Bottom-up and top-down drivers of herbivory

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"In the light of the moon a little egg lay on a leaf. One Sunday morning the warm sun came up… and POP, out of the egg came a tiny, very hungry caterpillar. He started looking for some food."

Eric Carle, *The Very Hungry Caterpillar*, 1969.

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SUMMARY

In the face of global biodiversity loss threatening natural ecosystems as well as provision of ecosystem services for humans, such as food production and well-being, Biodiversity-Ecosystem Functioning (BEF) research has proven to be of high importance in explaining and providing predictions of how the loss of species shapes the environment. As most ecosystems are built on plants as producers, herbivory is a key process in ecosystem functioning; it transfers material and energy from plants to yet higher trophic levels, and affects plant condition and productivity. Herbivory is affected by bottom-up mechanisms of plant functional traits and diversity, as well as by top-down mechanisms through predation and parasitism, which are themselves influenced by plant diversity and structure.

One question addressed in a plethora of studies is: Does herbivory increase or decrease with increasing plant species richness? Although the topic has been addressed from multiple angles, studies incorporating key groups of herbivores, top-down control, and direct measures of herbivory are rare, especially in forest ecosystems. The aim of this thesis is to address the relationship between tree species richness and herbivory in connection to a comprehensive set of variables that can interact with tree species richness modifying the herbivore, as well as predator, response. The herbivore response is addressed by estimating what kind of caterpillar community (based on their functional traits) is hosted on each tree species, and by the amount of herbivory the trees accumulate. In turn, predation response is addressed as predation pressure, estimated using artificial caterpillars. Leaf nutritional traits of trees are used to describe the quality of the herbivore food source. Forest structure is used to define the amount of biomass available for herbivores, and the environment that determines how effectively predators find their prey. Further, the bottom-up and top-down relationships affecting herbivory are addressed from a seasonal and topographic perspective. This is done in order to account for the changes they can cause in abundance and species composition of the herbivore and predator fauna, as well as in leaf quality.

Specifically, I conducted three studies in the subtropical BEF-China experiment. I investigated (1) how tree species richness, leaf traits, and seasonal progression shape caterpillar community trait composition between tree species. I further extended the scope of analyses to cover trees individually, in order to investigate (2) how the tree species richness and seasonal progression alongside forest structure and topography shape predation pressure on artificial caterpillars, and finally, (3) how the tree species richness, leaf traits, forest structure, topography and seasonal progression in combination drive herbivory on trees. The herbivory results are further interpreted in light of the observed patterns in caterpillar community composition and predation pressure.

I found that the tree species richness structures the caterpillar community, and shapes predation pressure and herbivory, but that these effects cannot be described as any simple single trend. Instead, tree species richness in combination with leaf traits and forest structure formed a complex network of interactions. However, despite the complexity, predictions made based on the ecological theory within the current BEF framework could explain the observed relationships with caterpillar trait composition, herbivory and predation. Increasing tree species richness demonstrated simultaneously higher caterpillar species richness and increased sharing of caterpillar species between tree species. The caterpillar community was more abundant, though less species-rich, and consisted of smaller and likely earlier instar as well as more generalist individuals on high nutritional quality trees. Caterpillars were also generally less defended (i.e. had more warning coloration and higher hair coverage) in high nutritional quality trees. Increasing tree species richness caused herbivory to concentrate more on the less abundant host tree types, the nutritionally highest quality deciduous trees and the most common tree species family in the BEF-China experiment, the Fagaceae. Herbivory further increased in lower nutritional quality trees when surrounded by higher quality trees, indicating that herbivores may 'spillover' from where they are most abundant.

Forest structure affected both predation pressure and herbivory, but in different ways. Predation pressure was shaped by the interrelationship of the neighborhood tree sizes, vegetation density, canopy vertical structure, and small spatial-scale variables that can work as visibility-enhancing variables and predator attractants. Overall, the results indicated that predation pressure in any

given location depends on the relationship between environmental determinants that shape the predator and prey abundance and those that shape the prey finding likelihood. Herbivory was instead generally promoted in lower branches, due to likely higher leaf quality, and by higher plant biomass. However, the latter effect was overturned when trees with more palatable leaves grew surrounded by large less palatable-leaved trees. Further, trees larger than their neighboring ones suffered higher herbivory when growing close to plot edges. Herbivory was also higher closer to plot edges in tree species mixtures, and closer to center in monocultures. Herbivores may favor higher resource base of their host plants, and immigration and emigration to and from plots can drive the difference in edge effects between tree species mixtures and monocultures. In turn, although predation pressure was indicated to respond to seasonally chancing abiotic conditions in respect to canopy vertical stratification and topography, shifting away from more sunny conditions in dry season, the overall seasonal response followed the pattern of higher caterpillar abundance and higher herbivory in the early to mid-summer period. However, predation by birds was an exception to this pattern, and may have increased towards autumn due to fledglings and winter migration.

These results demonstrate the highly dynamic nature of herbivory and predation pressure in forest environments, and offers insights into how they are determined especially in close neighborhood scale. Herbivory was shown to increase in particular by bottom-up effects of leaf nutritional quality, but the response was shaped by several other variables from tree species richness and forest structure to topography. Further, top-down control was demonstrated not to be a stagnant property in any specific habitat, but to be interactive between smaller and wider spatial-scales, and shift seasonally between habitats presumably due to preference for cooler microclimates. Investigation of caterpillar functional traits further brings insights into how the combination of leaf traits and tree species richness structures the community of an important herbivore group. Through this work, I contribute to improving the understanding of the BEF relationships driving bottom-up and top-down control of herbivory, and to determining the specific needs for future research.

ZUSAMMENFASSUNG

Angesichts des weltweiten Verlusts biologischer Vielfalt, der sowohl natürliche Ökosysteme als auch die Bereitstellung von Ökosystemdienstleistungen für den Menschen, z. B. hinsichtlich Nahrungsmittelproduktion und Gesundheit, bedroht, hat sich die Biodiversitäts-Ökosystemforschung (BEF) als äußerst wichtiger Forschungszweig für grundlegende Erkenntnisse und Prognosen erwiesen. Da die meisten Ökosysteme auf Pflanzen als Produzenten basieren, ist Herbivorie ein Schlüsselprozess, durch den Material und Energie von Pflanzen auf höhere trophische Ebenen übertragen werden und der sich zudem auf Fitness und Produktivität der Pflanzen auswirkt. Pflanzenfresser werden durch „Bottom-Up“-Mechanismen funktioneller Pflanzenmerkmale, Pflanzenvielfalt sowie durch „Top-Down“-Mechanismen (z. B. Prädation und Parasitismus) beeinflusst. Letztere werden wiederum von Pflanzenvielfalt und -struktur geprägt.

Eine Vielzahl von Studien befasst sich mit der Frage, ob Herbivorie mit steigendem Artenreichtum der Pflanzen zu- oder abnimmt. Doch obwohl das Thema bereits aus verschiedenen Blickwinkeln betrachtet wurde, sind Studien, die verschiedene Gruppen von Herbivoren, „Top-Down“-Kontrolle und Herbivorie gleichzeitig einbeziehen, selten, insbesondere in Waldökosystemen. Ziel dieser Arbeit ist es, die Beziehung zwischen Baumartenreichtum und Herbivorie unter Berücksichtigung eines umfassenden Sets an Variablen, welche mit Baumartenreichtum interagieren und die Reaktion von Pflanzenfressern und Raubtieren potentiell verändern können, zu untersuchen. Die Auswirkungen werden basierend auf Herbivorierate sowie anhand der Raupengemeinschaften, welche an den jeweiligen Baumarten zu finden sind, evaluiert (basierend auf ihren funktionellen Eigenschaften). Des Weiteren wird Prädationsdruck mithilfe künstlicher Raupen geschätzt. Die Qualität der Blätter als Nahrungsgrundlage für Herbivore wird anhand ihrer Nährstoffeigenschaften beschrieben. Die Waldstruktur wird einerseits verwendet, um die Menge an Biomasse, die Pflanzenfressern zur Verfügung steht, zu schätzen. Andererseits dient sie als Determinante (Strukturkomplexität), um abzuschätzen, wie effektiv Prädatoren ihre Beute lokalisieren können. Des Weiteren werden die „Bottom-Up“ - und „Top-Down“-Beziehungen, die sich auf Herbivorie auswirken, unter saisonalen und topografischen

Gesichtspunkten untersucht. Ziel dessen war es, sowohl bei den Herbivoren als auch bei den Prädatoren Änderungen in Abundanzen und Artenzusammensetzung sowie Änderungen in der Blattqualität zu berücksichtigen.

