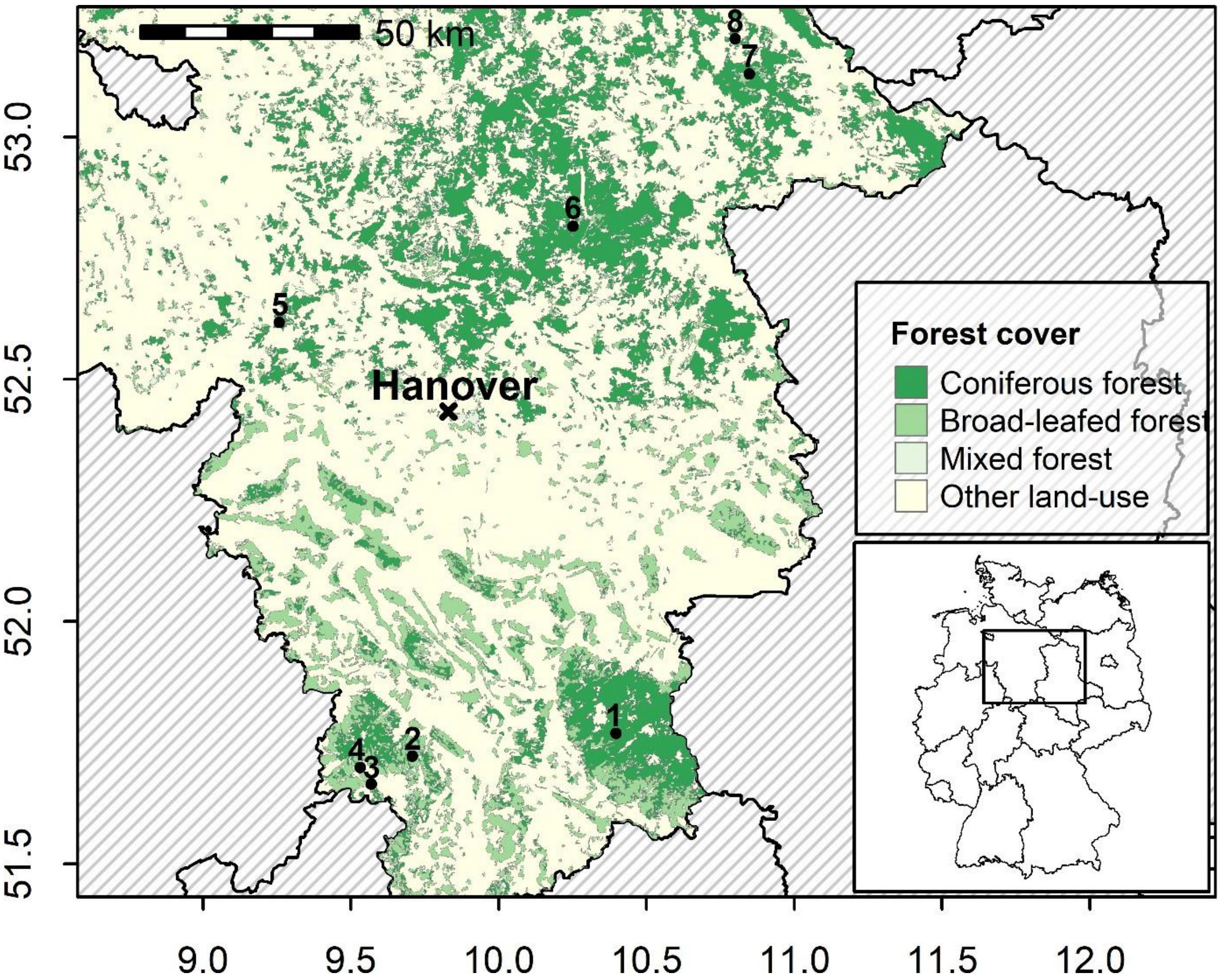

Fig. C1 Map with locations for all 8 of the quintets studied

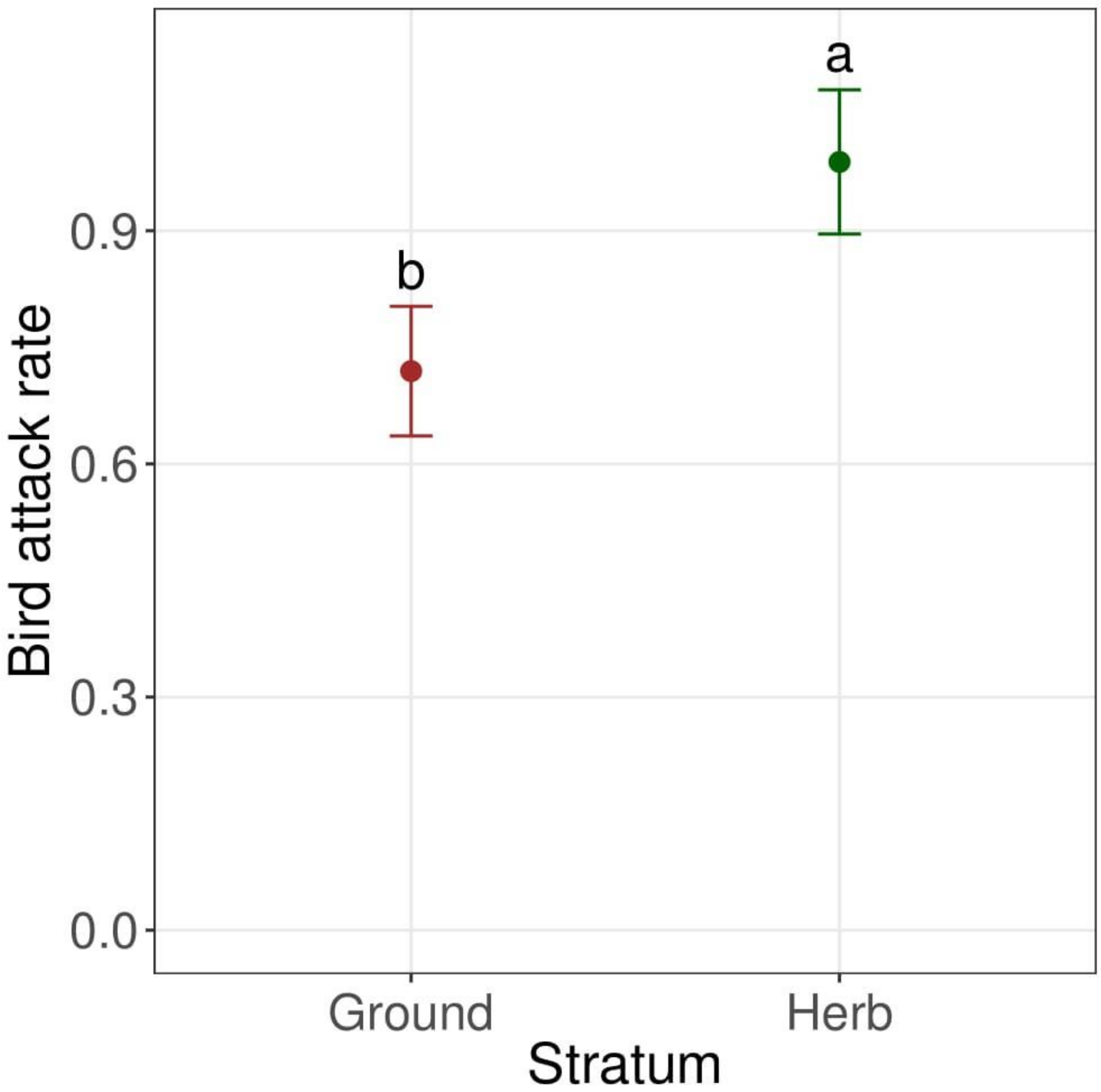

Fig. C2 Difference in bird attack rates (% of clay caterpillars attacked per day ± SE) between the ground and herb stratum. Significant difference marked with letters.