Konkret habe ich drei Studien im Rahmen des subtropischen BEF-China-Experimentes durchgeführt. Ich untersuchte (1), wie Baumartenreichtum, Blattmerkmale und Saisonalität die Zusammensetzung der Raupengemeinschaftsmerkmale zwischen Baumarten beeinflussen. Zudem habe ich den Umfang der Analysen auf die Ebene einzelner Bäume ausgeweitet, um (2) zu untersuchen, wie der Baumartenreichtum und der saisonale Verlauf zusammen mit der Waldstruktur und Topographie den Prädationsdruck auf künstliche Raupen beeinflussen, und (3), wie sich Baumartenreichtum, Blattmerkmale, Waldstruktur, Topographie und saisonaler Verlauf in Zusammenwirkung auf Herbivorie an Bäumen auswirken. Die Ergebnisse zur Herbivorie werden im Lichte der beobachteten Muster der Raupengemeinschaften und des Prädationsdruckes interpretiert.

Ich fand heraus, dass der Baumartenreichtum die Raupengemeinschaft strukturiert wie auch Prädationsdruck und Herbivorie beeinflusst. Diese Effekte lassen sich jedoch nicht als einfache Zusammenhänge beschreiben. Stattdessen ergaben sich komplexe Interaktionen und Wechselwirkungen zwischen Baumartenreichtum, Waldstruktur und Blattmerkmalen. Trotz der Komplexität konnten dennoch auf der Grundlage ökologischer Theorie innerhalb des BEF-Rahmens Vorhersagen gemacht werden, die die beobachteten Zusammenhänge zwischen Raupengemeinschaften, Herbivorie und Prädationsdruck erkären konnten. Der zunehmende Baumartenreichtum zeigte gleichzeitig einen höheren Raupenartenreichtum und gleichzeitiges Auftreten von Raupenarten an verschiedenen Baumarten. Die Abundanz von Raupengemeinschaften auf Bäumen mit hoher Nährstoffqualität war im Schnitt größer, wenn auch weniger artenreich. Zudem bestanden sie aus kleineren, wahrscheinlich jüngeren und eher generalistischen Individuen. Raupen auf Bäumen mit hoher Nährstoffqualität hatten zudem weniger stark ausgeprägte Verteidigungsmechanismen (d.h. hinsichtlich Warnfärbung und Behaarung). Der zunehmende Baumartenreichtum führte dazu, dass Herbivorie verstärkt an weniger häufig vorkommenden Baumarten auftrat. Zudem trat Herbivorie verstärkt an nährstoffreichen Arten und an Vertretern der häufigsten Baumartenfamilie im BEF-China-

Experiment, den Fagaceae, auf. Herbivorie nahm außerdem zu an Bäumen, die eine geringere Nährwertqualität aufweisen, sofern diese von solchen mit höherer Qualität umgeben waren, was darauf hindeutet, dass die Herbivoren von dort 'überlaufen', wo sie sich in größter Abundanz befinden.

Die Waldstruktur wirkte sich sowohl auf den Prädationsdruck als auch auf die Herbivorie aus, jedoch auf unterschiedliche Weise. Der Prädationsdruck wurde durch die Wechselbeziehung zwischen den Größen der Nachbarbäume, der Vegetationsdichte, der vertikalen Struktur des Blätterdachs und kleinräumlicher Variablen beeinflusst, welche sichtbarkeits- und prädationsfördernd wirken können. Insgesamt deuten die Ergebnisse darauf hin, dass der Prädationsdruck an einem bestimmten Ort von der Beziehung zwischen Umweltdeterminanten abhängt, die einerseits die Prädatoren- und Beutehäufigkeit und andererseits die Wahrscheinlichkeit, Beute zu finden, beeinflussen. Stattdessen wurde die Herbivorie aufgrund der wahrscheinlich höheren Blattqualität und der höheren Pflanzenbiomasse im Allgemeinen in den unteren Zweigen gefördert. Der letztgenannte Effekt wurde jedoch ausgehebelt, wenn Bäume mit nährstoffreichen Blättern von Bäumen mit großen, nährstoffärmeren Blättern umgeben waren. Darüber hinaus wiesen Bäume, die größer als ihre Nachbarbäume waren, eine stärkere Herbivorie auf, wenn sie in der Nähe der Plotränder wuchsen. In Baumartenmischungen nahm Herbivorie zu den Ploträndern hin zu, in Monokulturen zum Zentrum hin. Möglicherweise bevorzugen Herbivoren eine höhere Basis an Ressourcen in den sie behausenden Pflanzen; Immigration und Emigration zu und von einzelnen Plots kann den Unterschied in Randeffekten zwischen Baumartmischungen und Monokulturen forcieren. Obwohl es jedoch Hinweise gab, dass der Prädationsdruck auf saisonal wechselnde abiotische Bedingungen in Bezug auf vertikale Baumkronenstratifikation und Topographie reagiert, während er vor sonnigeren Bedingungen in der Trockensaison weicht, folgte die saisonale Gesamtwirkung dem Muster einer höheren Raupenabundanz und einer erhöhten Herbivorie im Früh- bis Mittelsommer. Prädation durch Vögel stellte jedoch eine Ausnahme von diesem Muster dar und dürfte zum Herbst hin aufgrund von Jungvögeln und Winterzug zugenommen haben.

Diese Ergebnisse zeigen die hochdynamische Natur von Herbivorie und Prädation in Waldökosystemen und bieten Einblicke, wie diese auf kleinräumiger Ebene bestimmt werden. Es zeigte sich, dass Herbivorie vor allem aufgrund von „Bottom-Up“-Effekten der Blattqualität zunahm. Sie wurde jedoch auch durch weitere Variablen beeinflusst: vom Baumartenreichtum über die Waldstruktur bis hin zur Topographie. Darüber hinaus wurde gezeigt, dass „Top-Down“-Kontrolle in keinem bestimmten Habitat eine feststehende Eigenschaft war, sondern, dass sie mit kleineren ebenso wie mit weiteren räumlichen Skalen interagiert und sich saisonal abhängig vom jeweiligen Habitat aufgrund einer Präferenz für kühlere mikroklimatische Bedingungen verändert. Die Untersuchung funktioneller Merkmale von Raupen liefert zudem Erkenntnisse darüber, wie Blattmerkmale und Baumartenreichtum in Kombination die Artengemeinschaft einer wichtigen Herbivorengruppe strukturieren. Diese Arbeit kann also dazu beitragen, das Verständnis der BEF-Beziehungen zu verbessern – insbesondere welchen Einfluss „Bottom-Up“- und „Top-Down“-Effekte auf Herbivorie haben – sowie Bedarf für zukünftige Forschungen zu spezifizieren.

CHAPTER 1

General introduction

Forests cover 31% of the world's land area (FAO, 2020). Forests richer in tree species provide a wider range of ecosystem services than monocultures, such as higher production of tree biomass, game, fruits and berries, and enhanced soil carbon storage (Gamfeldt et al., 2013; Brockerhoff et al., 2017). The human induced global biodiversity loss is causing massive changes to ecosystem functioning (Pereira et al., 2012), and further threatens human livelihoods and existence (IPBES, 2019). In forests, biodiversity loss is caused by deforestation and selective silviculture practices favoring monocultures (Bremer and Farley, 2010; Brockerhoff et al., 2017; Wang et al., 2022). Thus, it is of high importance to understand not just which effects deforestation has but also how loss of tree species richness in forests affects ecosystem functioning. Filling this need, BEF (Biodiversity-Ecosystem Functioning) research using experimental field studies with controlled plant species composition and richness gradients has extended from early experiments with grasslands to forests, demonstrating a similar high importance of biodiversity (Hooper et al., 2005; Tilman et al., 2014; Eisenhauer et al., 2019). However, though studies on forest ecosystems have been on the rise (Kozlov and Zvereva, 2017), these ecosystems still remain relatively poorly understood compared to grasslands and agroecosystems (Cardinale et al., 2011; Nakamura et al., 2017).

Plant diversity-higher trophic level interactions

Plant diversity is a highly important determinant of ecosystem functioning, leading to increased primary production (Cardinale et al., 2011; Liang et al., 2016; Duffy et al., 2017) and higher arthropod diversity (Siemann et al., 1998; Haddad et al., 2009; Ebeling et al., 2018). Especially herbivore insect diversity is strongly dependent on plant diversity (Siemann et al., 1998; Scherber et al., 2010; Ebeling et al., 2018), as plants do not just provide food for herbivorous insects, but form a major part of their whole environment (Price, 2002). The vast majority of terrestrial food webs are based on living plants (Price, 2002), which makes herbivores a key mediator in trophic webs. Herbivores do not just hinder plant growth but under moderate levels of herbivory can enhance ecosystem services and lead to an increase in plant biomass production through enhancing nutrient cycling and soil formation (Maguire et al., 2015; Kozlov and Zvereva, 2017). Herbivory can further modify plant species competition and lead to increased plant diversity (Huntly, 1991).

Plant species richness is expected to affect the amount of herbivory by promoting herbivore populations in low plant richness levels through increased host species abundance (Root, 1973; Jactel et al., 2021), or by leading the herbivores to concentrate more on the less abundant host plants in higher plant richness (Otway et al., 2005; Plath et al., 2012). Herbivores can further respond to variation in plant species composition in close surroundings through associational neighborhood effects, since neighboring plants can mask a focal plant by visual and/or olfactory obstruction of herbivore searching, or additionally, herbivores can 'spillover' to surrounding vegetation from their host plants (White and Whitham, 2000; Plath et al., 2012; Jactel et al., 2021).

Similar to herbivores, predator and parasite richness also usually increases with increasing plant richness (Haddad et al., 2009; Wan et al., 2020). Yet, the effects of plant diversity can weaken along increasing trophic level, with the higher levels being affected mainly through bottom-up trophic cascades (Scherber et al., 2010). Besides bottom-up effects of herbivores toward higher trophic levels, predators and parasites can reciprocally suppress herbivore populations, and while the relative strength of the top-down and bottom-up effects on herbivore populations has been long a matter of debate, herbivore populations can be expected to be modified by both (Hunter, 2001; Walker and Jones, 2001). Moreover, besides top-down suppression of herbivore populations, predators and parasites can have diversifying effects on herbivore fauna (Siemann et al., 1998). Plant richness effects on herbivores and predators are further expected to be modified by the vegetation patch size through resource abundance, source-sink dynamics, and arthropod immigration-emigration rates (Root, 1973; Pulliam, 1988; Bommarco and Banks, 2003; Hambäck and Englund, 2005). However, despite decades of research and a wealth of accrued knowledge, many specific mechanisms in plant richness-higher trophic level interactions require further elucidation.

Biomass and forest structural effects on herbivores and predators

Whereas plant diversity can increase vegetation biomass and shape the arthropod community, the biomass itself can influence arthropod communities and herbivory. Higher foliage biomass can increase herbivore abundances (Marques et al., 2000; Whitfeld et al., 2012), but larger trees may also promote herbivory through being more apparent in their surroundings (Floater and Zalucki, 2000; Castagneyrol et al., 2013). Besides plant biomass, vegetation structure shapes the environment that animals experience. Canopy structure can, for example, modify the microclimate (Ehbrecht et al., 2017; Menge et al., 2023). More complex vegetation can also affect predators and parasitoids by offering them more abundant food sources and reducing their competition (Langellotto and Denno, 2004), or by hindering their host searching (Andow and Prokrym, 1990; Clark and Messina, 1998). Further, small-scale factors such as visibility and cues from the vegetation can influence predator behavior and prey-finding success (Heinrich and Collins, 1983; Tschanz et al., 2005; Turlings and Erb, 2018). Due to the complexity and alternative mechanism on how forest structure can affect herbivory and predation, further studies that address the topic in a comprehensive manner are needed. In addition, as plant diversity can affect biomass and forest structure (Cardinale et al., 2011; Kunz et al., 2019), careful consideration of these effects is required in plant-higher trophic level studies.

Producer and consumer functional traits and seasonality

When trying to understand the complexity of plant diversity and higher trophic level interactions, studies of species compositions can describe the observed patterns but are limited in scope of as to what the underlying mechanisms are. Whereas taxonomic diversity is commonly used to measure changes in community assembly and trophic interactions (Wong et al., 2018), functional traits and functional diversity, by contrast, can provide deeper insight to the underlying mechanisms (Cadotte et al., 2011; Mouillot et al., 2011). Therefore, functional traits represent a useful tool to unveil drivers of community structure and food webs across trophic levels (Hooper et al., 2005; McGill et al., 2006; Wong et al., 2018). Limited set of plant functional traits have been successfully used to explain plant form and function on a global scale (Díaz et al., 2016) and relationships between local and global plant community structures (Bruelheide et al., 2018).

Leaf nutritional traits are key plant functional traits, which are known to affect herbivore arthropods. Especially the high importance of nitrogen for herbivores is well established, as they need it in much higher amounts for their own tissue when compared to what is present in the same amount of plant tissue (Mattson, 1980; Elser et al., 2000). However, nitrogen can also have adverse effects on herbivores as defensive compounds (War et al., 2012; Campbell and Vallano, 2018). Notably, also nutrients that are needed by animals in much smaller amounts, such as magnesium, can modify the plant-consumer interactions (Prather et al., 2020; Zhu et al., 2021). Carbon, in turn, is the most abundant element in leaves. It is largely present as herbivore feeding and growth inhibiting structural carbon as well as tannins, but is also important for herbivores as sugars (Feeny, 1970; Elser et al., 2000; Chapman, 2013). Although the potential importance of plant nutritional traits was recognized early for plant neighborhood interactions (Feeny, 1976), direct comparisons of how the difference in focal and neighborhood plant species' nutritional content affects herbivory has not been addressed.

In turn, arthropods as consumers respond to plant quality through their functional response traits (Wong et al., 2018). Body size and defensive traits are key functional traits of herbivorous insects, affecting their survival, dispersal, and fecundity, and body size is further simultaneously a response trait to host plant quality (Bowers, 1993; Coley et al., 2006; Chown and Gaston, 2010; Brousseau et al., 2018). Additionally, diet breadth of arthropods is an overarching trait that defines a large part of their ecological niche and guides the herbivory co-evolution with their host plants (Singer, 2008). Plant diversity can affect specialist and generalist herbivore insects differently, as increasing host plant abundance in low vegetation diversity is expected to be most beneficial for specialists due to higher resource base (Root, 1973; Jactel et al., 2021), whereas generalists can benefit from dietary mixing in plant species mixtures (Singer et al., 2004; Karban et al., 2010; Lefcheck et al., 2013). Thus, specialist dominance may decrease and occurrence of rare generalist species may increase in high plant diversity patches (Ebeling et al., 2018). However, even though development of generalized methods for measuring functional traits of arthropods has been attempted (Moretti et al., 2017; Brousseau et al., 2018), the conceptual framework across taxonomic groups has not yet been well established (Wong et al., 2018).

Additionally, the influence that plant diversity and plant functional traits have on higher trophic levels is seasonally dependent. Plant nutritional quality declines as foliage matures (Mattson, 1980; Scriber and Slansky, 1981; Chavana-Bryant et al., 2017), and abiotic conditions change amid the growing season. The changes in foliage quality lead to herbivore populations being highest in the early season (Feeny, 1976; Murakami et al., 2005); and although predator populations commonly follow the changes in herbivore prey populations (Polis, 1999), seasonal changes in abiotic conditions between habitats can cause deviations from this pattern (Janzen, 1973; Richards and Windsor, 2007). Overall, though leaf traits and seasonal patterns in herbivore and predator abundances are studied in themselves, studies incorporating these variables in a comprehensive approach along forest diversity and structure are rare.

BEF-China

Subtropical regions hold the lowest percentage (11%) of forest cover of all climatic domains but have the second highest deforestation rates (FAO, 2020). The deforestation rate has, however, significantly slowed down in the recent years (FAO, 2020), and further knowledge of ecosystem functioning in respect to tree diversity is needed in this climatic domain to aid the reduction of further forest diversity and promotion of forest restoration. Therefore, BEF experiments are highly valuable for understanding how ecosystem functioning changes with the loss of species and can guide ecological restoration (Eisenhauer et al., 2019). The BEF-China experiment is the currently the world's largest biodiversity-ecosystem functioning experiment, planted in 2009-2010 (Bruelheide et al., 2014). It is situated in a mountainous area in the subtropical climate zone in south-east China in Jiangxi province, Dexin City, Xingangshan township, (29°08'-29°11', 117°90 '-117°93') (Yang et al., 2013). The BEF-China experimental design follows controlled tree species richness extinction scenarios. The study plots in the experiment are divided between singletons and ones that are part of four times greater "superplots" (Bruelheide et al., 2014), allowing estimations of plot size effects in relation to tree species richness. Research in the BEF-China experiment produces valuable information of biodiversity functioning in general and for subtropical forests in particular, but also provides guidance for large scale-deforestation prevention and reforestation programs in China (Bryan et al., 2018), which have favored monoculture plantations over tree species mixtures (Wang et al., 2019).