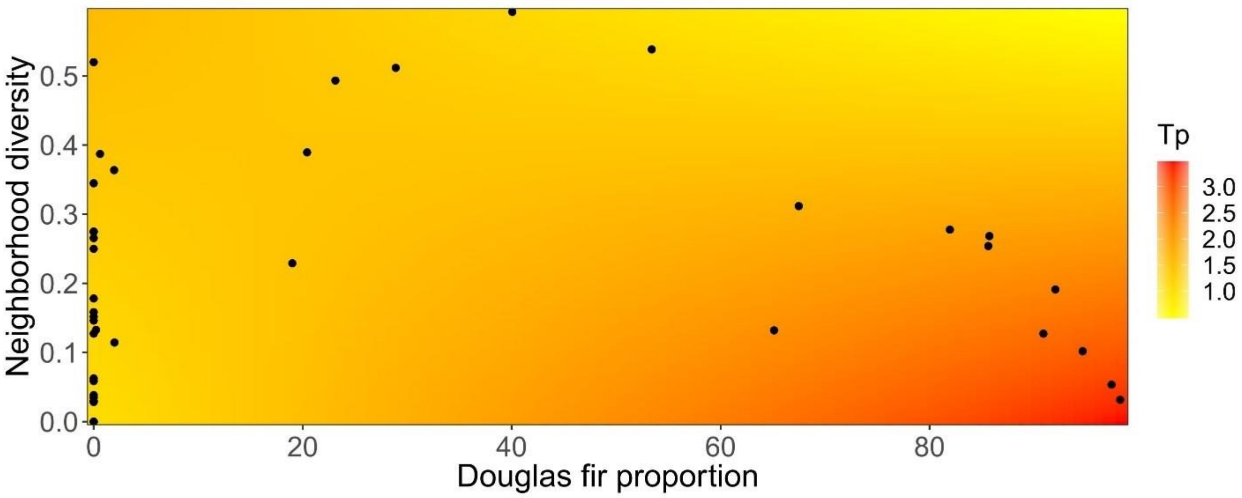

Fig. C3 Interaction of neighborhood diversity and Douglas fir proportion (in %) effects on total attack rates (% of clay caterpillars attacked per day)

Appendix D

Supplementary material for Chapter 5

Introduction of non-native Douglas fir reduces leaf damage on both saplings and mature trees in European beech forests

Table D1. Data on soil type (Foltran,, unpublished), stand age (years, provided by the local forest management authority), proportion of tree species (Do - Douglas fir, Sp – Norway spruce, Be – European beech) and total basal area, mean annual average temperature (MAAT) and mean annual precipitation (MAP) calculated since 1980 from interpolated data from the German weather service (Deutscher Wetterdienst, DWD), as well as data on latitude, longitude (ETRS89/UTM32N; EPSG:25832) and elevation of all sites.

Quintet	Stand	Soil	Age	Do %	Sp %	Conifer %	Be %	Basal Area (m² .ha^{-1})	MAAT °C	MAP mm/yr	Latitude	Longitude	elevation m.a.s.l
1. Dassel	Do/Be	Dystric Cambisols from quartzitic sandstones and conglomerates with low base status	90	8	-	8	92	38.3	8.6	823	5730316	549045	442
	Be		89	-	-	0	100	24.9	8.6	823	5730430	548875	442
	Sp/Be		89	-	9	9	91	22.7	8.6	823	5730338	548791	442
2. Winnefeld	Do/Be	Dystric Cambisols from quartzitic sandstones and conglomerates with low base status	91	16		16	84	30.4	8.9	818	5723181	540118	339
	Be		91	-		0	100	27.8	8.9	818	5723255	540025	379
	Sp/Be		96	-	18	18	82	26.3	8.9	818	5723033	540382	345
3. Nienover	Do/Be	Dystric Cambisols from quartzitic sandstones and conglomerates with low base status	74	27	1	28	72	38.5	9.1	870	5726824	536587	282
	Be		88	-	-	0	100	28.3	9.1	870	5727251	536091	320
	Sp/Be		86	-	15	15	85	37.5	9.1	870	5727849	537565	310
4. Nienburg	Do/Be	Haplic Podzols / Dystric Regosols from dry dystrophic sand deposits	108	58	-	58	42	39.3	9.7	733	5828882	518483	89
	Be		79	-	-	0	100	28.6	9.7	733	5832537	520245	101
	Sp/Be		79	-	17	17	83	31.2	9.7	733	5832258	520183	98
5. Ghörde II	Do/Be	Haplic Podzols / Dystric Regosols from dry dystrophic sand deposits	67	46	5	51	49	35.4	9.2	682	5888393	620255	126
	Be		97	-	11	11	89	34.5	9.2	682	5888973	620345	117
	Sp/Be		118	-	28	28	72	37.8	9.2	682	5886878	622986	138
6. Ghörde I	Do/Be	Spodic Arenosols from dry dystrophic sand deposits	75	48		48	52	39.7	9.2	673	5896024	620099	125
	Be		131	-	2	2	98	24.3	9.2	673	5896425	620270	115
	Sp/Be		81	-	32	32	68	32.7	9.2	673	5896221	620524	113