Thesis outline

In this dissertation, I have investigated how bottom-up mechanisms of tree species richness and tree nutritional traits affect herbivore (caterpillar) functional trait composition and, with the addition of forest structure, the amount of herbivory. I have further investigated how tree species richness and forest structure shape the top-down control through measures of predation pressure. The studies were conducted in the BEF-China experiment using a random extinction scenario following a tree species richness gradient from 24-species mixtures to monocultures, with highly overlapping sets of tree individuals and time frames, allowing for a high degree of comparability. Incorporation of these research topics allows much more detailed predictions of the underlying BEF mechanisms affecting herbivory in response to forest environment than a focus on any of the topics alone can. The selected broad approach will, thus, provide novel insights into the bottom-up and top-down drivers of herbivory, which is highly beneficial for understanding how loss of tree species in forests moderates ecosystem functioning.

In chapter 2, "Leaf nutritional content, tree species richness, and season shape the caterpillar functional trait composition hosted by trees", I evaluate (I) how individual caterpillar traits related to growth, defenses, and host plant utilization (generalism and head size), and the functional diversity of these traits, are shaped across the caterpillar fauna which is hosted seasonally on each tree species per richness level. Higher leaf nutritional content is expected to affect the average caterpillar body size through enhanced growth rates, and to reduce the need for defensive traits due to faster development. Leaf quality is further expected to affect caterpillar head capsule size through palatability. Higher leaf nutritional content and increasing tree species richness are both expected to favor generalist species. (II) The analysis of the change in caterpillar traits is followed by an estimation of the trait variances in respect to tree species richness and season. The variance patterns are further compared to the change in caterpillar species sharing between tree species along the tree species richness gradient. Increased species sharing between neighboring trees at high tree species richness is expected to lead to an increase in caterpillar species richness per tree species and thus to a simultaneous decrease in caterpillar trait variation between tree species.

In chapter 3, “Predation pressure by arthropods, birds, and rodents is Interactively shaped by tree species richness, vegetation structure, and season”, I evaluate how tree species richness, forest structure, plot size, topography, and seasonal progression shape the top-down control by estimating predation pressure from bite marks left by various predator taxa on artificial caterpillars. Whereas tree species richness is expected to influence predation mainly through predator and herbivore prey abundances, forest structure can additionally influence host finding probability through cues from vegetation and visibility. Variables influencing predator and prey abundances, and variables influencing prey finding probability, are expected to interact between spatial scales. Specific attention is given to the relationship between tree species richness and forest structure, as increasing tree species richness can cause systematic changes in specific forest structural attributes, such as tree size and canopy vertical stratification. This is further addressed in a seasonal context, as forest structure, along topography, is expected to shape the abiotic environment, which can have profound effects on predator activity between rainy and dry seasons. Finally, comparisons are carried out to evaluate the importance of overall forest structural complexity in contrast to individual structural measures.

Chapter 4, “Tree species richness, leaf quality, and topography shape herbivory in a subtropical Biodiversity-Ecosystem Functioning experiment” evaluates the change in the amount of herbivory as per branch averages with respect to tree species richness, leaf nutritional quality, forest structure, plot size and tree position within plot, topography, and seasonal progression. Earlier studies in the field site have demonstrated the herbivory to increase in higher tree species richness levels (e.g. Schuldt et al., 2017), and the current approach aims to elucidate the patterns driving this relationship. Leaf quality is expected to be a key element in herbivory accumulation with herbivores being more concentrated on high quality trees as their frequency declines, and through associational neighborhood effects where herbivores can ‘spillover’ from high quality hosts to lower ones, or low quality hosts can mask the high quality ones. Herbivory is expected to be promoted by forest structure through positive biomass relationship, and by topography through presumed changes in plant defenses and intra-individual leaf trait variation. Forest structure and topography can further interact by shaping the vertical distribution of herbivory within the canopy through presumed changes in light availability and soil quality. Further, plot size and edge effects are expected to be important in driving differences in herbivory between high and low tree species richness, as herbivores are expected to concentrate in larger monocultures and central positions within them due to high host tree abundances.

In chapter 5, I discuss the key findings of the thesis, the links between the individual chapters' results, and specific needs for future studies. Particular attention is given to the broader applicability of the results, and their benefits for BEF research, and more specifically, for future studies in the BEF-China experiment.

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CHAPTER 2

Leaf nutritional content, tree species richness, and season shape the caterpillar functional trait composition hosted by trees

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Leaf Nutritional Content, Tree Richness, and Season Shape the Caterpillar Functional Trait Composition Hosted by Trees

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Simple Summary: The nutritional content of food plants can, to a large extent, determine the physical attributes of herbivorous insects, from growth rates to the need for defenses against predators. In forests, tree species richness may influence these plant-mediated effects through increasing variation in the nutritional quality that herbivorous insects encounter. Seasonal progression can also shape the plant–herbivore relationship, with lowered leaf quality in later seasons. It is expected that specialist herbivores fare better than generalists in poorer nutritional-quality host plants, whereas generalists can benefit from dietary mixing in more variable neighborhoods. However, a clear understanding of how these factors interact to influence the diversity and functionality across multiple traits of herbivorous insect communities is lacking. In this study, we found support for the expectation of higher generalism of caterpillars in high-nutrition content trees, which also promoted higher abundance but lowered caterpillar species richness and smaller and less defended individuals. Increasing tree richness led to higher caterpillar species sharing between tree species, decreased trait variation, and increased caterpillar species richness per tree species. Our findings shed light on how leaf traits and changes in tree richness interact to influence the trait composition of key herbivores through fine-scale habitat partitioning in host plant neighborhoods.

Abstract: Nutritional content of host plants is expected to drive caterpillar species assemblages and their trait composition. These relationships are altered by tree richness-induced neighborhood variation and a seasonal decline in leaf quality. We tested how key functional traits related to the growth and defenses of the average caterpillar hosted by a tree species are shaped by nutritional host quality. We measured morphological traits and estimated plant community-level diet breadth based on occurrences from 1020 caterpillars representing 146 species in a subtropical tree diversity experiment from spring to autumn in one year. We focused on interspecific caterpillar trait variation by analyzing presence-only patterns of caterpillar species for each tree species. Our results show that tree richness positively affected caterpillar species-sharing among tree species, which resulted in lowered trait variation and led to higher caterpillar richness for each tree species. However, community-level diet breadth depended more on the nutritional content of host trees. Higher nutritional quality also supported species-poorer but more abundant communities of smaller and less well-defended caterpillars. This study demonstrates that the leaf nutritional quality of trees shapes caterpillar trait composition across diverse species assemblages at fine spatial scales in a way that can be predicted by ecological theory.

Keywords: body weight; carbon; defense; generalist; leaf traits; Lepidoptera; magnesium; nitrogen; plant richness; specialist

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1. Introduction

Herbivorous insect abundance and species richness tend to increase with increasing plant richness [1,2]. Besides plant richness per se, changes in the plant composition may influence the herbivore fauna through plant functional traits [2,3], of which leaf nutritional quality is of especially high importance [4,5].

The Resource Concentration Hypothesis [6] predicts that specialists concentrate in patches of low plant richness based on resource abundance. In turn, higher plant richness may offer possibilities for dietary mixing for herbivores [7,8], and some studies have demonstrated such nutrient-balancing behavior to be stronger with generalist than specialist herbivores [9,10] (but see [11]). Other ecological factors than balancing nutritional intake are, however, likely also to lead to mixed diets [8]. For example, the Optimal Foraging Hypothesis [12] posits that herbivores make diet choices to optimize energy, nutrient, and time demands [13,14]. Higher plant richness can then enable host plant shifts through increased options in the host plant neighborhood.

Caterpillars represent a substantial component of total insect diversity in forest ecosystems [15] and are a common model group in nutritional ecological studies (e.g., [10,16,17]). Host plants are selected both by ovipositing female Lepidoptera and by caterpillars [18]. Caterpillars can switch among host plants either through ballooning (via silken thread) or by locomotion [19,20]. Through host plant shifts, caterpillars can offset poor oviposition choices [18,21], balance nutritional intake [22–24], shift from the high protein demand of early instars to the high carbohydrate demand of later stages [9,25], and increase food resources (e.g., feeding habit shift from miner to external feeder [26]). Conversely, caterpillars may be directed towards suboptimal food sources in order to escape parasitism and predation through host plant shifts [27–29].

The positive effect of high nutritional quality on herbivorous insect preference has been demonstrated to be strong [5]. Nitrogen (N) especially is a major limiting factor in the growth of herbivorous insects [4,30], and the lower use efficiency of generalists can lead them to favor high N diets or to rely on over-ingestion [24,31,32]. Required carbohydrates can also be limiting, as carbon (C) is largely present in less usable structural carbohydrates and as digestibility-reducing and feeding-inhibiting tannins [30,31]. Tougher, high C-content plant material can affect the caterpillar feeding traits by requiring stronger head musculature [33–35] or by selecting for smaller species or individuals that can selectively consume the more palatable portions within the leaf (reviewed in [36]). C content increases while N often decreases with leaf maturation [4,17,37] (but see [38]). A similar pattern follows for leaves produced later in the season [39], and these changes can have profound effects on caterpillar growth and defenses [16]. While more nutrient-rich, early-season leaves increase the growth rates of caterpillars [16,39], they have been found to particularly favor smaller herbivore species [4,40]. A decrease in content by leaf age has also been shown for other nutrients, such as magnesium (Mg), phosphorus (P), and potassium (K) [38,41,42] (but see opposing results for Ca [43]). N, P, K, Mg, and Ca are all essential nutrients for herbivorous insects [35,44], and micronutrients, such as Mg, have been shown to modify caterpillar species composition [45] and amplify the effect of macronutrients (N, P, K) on arthropod abundance [46]. Mg, specifically, is an important element in hemolymph, cuticle formation, and tissues, including the nervous system [31,44,47]. However, leaf nutrients other than N have received much less attention in nutritional ecology studies so far.

Leaf traits and plant species richness can also influence caterpillar traits that are indirectly linked to resource use. Plants or older leaves with lower nutritional quality can reduce the growth rate of caterpillars and, thus, prolong development time and increase their vulnerability to predation, which, in turn, may demand greater investment in defense mechanisms [4,16,48]. Hairs offer physical repellence against predators [49,50], and coloration can work as a defensive trait through camouflage and aposematism (e.g., [49,51]). Higher conspicuousness in later instars can promote aposematism due to increased size and mobility [51,52]. Aposematism can also be more useful in later seasons outside the naïve fledgling period [53]. Increasing plant richness may promote predator abundance (the Enemies Hypothesis [6]), which may lead to a higher need for defensive traits. However, empirical knowledge on how plant richness, leaf traits, and seasonal change together influence the caterpillar community via the caterpillars' body size, diet breadth, and defensive traits is still lacking.

In this study, we aimed to test how the leaf nutritional content of trees affects the trait composition of caterpillar communities and how this relationship is altered by the surrounding tree richness and seasonal progression in a subtropical tree diversity experiment. We tested what kind of caterpillar fauna, on average, a tree species hosts at a given point in time, along with increasing tree neighborhood richness, by sampling over spring, summer, and autumn during a single year. Presence-only sampling units for trait analysis were formed by averaging the caterpillar traits across species for each tree species per tree richness level per season. Changes in trait variation were tested as functional diversity of caterpillar fauna within each tree species and between the caterpillar trait averages among tree species. We expected that: (i) tree richness increases sharing of caterpillar species between tree species (measured as tree richness level–specific beta diversity), which also shows as increased caterpillar generalism (measured as occurrences between all sampling units) and as an increase in caterpillar richness per each tree species; (ii) increased caterpillar species-sharing among tree species at higher tree richness results in reduced caterpillar trait variation. Similarly, it reduces within-tree species functional diversity (functional dispersion, FDis); (iii) higher nutritional content (N and Mg), which is promoted in early seasons, leads to lower body weights by favoring earlier instars and smaller species, and lower defensive traits due to faster development. Carbon content (C) is expected to have the opposite effect of N and Mg on body weight due to tougher and palatability-reducing structural carbohydrates and tannins, but, alternatively, can lead to increased growth rates because of the higher amount of shorter, more usable carbohydrates. Similarly, the effect of C on head size may be positive or negative, either by promoting reduced head size and selective feeding or by increasing head musculature. By linking tree richness and leaf nutritional traits, and the functional composition of a highly diverse herbivore larval community in a controlled tree richness setup, our study provides insights into how bottom-up effects shape caterpillar communities through fine-scale habitat selection.

2. Materials and Methods

2.1. Study Region and Experimental Design

This study was carried out in the subtropical region of southeast China (Jiangxi Province, 29°08′–29°11′ N, 117°90′–117°93′ E, 105 to 275 m above sea level) as part of the BEF-China biodiversity experiment. BEF-China is currently the largest tree diversity experiment in the world, where tree richness and tree species composition of individual plots were manipulated following a strict design (see also map of the area [54]). The study area used was site A of the BEF-China experiment, which has a stand-alone tree diversity setup planted in 2009. The 26.7 ha study site comprises 271 plots, of which 69 were used in this study. The plot size is 25.82 m × 25.82 m, which corresponds to the traditional Chinese unit of 1 mu (666.7 m^2). Within each plot, 400 trees were planted in a 20 × 20 (rows by columns) design. The selection of species followed a random broken stick design for extinction scenarios with mixtures of 24, 16, 8, 4, and 2 species and monocultures. The 24-species mixtures are an additional treatment on top of the gradual extinction scenario design starting from the 16-species mixture [54]. The richness levels 16 and 24 were combined to form a single 'high richness' level that was named '16' in the analyses and results and used in order to avoid crowding tree replicates closely together (fewer plots towards higher richness levels as tree species appear on same plots). From the species pool involving 24 tree species, 16 were used in this study. The species used in the study consisted of deciduous species: *Castanea henryi* Rehd. and Wils., *Choerospondias axillaris* Roxb., *Koelreuteria bipinnata* Franch., *Liquidambar formosana* Hance, *Nyssa sinensis* Oliver, *Quercus fabri* Hance, *Quercus serrata* Murray, *Rhus chinensis* Mill., *Sapindus mukorossi* Gaertn., and *Triadica sebifera* L.; and of evergreen species: *Castanopsis eyrie* Champ. ex Benth., *Castanopsis sclerophylla* Lindl. and Paxt., *Cyclobalanopsis glauca* Thunb., *Cyclobalanopsis myrsinifolia* Blume, *Lithocarpus glaber* Thunb., and *Schima superba* Gardner and Champ. No living individuals of *Rhus chinensis* Mill. were found in 2-species mixtures, so these plots were reassigned as *Schima superba* Gardner and Champ. monocultures. Some individuals of *Castanopsis eyrei* Champ. were recognized to belong to *Castanopsis fargesii* Franch. and were excluded from the data. The number of sampled trees per species per richness level varied from 1 to 16 with an average of 5.9 (SD = 2.5) (see Table S1 for all tree replicate numbers). The replicate numbers vary to some extent, besides tree species and richness level corrections, due to self-thinning making some trees very rare in certain richness levels. Moreover, we followed a sampling scheme that matches the sampling of leaf traits [55], which increases the intended tree replicate numbers per tree richness level from 5 to 6 in monocultures and to 9 in 2-species mixtures. Effects of differences in tree replicate numbers were accounted for in the analyses by using replicate numbers as a covariate in caterpillar richness analyses (see Section 2.5.1).

2.2. Sampling Strategy

The caterpillar samples were collected three times in 2019 (April–May, June–July, and August–September), from 449 tree individuals in spring, 465 in summer, and 463 in autumn, with the campaign lasting 12, 16, and 16 days, respectively. Caterpillars were collected by beating the tree crown seven times with a padded stick over a suspended white sheet (1.0 m × 1.0 m) that was lifted as close as possible to the branches under collection by a telescopic pole reaching a maximum of 8 m height. Due to this collection method, the caterpillars represent only external feeders. All dislodged caterpillars were collected and stored separately in tubes with 99.5% ethanol.

Given the throughput limitations in the morphological identification of caterpillars, DNA barcodes were sequenced from all caterpillar individuals and clustered into Molecular Operational Taxonomic Units (MOTU, hereafter referred to as species) for further analyses. Threshold-based hierarchical clustering with BLASTclust [56] (threshold of 97.8% identity [57]) was adopted as the species delimitation method following the pipeline of [58] due to the threshold-based method's conservatism with datasets consisting of many singleton sample species, which can lead to poor performance of variance-based methods [59].

One sample was excluded from the data, as leaf traits were unavailable for *Koelreuteria bipinnata* Franch. for the high richness level. One sample was recognized to have an obvious measurement or recording error in weight and was excluded. Finally, 57 caterpillars were removed because of inability to measure some trait values due to tissue damage. After these exclusions, 1020 caterpillar–plant interactions (i.e., caterpillar) samples were retained for subsequent analyses.

2.3. Caterpillar Trait Measurements

We measured the diet breadth of each caterpillar species as occurrences across all tree species within the plant community (generalism). Body weight, head capsule width, hair coverage, and aposematism were measured from each caterpillar individual. Body weight (with an accuracy of ±0.1 mg) was measured from the ethanol-stored caterpillars first air-dried on Petri dishes. Head capsule width was measured under a stereoscopic microscope with a measuring scale with 10× to 40× magnification. An increase in head capsule width is highly correlated with an increase in body weight. In addition, head size may be hypoallometric (decrease relatively as the body grows) because body weight increases continuously during the instar development, but the sclerotized head capsule size increases when molting and is assumed to follow a geometric growth ratio along instars (named Dyar's rule [60,61]). The difference in head and body size is expected to be most pronounced at the end of each instar prior to molting [62]. For this reason, in addition to using body weight as a covariate in the head capsule width analysis (see Section 2.5), relative head capsule width was calculated (head capsule width divided by body weight). Further, the body weight (mg) values were cube root-transformed to increase linearity and correlation to the one-dimensional head capsule width (correlations of original and cube root transformed values shown in Figure S1).