Table D2. Pearson correlation between the two principal components of the soil variables PCA and the soil variables used for the PCA. High correlations in bold

	pH (KCl)	C	N	CN
PC1	-0.43	**-0.65**	**-0.96**	**0.82**
PC2	**-0.75**	**0.78**	**0.33**	0.37

Table D3. Differences in leaf damage rates/CV of leaf damage rates between stand types supported by a post-hoc Tukey test adjusted by Holm test

Type of leaf damage/CV of leaf damage	Beech/Douglas fir-Beech			Beech/Norway spruce-Beech			Beech/Norway spruce-Beech/Douglas			Monoculture-Mixture		
	Est. (±SE)	z	*P*	Est. (±SE)	z	*P*	Est. (±SE)	z	*P*	Est. (±SE)	z	*P*
Sapling herbivory damage	-0.31 (±0.13)	-2.4	**0.044**	-0.26 (±0.13)	-2.1	0.072	0.04 (±0.12)	0.4	0.714			
Sapling pathogen damage	-0.16 (±0.19)	-0.8	0.406	0.35 (±0.19)	1.8	0.137	0.51 (±0.18)	2.9	0.**013**			
Sapling sucking damage										0.52 (±0.16)	3.3	**0.001**
CV of sapling herbivory damage	0.17 (±0.04)	4.4	**<0.001**	0.07 (±0.04)	1.8	0.067	-0.10 (±0.04)	-2.7	**0.013**			

Table D4. Output of the beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture) on mean leaf damage leveled for European beech monoculture with AICc and conditional R squared values (cR)^2. When stand type was not significant it was replaced by the contrast between linear models for stand type effects (Be/Do – European monoculture/mixture. Significant effects indicated in bold.

Saplings																				
	Log(Total damage+1)				Log(Herbivory damage+1)				Log(Pathogen damage+1)				Log(Sucking damage+1)				Log(Chewing damage+1			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	2.24 (±0.11)	265	19.5	**<0.001**	2.05 (±0.09)	265	22.0	**<0.001**	0.89 (±0.18)	265	4.9	**0.001**	1.24 (±0.08)	265	14.9	**<0.001**	0.67 (±0.08)	265	8.1	**<0.001**
Be/Do	-0.30 (±0.13)	7	-2.3	0.053	-0.31 (±0.13)	7	-2.4	**0.045**	-0.15 (±0.19)	7	-0.8	0.434					0.04 (±0.12)	4	0.4	0.728
Be/Sp	-0.06 (±0.13)	7	-0.5	0.660	-0.26 (±0.13)	7	-2.1	0.074	0.35 (±0.19)	7	1.8	0.111					0.10 (±0.11)	4	0.9	0.415
Mixture/ Monoculture													0.52 (±0.16)	6	3.3	**0.016**				
Nutrient capacity													-0.08 (±0.06)	6	0.3	0.805	-0.07 (±0.08)	4	-0.9	0.422
Be/Do: Nutrient capacity																	0.37 (±0.12)	4	3.2	**0.034**
Be/Sp: Nutrient capaciy																	0.17 (±0.11)	4	-1.6	0.195
Mixture/ Monoculture: Nutrient capacity													-0.06 (±0.13)	6	1.5	0.174				
cR^2 / AICc	0.291/315.975				0.197/ 342.437				0.448/411.495				0.365/413.242				0.200/444.036			
Trees																				
	Log(Total damage+1)				Log(Herbivory damage+1)				Log(Pathogen damage+1)				Log(Sucking damage+1)				Log(Chewing damage+1)			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*				
Intercept	1.78 (±0.10)	126	16.9	**<0.001**	0.65 (±0.15)	126	4.4	**<0.001**	0.65 (±0.15)	126	4.4	**<0.001**	1.43 (±0.09)	126	15.5	**<0.001**	0.45 (±0.04)	126	12.6	**<0.001**
Be/Do					-0.26 (±0.07)	7	-3.6	**0.009**					-0.29 (±0.08)	7	-3.5	**0.009**				
Be/Sp					-0.17 (±0.06)	7	-2.7	**0.032**					-0.15 (±0.07)	7	-2.1	0.073				
Nutrient capacity	0.13 (±0.08)	11	1.7	0.113	0.22 (±0.06)	7	3.6	**0.008**					0.29 (±0.07)	7	4.2	**0.004**				