Hair coverage and aposematism were evaluated by using similar methods to those in other studies of caterpillar defenses, e.g., [16,27], but with adding one more class to hair coverage evaluation (<25%) and simplifying the aposematism to two classes instead of three (Figure 1), as compared to methods in [16]. The hair coverage was estimated visually under a stereomicroscope and it informs how much of the caterpillar cuticle is covered due to the combination of hair density and hair length. Hair coverage was classified into four levels: 0 (Figure 1a), 1 (<25%; Figure 1b), 2 (<50%; Figure 1c,e), and 3 (>50%; Figure 1d,f). The color of the caterpillars was visually recorded as the coloration that covers at least 80% of the body surface (mainly excluding the head). Observed colors varied from black to light yellow and were divided into camouflage (singular colors, e.g., green, grey, and black) (Figure 1a–d) and warning colors (bright coloration and high contrasts such as bright yellow and red, and black and yellow stripes) (Figure 1e,f). The color classification was intentionally robust, focusing on the color contrasts rather than specific color shades to account for potential fading because of storing the samples in ethanol.

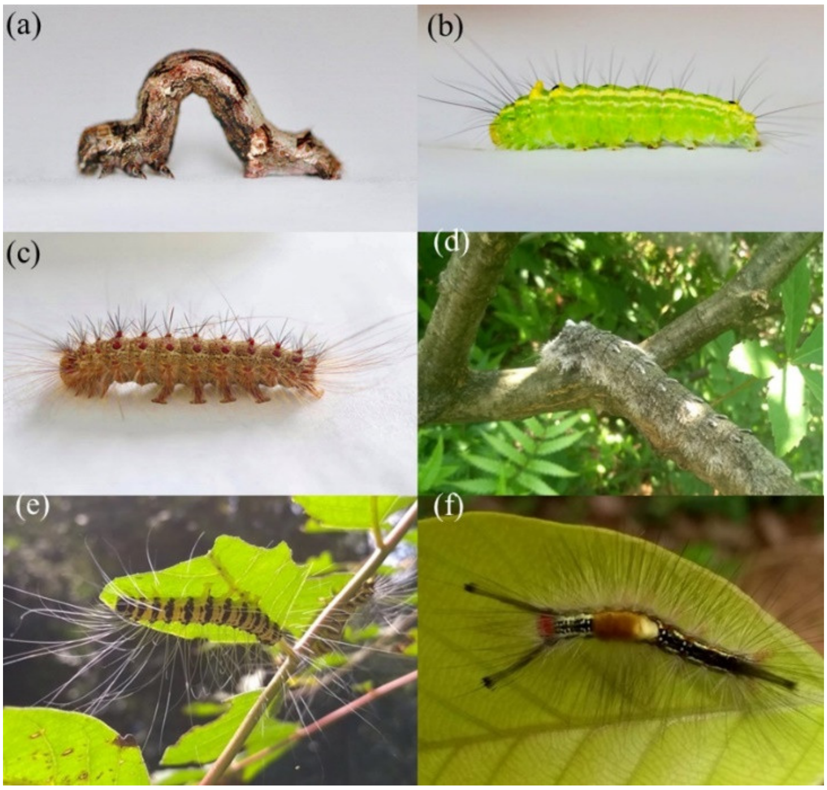

Figure 1. Hair coverage and coloration categories employed in this study, presented by example species encountered in BEF-China: (**a**) 0, (**b**) <25%, (**c**,**e**) <50%, and (**d**,**f**) >50% hair coverage. Pictures (**a**–**d**) represent camouflage, and (**e**,**f**) aposematism. Photo credit: (**a**–**c**) Y. Li, (**d**–**f**) P. Anttonen.

2.4. Leaf Trait Selection

Specific leaf area (SLA), leaf dry matter content (LDMC), nitrogen (N), carbon (C), magnesium (Mg), calcium (Ca), potassium (K), and phosphorus (P) were measured on all trees used in the study (details on leaf trait measurements are provided in Supplement S1; see also [55,63]). The selection of leaf traits from candidates for analysis was based on internal collinearities (Pearson $r < 7$; see Figure S1 for trait correlations). Many nutritional leaf traits were highly correlated with each other: N and Mg with K and P, and Mg also with Ca. For this reason, N and Mg were considered the most suitable overall estimators of nutritional quality. C content was also included for further information on leaf quality. The structural leaf traits SLA and LDMC were not included in analyses because of their high correlation with each other, and of SLA with N and LDMC with C. Leaf samples were collected from multiple tree individuals per tree species between August and October 2018 and comprised only fully developed, non-senescent leaves free of damage from herbivores, pathogens, or mechanical stress. Leaf traits were averaged for statistical analyses for each tree species per tree richness level in order to account for neighborhood richness-induced changes in leaf traits [55,64].

2.5. Statistical Analyses

2.5.1. Caterpillar Trait Data Processing and Linear Analysis

In order to focus on interspecific variation, the study sampling unit was formed by averaging caterpillar intraspecific trait values, followed by interspecific averaging for each tree species and season (see Figure A1 for the process pipeline of the study). Intraspecific caterpillar trait values were first averaged for each caterpillar species per tree individual to account for differences in traits caused by solitary and gregarious individuals of different group sizes [65], followed by averaging between tree individuals per tree richness level per season.

The averaged caterpillar data were analyzed using linear mixed-effects models using package lmerTest [66] in R v 4.0.5 environment [67]. Response variables used were: caterpillar species richness, abundance, generalism, body weight, head capsule width, relative head capsule width, aposematism, and hair density. All caterpillar trait models were analyzed using tree richness, sampling season, leaf traits (N, Mg, and C), and two-way interactions of tree species richness and season with each other and leaf traits as explanatory variables. Tree species identity was used as a random factor in all trait models. The number of replicates for each tree species per richness level was included as a covariate for caterpillar species richness and abundance models. Species richness was used as a covariate for caterpillar trait analyses to account for the directional effect caused by lower caterpillar species numbers on specific tree species. Because the likelihood of being caught increases by the number of tree species a caterpillar species occurs on, no exclusions of rare species (based on abundances) in the data were performed in order to not disproportionately weight the effect of generalist species. The correlation of body size to other caterpillar traits was tested by including body weight as a covariate. The correlation of defensive traits (aposematism and hair density) was tested by including them in each other's models.

All models were reduced using backward selection with function 'step' in the package lmerTest [66] to obtain the most parsimonious model. All fixed factors, but not the random factors, were allowed to be dropped from the model with selection criterion $p < 0.05$. All predictors were tested for collinearity with Pearson's correlation $r > 0.7$ (Figure S1). Variance inflation factors (VIFs) were calculated using the package car [68] to ensure no strong collinearity among the predictor variables (all VIFs < 5; see also [69]). In order to improve the normality and variance homogeneity of the model residuals, leaf trait values and all response variables were log $(x + 1)$-transformed. The cube root transformed body weight values were used in all analyses to increase linearity.

Single factors in linear mixed effect models can have significant F-test values but improve the overall information value of the model only marginally, or even increase the

AIC value by increasing the number of explanatory variables. In order to evaluate whether leaf traits and other factors of interest improve the overall models, random variable- and covariate-only models were run for each model with (1) only tree species identity as a random variable and (2) with the following non-hypothesis covariates: tree replicates for caterpillar species richness, tree replicates and caterpillar species richness for abundance, caterpillar species richness and body weight for head capsule width, and only caterpillar species richness for the other trait models and FDis (see below). All models were evaluated by comparing the AIC-values (Akaike Information Criterion value) [70] against the random variable- and covariate-only models, with ΔAIC > 2 interpreted to offer an improved model.

Further, sensitivity comparisons of the effect of the most common and widely spread caterpillar species between tree species were conducted. This was conducted for all caterpillar traits and FDis by removing all species that appeared on more than half of the tree species. This accounted for 11 species with a total of 621 individuals (~60.6% of all samples).

2.5.2. Caterpillar Functional Diversity within Tree Species

Functional dispersion (FDis), which works without abundance-weighing as a measure of functional diversity [71], was used for measuring within-study unit caterpillar functional diversity. Caterpillar FDis was calculated based on caterpillars' body weight, head capsule width, hair coverage, aposematism, and generalism. Increasing FDis values indicate higher overall trait variation around the trait centroid [71]. The abundance of each species was set as one to focus on the effects of interspecific trait variation. The change in FDis between sampling units was analyzed using tree richness, sampling season, leaf traits, and interaction between them as explanatory variables, and caterpillar species richness was included as a covariate.

2.5.3. Caterpillar Trait Variation and Species-Sharing between Tree Species

In addition to functional trait diversity within tree species, the caterpillar trait variation between tree species was estimated by calculating the standard deviation (SD) of the caterpillar trait values between sampling units. The change in standard deviation was analyzed with linear models with the function 'lm' in the R environment. Explanatory variables used were tree richness, sampling season, and caterpillar species richness. Body weight averages for the respective tree richness levels were also included in the relative head capsule width model to test if systematic changes in body weight lead to increasing variation in the head capsule width.

Caterpillar beta diversity between tree species for each tree richness level was estimated for comparison to caterpillar trait variation between tree species and species richness per tree species. The change in community assembly was tested using Sørensen dissimilarity and, separately, its two components, species turnover using Simpson's dissimilarity and nestedness, with the R package 'betapart' [72]. These richness level-specific values were tabulated and analyzed with the function 'lm' in the R environment. Explanatory variables used were tree richness, sampling season, and the number of sampled plots per richness level in order to account for decreasing spatial variation towards higher tree richness (more monoculture plots than species mixture plots). Due to the low number of data points in the between-tree species analyses (15), no interactions between explanatory factors were included.

2.5.4. Caterpillar Intra- and Inter-Specific Trait Variation

Because caterpillar traits can vary both between and within species, a robust comparison of intra- and inter-specific trait variation was conducted in order to test their relative effect on the underlying trait patterns. Overall, caterpillar intra-specific trait variation was estimated for each caterpillar trait as the average of standard deviations (SD) of each species that had more than one individual. The inter-specific variation was estimated as the standard deviation between caterpillar trait averages of each caterpillar species across all sampling units.

3. Results

In total, we analyzed 1020 successfully sequenced and trait-evaluated caterpillar samples. Sequencing failed for 15 samples of 1092 caught. The caterpillars were delineated to 176 species by BLASTClust, of which 146 were retained for further analysis after the exclusion of missing trait values and incorrect tree species. Caterpillar species richness and abundance with respective tree replicates for each sampling unit are shown in Table S1. In total, caterpillar species were assigned to 17 Lepidoptera families, in which Erebidae (48 species, 309 individuals) was the most species-rich and Geometridae (33 species, 573 individuals) the most abundant (Table S2). Other families had much lower species numbers and abundances, with the third most species-rich family (Notodontidae) having 11 species and an abundance of 22, and the third most abundant family (Sphingidae) having 2 species and an abundance of 33. Around 17% of the caterpillar species (25 species, 33 individuals) could only be assigned reliably to the rank of order (Lepidoptera) and thus were labeled as unassigned Lepidoptera.

3.1. Caterpillar Traits

3.1.1. Diversity and Generalism

Caterpillar species richness was positively affected by the number of tree replicates and tree richness and negatively by leaf Mg content (see Table 1 for full model results). Abundance was highest in summer (693), as compared to spring (150) and autumn (177), and was best explained by increasing caterpillar species richness. Abundance also increased with increasing leaf Mg and with the interaction of leaf C content and season (Figure 2a), with increased abundance in high C content in the summer.

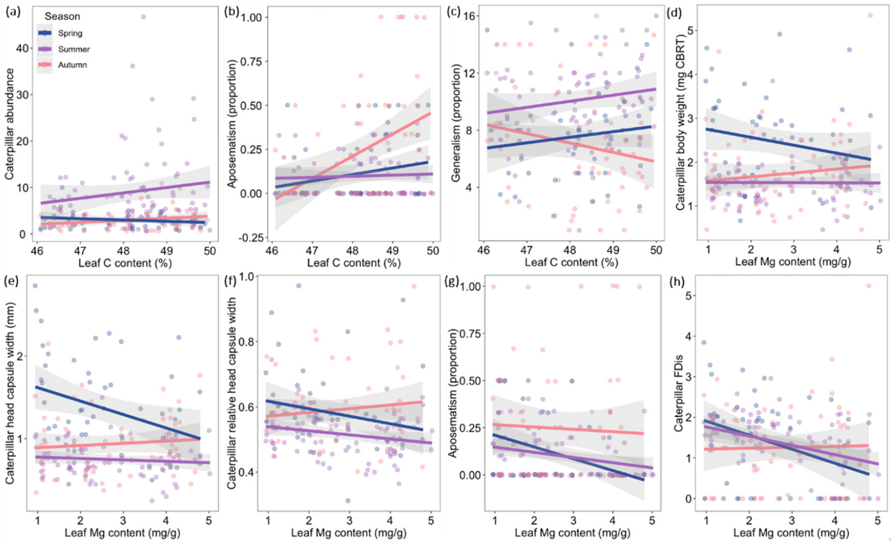

Figure 2. Relationships between leaf traits (leaf C and Mg content) with caterpillar (**a**) abundance and traits, (**b**) body weight, (**c**) head capsule width, (**d**) relative head capsule width, (**e**,**f**) aposematism, (**g**) generalism, and (**h**) FDis.

Generalism of caterpillar species varied between 1 and 16 host tree species, but with the vast majority of species being found only from one (92 species) or two (20 species) tree species (Table S3). Average generalism between sampling units was 8.42 (SD = 3.56). Generalism per tree species was positively correlated with caterpillar species richness and promoted by high leaf Mg content (see Table 1 for full model results). Tree richness showed only a weak direct positive effect on generalism, but the negative effect in low richness was stronger with low Mg content, with little to no effect of Mg in high richness (Figure 3a). A negative effect for generalism was shown by body weight and season, with the latter especially, in high C-content tree species (Figure 2c). However, C content showed a positive trend for generalism in spring and summer.

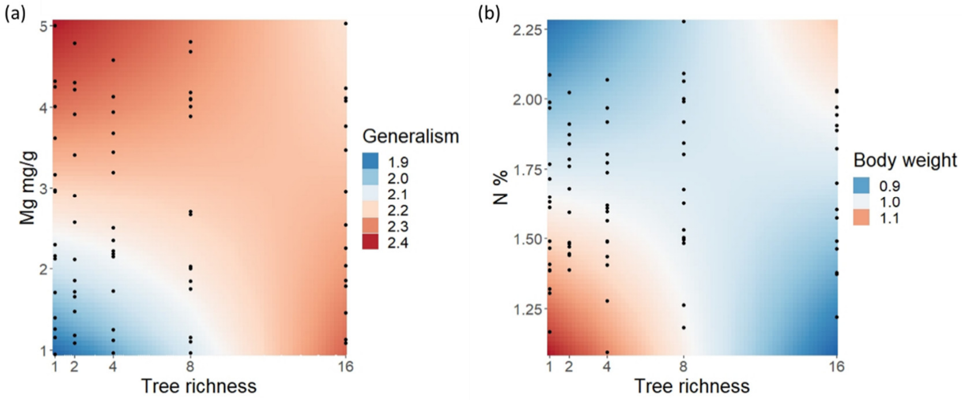

Figure 3. Relationship of caterpillar traits to interaction of leaf traits and tree richness. Color gradient represents estimated change in response values in the lme models retrieved by package 'effects' [68], and point clouds show observed values. (**a**) Change in generalism through interaction of tree richness and leaf Mg content, and (**b**) caterpillar body weight change through interaction of tree richness with leaf N content. All factors except tree richness are log + 1 transformed. Body weight values are also cube root transformed.

3.1.2. Growth-Related Traits

Body weight was higher in spring and especially in low Mg content tree species that, in turn, hosted slightly smaller caterpillars in autumn (Figure 2d) (see Table 1 for full model results of all growth-related traits). Nitrogen and tree species richness had only a weak negative overall effect on body weight, but the negative effect of N in the low tree richness levels was stronger (Figure 3b).

Head capsule width increased strongly with increasing body weight and decreased with increasing C, N, and Mg content. The negative effect of Mg was especially strong in spring, with a weak positive trend in autumn (Figure 2e). Head capsule width was also negatively correlated to caterpillar species richness.

The relative head capsule width was negatively affected by body weight and caterpillar species richness. Relative head capsule width decreased with increasing Mg and its interaction with the season (Figure 2f), with a negative effect of increasing Mg in spring and summer and a positive effect in autumn.

3.1.3. Defensive Traits

Hair coverage and aposematism were strongly positively correlated with each other (see Table 1 for full model results). C content had a negative effect on hair coverage, and a positive effect on aposematism, with the strongest effect in autumn (Figure 2b). Increasing N content also had a negative effect on hair coverage. Hair coverage was reduced in later seasons, and aposematism increased. Mg content had an overall negative effect on aposematism in spring and summer, with the overall higher autumn values being affected only slightly (Figure 2g). Body weight had a positive effect on aposematism.