Be/Do Nutrient capacity					-0.00 (±0.06)	7	-0.0	0.991					-0.06 (±0.08)	7	-0.8	0.451				
Be/Sp nutrient capacity					-0.14 (±0.06)	7	-2.1	0.070					-0.17 (±0.07)	7	-2.4	**0.046**				
cR^2 / AICc	0.439/150.968				0.386/110.391				0.497/209.854				0.446/135.655				0.145/69.933			

Table D5. Output of the linear models for stand type effects (Be/Do – European beech/Douglas fir mixture, Be – European beech monoculture, Be/Sp – European beech/Norway spruce mixture) on CV (coefficient of variation) of mean plant damage leveled for European beech monoculture with AICc and conditional R squared values (cR)^2. When stand type was not significant it was replaced by the contrast between monoculture/mixture. Significant effects indicated in bold.

	Saplings																			
	CV of total damage				CV of herbivory damage				CV of pathogen damage				CV of sucking damage				CV of chewing damage			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	0.48 (±0.05)	9	8.8	**<0.001**	0.44 (±0.06)	7	8.0	**<0.001**	0.95 (±0.14)	9	6.7	**<0.001**	0.63 (±0.04)	8	17.4	**<0.001**	0.97 (±0.06)	9	15.6	**<0.001**
Be/Do					0.17 (±0.04)	7	4.4	**0.003**												
Be/Sp					0.07 (±0.04)	7	1.8	0.109												
Nutrient capacity													-0.08 (±0.03)	8	-2.3	0.054				
cR^2 / AICc	0.719/-18.771				0.834/ -8.131				0.060/27.299				0.465/-5.850				0.005/7.429			
	Trees																			
	CV of total damage				CV of herbivory damage				CV of pathogen damage				CV of sucking damage				CV of chewing damage			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	0.46 (±0.06)	11	8.2	**<0.001**	0.37 (±0.03)	12	11.7	**<0.001**	0.76 (±0.13)	12	6.0	**<0.001**	0.41 (±0.03)	12	12.7	**<0.001**	0.78 (±0.08)	12	9.3	**<0.001**
Mixture/ Monoculture	-0.18 (±0.10)	11	-1.8	0.092																
cR^2 / AICc	0.184/-1.934				<0.001/-11.540				<0.001/36.070				<0.001/-10.098				<0.001/22.123			

Table D6. Output of the linear models for NDiv (neighborhood diversity) effects on mean plant damage with AICc and conditional R squared values (cR)2. Significant effects indicated in bold.

Saplings																				
	Log(Total damage+1)				Log(Herbivory damage+1)				Log(Pathogen damage+1)				Log(Sucking damage+1)				Log(Chewing damage+1			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	2.14 (±0.07)	265	30.6	**<0.001**	1.84 (±0.05)	265	15.3	**<0.001**	0.99 (±0.12)	265	8.0	**<0.001**	1.38 (±0.06)	265	23.5	**<0.001**	0.79 (±0.05)	265	15.1	**<0.001**
NDiv	-0.01 (±0.06)	5	-0.2	0.851	-0.09 (±0.05)	7	-1.8	0.116	0.17 (±0.11)	5	1.5	0.188	-0.26 (±0.06)	6	-4.4	**0.005**	0.24 (±0.07)	6	3.5	**0.012**
Nutrient capacity	-0.15 (±0.08)	5	-2.0	0.107					-0.41 (±0.14)	5	-2.9	**0.036**	0.08 (±0.06)	6	1.4	0.208	-0.16 (±0.07)	6	-2.1	0.076
PC1	-0.21 (±0.08)	5	-2.5	0.056	-0.07 (±0.05)	7	1.4	0.193	0.34 (±0.15)	5	-2.2	0.075					-0.18 (±0.08)	6	-2.3	0.065
NDiv: Nutrient capacity	-0.11 (±0.05)	5	-2.4	0.063					-0.15 (±0.09)	5	-1.7	0.155	-0.10 (±0.06)	6	-1.6	0.166				
cR^2 / AICc	0.302/323.313				0.194/ 344.193				0.478/420.465				0.353/412.523				0.199/442.939			
Trees																				
	Log(Total damage+1)				Log(Herbivory damage+1)				Log(Pathogen damage+1)				Log(Sucking damage+1)				Log(Chewing damage+1)			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	1.78 (±0.10)	126	16.9	**<0.001**	1.58 (±0.06)	126	25.4	**<0.001**	0.65 (±0.15)	126	4.4	**<0.001**	1.31 (±0.08)	126	16.9	**<0.001**	0.45 (±0.02)	126	18.0	**<0.001**
NDiv					-0.06 (±0.04)	10	-1.7	0.115					-0.07 (±0.05)	10	-1.5	0.165	0.06 (±0.03)	9	1.9	0.084
Nutrient capacity	0.13 (±0.08)	11	1.7	0.113	0.15 (±0.05)	10	2.9	**0.017**					0.19 (±0.07)	10	2.8	**0.017**				
PC1																	-0.11 (±0.03)	9	-3.9	**0.003**
PC2																	0.04 (±0.03)	9	1.8	0.114
cR^2 / AICc	0.439/150.968				0.342/105.570				0.497/209.854				0.423/130.780				0.157/76.951			

Table D7. Output of the linear models for Ndiv (neighborhood diversity) effects on CV (coefficient of variation) of mean plant damage with AICc and conditional R squared values $(cR)^2$. Significant effects indicated in bold.

Saplings																				
	CV of total damage				CV of herbivory damage				CV of pathogen damage				CV of sucking damage				CV of chewing damage			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	0.48 (±0.05)	9	8.8	**<0.001**	0.51 (±0.03)	6	14.9	**<0.001**	0.95 (±0.14)	9	6.7	**<0.001**	0.62 (±0.02)	6	12.7	**<0.001**	0.97 (±0.06)	8	17.5	**<0.001**
NDiv					0.07 (±0.02)	6	3.8	**0.009**					0.04 (±0.02)	6	12.7	0.109	0.12 (±0.06)	8	2.0	0.075
Nutrient capacity					-0.03 (±0.03)	6	-1.3	0.249					-0.08 (±0.02)	6	12.7	**0.017**				
NDiv: Nutrient capacity					0.07 (±0.02)	6	3.7	**0.010**					0.07 (±0.03)	6	12.7	**0.039**				
cR^2 / AICc	0.719/-14.677				0.834/ -2.061				0.060/27.299				0.660/0.919				0.243/9.464			
Trees																				
	CV of total damage				CV of herbivory damage				CV of pathogen damage				CV of sucking damage				CV of chewing damage			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	0.40 (±0.05)	12	8.2	**<0.001**	0.37 (±0.03)	12	11.7	**<0.001**	0.76 (±0.12)	11	6.6	**<0.001**	0.41 (±0.03)	12	12.7	**<0.001**	0.78 (±0.08)	12	9.3	**<0.001**
PC1									0.24 (±0.12)	11	2.0	0.067								
cR^2 / AICc	<0.001/3.759				<0.001/-11.540				0.196/36.586				<0.001/-10.098				<0.001/22.123			

Table D8. Output of the linear models for conifer proportion (Do=Douglas fir, Sp=Norway spruce) and effects not directly related to standtype on mean plant damage with AICc and conditional R squared values (cR)2. Significant effects indicated in bold.

	Saplings																			
	Log(Total damage+1)				Log(Herbivory damage+1)				Log(Pathogen damage+1)				Log(Sucking damage+1)				Log(Chewing damage+1			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	2.10 (±0.05)	263	39.4	<**0.001**	1.83 (±0.04)	264	42.9	<**0.001**	0.94 (±0.16)	263	5.8	<**0.001**	1.38 (±0.08)	265	16.9	<**0.001**	0.76 (±0.04)	263	17.5	<**0.001**
Do proportion	-0.18 (±0.06)	4	-3.1	**0.038**	-0.15 (±0.05)	2	-3.0	0.097					-0.19 (±0.09)	6	-2.1	0.086	0.16 (±0.06)	4	2.7	0.055
Sp proportion					-0.06 (±0.05)	2	-1.0	0.413	0.16 (±0.06)	5	2.6	0.051								
Canopy openness	-0.13 (±0.06)	4	-2.3	0.082	-0.13 (±0.05)	2	-2.8	0.112	0.14 (±0.08)	5	1.9	0.122								
Sapling height	-0.10 (±0.03)	263	-3.2	**0.001**	-0.07 (±0.03)	264	-2.3	**0.025**	0.05 (±0.04)	263	-1.2	0.214					-0.14 (±0.04)	263	-3.8	<**0.001**
Nutrient capacity	0.04 (±0.06)	4	-2.2	0.523	0.04 (±0.05)	2	0.8	0.527	-0.11 (±0.11)	5	-1.0	0.355	0.04 (±0.08)	6	0.5	0.645	-0.06 (±0.08)	4	-0.8	0.477
PC1									-0.18 (±0.11)	5	-1.6	0.170					-0.18 (±0.09)	4	-2.0	0.117
PC2	-0.13 (±0.06)	4	-2.1	0.100	-0.08 (±0.05)	2	-1.8	0.217									0.10 (±0.07)	4	1.5	0.212
Nutrient capacity: Do proportion:	-0.13 (±0.07)	4	-1.9	0.129	-0.12 (±0.05)	2	-2.1	0.167					-0.24 (±0.10)	6	-2.4	0.057	0.32 (±0.07)	4	4.7	**0.009**
Nutrient capacity: Sp proportion					-0.09 (±0.07)	2	-1.3	0.311												
Sapling height: Nutrient capacity	0.09 (±0.03)	263	2.7	**0.007**					0.08 (±0.04)	263	2.1	**0.039**					0.08 (±0.04)	263	2.0	**0.047**
cR^2 / AICc	0.348/332.398				0.231/ 369.086				0.546/425.897				0.377/418.968				0.220/452.051			
	Trees																			

	Log(Total damage+1)				Log(Herbivory damage+1)				Log(Pathogen damage+1)				Log(Sucking damage+1)				Log(Chewing damage+1)			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*				
Intercept	1.78 (±0.11)	126	15.6	**<0.001**	1.56 (±0.05)	126	31.0	**<0.001**	0.68 (±0.18)	126	3.7	**<0.001**	1.29 (±0.09)	126	15.1	**<0.001**	0.45 (±0.03)	126	17.1	**<0.001**
Do proportion	-0.08 (±0.05)	9	-1.6	0.139	-0.10 (±0.03)	6	-3.0	**0.024**					-0.09 (±0.04)	8	-2.2	0.062	-0.06 (±0.03)	10	-2.2	0.053
Sp proportion					-0.07 (±0.04)	6	-2.1	0.082	0.13 (±0.07)	6	2.0	0.095	-0.06 (±0.04)	8	-1.4	0.198				
Openness					-0.07 (±0.03)	6	-2.1	0.081	0.11 (±0.07)	6	1.5	0.182								
Nutrient capacity					0.11 (±0.04)	6	2.4	0.052	-0.71 (±0.36)	6	-2.0	0.093	0.16 (±0.06)	8	2.5	**0.036**				
PC1									-0.11 (±0.09)	6	-1.3	0.234					-0.08 (±0.03)	10	-3.2	**0.010**
PC2	-0.29 (±0.29	9	-1.1	0.282																
Do proportion: Nutrient capacity					-0.06 (±0.04)	6	-1.4	0.204												
Sp proportion: Nutrient capacity					-0.10 (±0.04)	6	-2.2	0.070	0.10 (±0.08)	6	1.2	0.275	-0.11 (±0.05)	8	-2.1	0.073				
Canopy openness: Nutrient capacity	0.02 (±0.01)	9	1.9	0.083					0.03 (±0.01)	6	2.7	**0.034**								
cR^2 / AICc	0.518/160.882				0.334/121.159				0.651/230.929				0.454/138.125				0.153/72.201			

Table D9. Output of the linear models for conifer proportion (Do=Douglas fir, Sp=Norway spruce) and effects not directly related to standtype on CV (coefficient of variation) of mean plant damage with AICc and conditional R squared values (cR)^2. Significant effects indicated in bold.

Saplings																				
	CV of total damage				CV of herbivory damage				CV of pathogen damage				CV of sucking damage				CV of chewing damage			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	0.48 (±0.05)	9	8.8	**<0.001**	0.52 (±0.03)	6	19.4	**<0.001**	0.95 (±0.14)	9	6.7	**<0.001**	0.63 (±0.02)	6	25.6	**<0.001**	0.97 (±0.05)	7	19.7	**<0.001**
Do proportion					0.11 (±0.03)	6	4.3	**0.005**					0.06 (±0.03)	6	1.9	0.106	0.14 (±0.05)	7	2.8	**0.025**
Sp proportion																	0.17 (±0.05)	7	3.3	**0.014**
Nutrient capacity					-0.03 (±0.03)	6	-1.0	0.349					-0.07 (±0.04)	6	-2.9	0.027				
Nutrient capacity: Do proportion					0.10 (±0.03)	6	3.5	**0.013**					0.09 (±0.03)	6	2.7	**0.038**				
cR^2 / AICc	0.719/-14.677				0.708/ -0.233				0.060/27.299				0.593/2.420				0.545/9.773			
Trees																				
	CV of total damage				CV of herbivory damage				CV of pathogen damage				CV of sucking damage				CV of chewing damage			
	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*	Est. (±SE)	DF	*t*	*P*
Intercept	0.44 (±0.06)	7	7.9	**<0.001**	0.36 (±0.04)	10	9.9	**<0.001**	0.74 (±0.11)	11	6.8	**<0.001**	0.42 (±0.02)	9	16.8	**<0.001**	0.78 (±0.08)	11	10.2	**<0.001**
Do proportion	0.14 (±0.03)	7	4.0	**0.005**	0.06 (±0.02)	10	2.7	**0.023**					0.06 (±0.03)	9	2.4	**0.042**				
Sp proportion																	0.17 (±0.08)	11	2.1	0.056
Canopy openness	0.16 (±0.04)	7	4.0	**0.005**	0.08 (±0.02)	10	3.1	**0.011**												
Tree height	0.12 (±0.04)	7	2.7	**0.031**																
Nutrient capacity	0.01 (±0.05)	7	0.1	0.916									-0.02 (±0.03)	9	-0.7	0.481				
Do proportion: Nutrient capacity													-0.08 (±0.04)	9	-2.2	0.058				

Tree height: Nutrient capacity	-0.14 (±0.05)	7	-2.7	**0.031**																
cR^2 / AICc	0.753/19.852				0.631/-5.353				<0.001/36.070				0.476/-0.579				0.212/23.131			

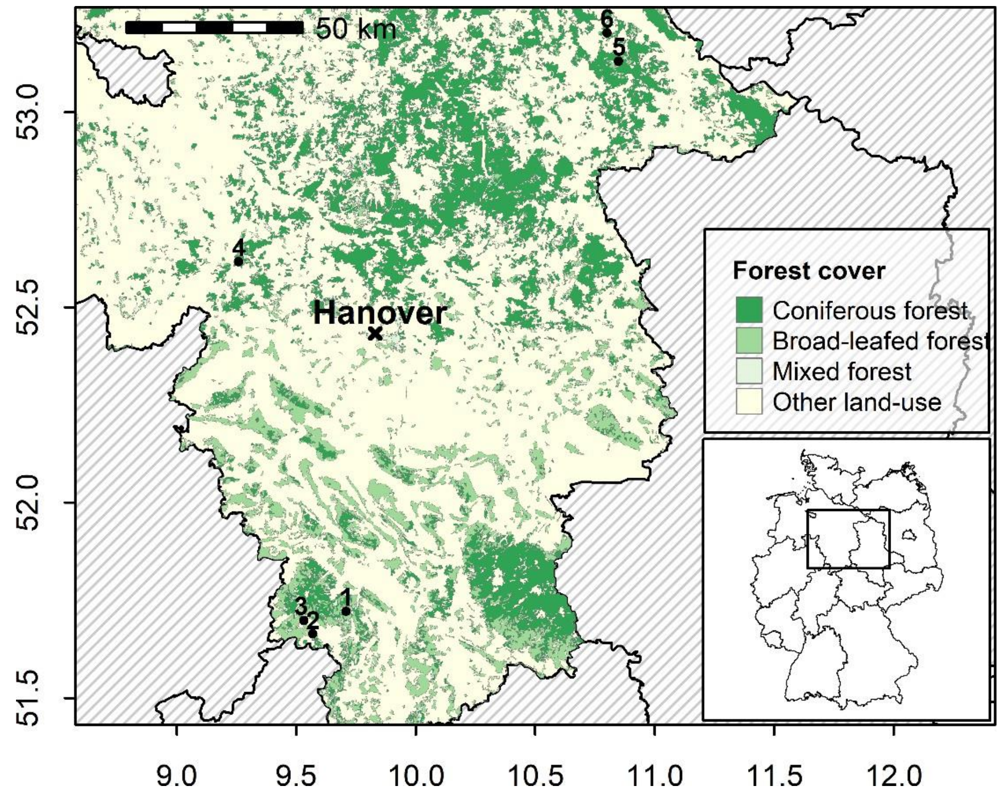

Fig. D1 Map with locations of the 6 triplets studied