3.1.4. Functional Diversity within Tree Species and Sensitivity Comparison

FDis of the caterpillar traits was strongly positively affected by caterpillar species richness (see Table 1 for full model results). Mg content had a negative effect on FDis in spring and summer (Figure 2h).

Our sensitivity comparison, with the most common species removed, led to similar overall results but with several of the weaker explanatory factors being dropped (Table S4). Additionally, in the case of relative head capsule width, seasonal interaction with Mg was replaced with tree richness interaction with Mg, and C content showed a negative effect. All random variable- and covariate-only models had a clearly worse fit (higher AIC values) than the fixed effect predictor models. Interspecific variation (SD) of caterpillar trait values was about twice as large as intraspecific variation, except for relative head capsule width, where they were nearly equal, and aposematism and hair coverage, which had no intraspecific variation (Table S5).

Table 1. Summary results of linear mixed-effects models after fixed factor reduction using backward selection with criterion $p < 0.05$ for the averaged caterpillar traits per tree species per richness level per season. All factors are scaled by subtracting the mean and dividing by standard deviation. All variables except tree replicates, sampling season, and tree richness are log + 1 transformed. Body weight values are also cube root transformed. Standardized parameter estimates (with standard errors, t and p values) are shown for the variables retained in the minimal models. p-values in bold mean $p \leq 0.05$, p-values of italic mean $p \leq 0.1$.

	Caterpillar Species Richness			**Caterpillar Abundance**		
	Est ± *SE*	*t*	*p*	*Est* ± *SE*	*t*	*p*
(Intercept)	1.382 ± 0.035	39.759	**<0.001**	1.592 ± 0.018	88.861	**<0.001**
Tree replicates	0.178 ± 0.039	4.607	**<0.001**	-	-	-
Caterpillar species richness	-	-	-	0.656 ± 0.018	35.668	**<0.001**
Tree species richness	0.101 ± 0.039	2.610	**0.010**	-	-	-
Sampling season	-	-	-	0.016 ± 0.018	0.863	0.390
Leaf C content	-	-	-	0.030 ± 0.021	1.450	0.149
Leaf Mg content	−0.097 ± 0.035	−2.774	**0.006**	0.044 ± 0.021	2.073	**0.040**
Season: leaf C content	-	-	-	0.056 ± 0.018	3.070	**0.002**
	Caterpillar FDis			**Caterpillar generalism**		
	Est ± *SE*	*t*	*p*	*Est* ± *SE*	*t*	*p*
(Intercept)	0.747 ± 0.025	29.911	**<0.001**	2.164 ± 0.040	53.703	**<0.001**
Caterpillar species richness	0.298 ± 0.026	11.640	**<0.001**	0.098 ± 0.031	3.135	**0.002**
Caterpillar body weight	-	-	**-**	−0.085 ± 0.032	−2.643	**0.009**
Sampling season	−0.004 ± 0.025	−0.149	0.882	−0.092 ± 0.032	−2.890	**0.004**
Tree species richness	-	-	-	0.040 ± 0.030	1.328	0.186
Leaf C content	-	-	-	0.060 ± 0.044	1.359	0.187
Leaf Mg content	−0.048 ± 0.026	−1.885	*0.061*	0.099 ± 0.045	2.216	**0.036**
Season: C	-	-	-	−0.074 ± 0.030	−2.421	**0.017**
Season: Mg	0.063 ± 0.025	2.468	**0.015**	-	-	-
Tree richness: Mg	-	-	-	−0.072 ± 0.032	−2.276	**0.024**
	Caterpillar body weight			**Caterpillar head capsule width**		
	Est ± *SE*	*t*	*p*	*Est* ± *SE*	*t*	*p*
(Intercept)	0.997 ± 0.019	51.275	**<0.001**	0.655 ± 0.007	99.980	**<0.001**
Caterpillar body weight	-	-	-	0.189 ± 0.006	30.412	**<0.001**
Caterpillar species richness	-	-	-	−0.023 ± 0.006	−3.834	**<0.001**
Sampling season	−0.087 ± 0.019	−4.537	**<0.001**	−0.007 ± 0.006	−1.197	0.233
Tree species richness	−0.018 ± 0.020	−0.909	0.365	-	-	-
Leaf C content	-	-	-	−0.019 ± 0.008	−2.394	**0.030**
Leaf N content	−0.033 ± 0.021	−1.551	0.123	−0.020 ± 0.007	−2.641	**0.015**
Leaf Mg content	−0.004 ± 0.021	−0.204	0.839	−0.025 ± 0.008	−3.155	**0.007**
Season: Mg	0.043 ± 0.020	2.178	**0.031**	0.017 ± 0.006	2.950	**0.004**
Tree richness: N	0.040 ± 0.020	1.998	**0.047**	-	-	-
	Caterpillar relative head capsule width					
	Est ± *SE*	*t*	*p*			
(Intercept)	0.440 ± 0.005	82.459	**<0.001**			
Caterpillar species richness	−0.010 ± 0.005	−2.082	**0.039**			
Caterpillar body weight	−0.017 ± 0.005	−3.430	**<0.001**			
Sampling season	−0.001 ± 0.005	−0.216	0.829			
Leaf Mg content	−0.012 ± 0.005	−2.298	**0.033**			
Season: Mg	0.014 ± 0.005	2.902	**0.004**			

Table 1. *Cont.*

	Caterpillar hair coverage			Caterpillar aposematism		
	Est ± *SE*	*t*	*p*	*Est* ± *SE*	*t*	*p*
(Intercept)	0.565 ± 0.029	19.980	**<0.001**	0.145 ± 0.014	11.245	**<0.001**
Caterpillar body weight	-	-	**-**	0.038 ± 0.015	2.766	**0.006**
Aposematism	0.203 ± 0.030	6.796	**<0.001**	-	-	-
Hair coverage	-	-	-	0.091 ± 0.015	6.430	**<0.001**
Sampling season	−0.142 ± 0.029	−4.883	**<0.001**	0.084 ± 0.015	5.510	**<0.001**
Leaf C content	−0.091 ± 0.033	−2.775	**0.006**	0.054 ± 0.016	3.095	**0.002**
Leaf N content	−0.074 ± 0.032	−2.297	**0.023**	-	-	-
Leaf Mg content	-	-	-	−0.003 ± 0.016	−0.577	0.564
Season: C	-	-	-	0.058 ± 0.017	3.133	**0.002**
Season: Mg	-	-	-	0.043 ± 0.017	2.313	**0.022**

3.2. Functional Trait Variation and Species Sharing between Tree Species

Increasing caterpillar species richness had a positive effect on variation of abundance, and a negative effect on other traits, with significant trends on body weight, head capsule width, hair coverage, aposematism, and FDis (see Table A1 for all SD model results). Tree richness had a strong negative effect on SD of head capsule width, a marginally significant negative effect on hair coverage, aposematism, and FDis, and a moderately negative trend on body weight. Season had a positive effect on SD of generalism and aposematism. None of the explanatory factors had a strong effect on variation of caterpillar species richness and relative head capsule width.

Beta diversity was more strongly driven by species turnover than by nestedness (see Table A2 for linear model results of changes in beta diversity). The number of sampled plots showed only a weak negative trend on caterpillar species turnover and nestedness but moderately stronger on beta diversity. Tree species richness had a strong negative effect on beta diversity and species turnover and a moderately positive trend on nestedness. Season also had a strong positive effect on beta diversity and species turnover and a moderately negative trend on nestedness.

4. Discussion

By using functional traits of leaves with corresponding traits of herbivores (caterpillars) in a tree diversity experiment with controlled tree richness and freely assembled insect fauna, our study provides insight into how functional traits determine interactions between consumer insects and primary producers through bottom-up effects. Our study answers what kind of caterpillar fauna, on average, is observed in tree species with varying nutritional quality at a given point in time along a tree richness gradient, and how tree richness affects caterpillar trait variation between the tree species. Caterpillar traits, especially body size, may change along the caterpillars' development, and it should be noted that the scope of the study is limited to comparisons between tree species at specific time points without extending to what ultimate body sizes or other trait values would be reached by specific caterpillar species on variations of diets. However, seasonal and body size-dependent trait patterns show that caterpillar functional traits are dynamic and deserve consideration beyond simple species-to-species connections. The tree richness gradient and leaf traits in this study reflect habitat quality at fine spatial scales, enabling a better understanding of how local conditions shape the community assembly of the caterpillar fauna via trait matching.

4.1. Tree Richness Effects on Caterpillar Trait Composition

The direct effects of tree richness on caterpillar functional traits remained weak in our study. This is in concordance with earlier results from the same field site, which demonstrated the higher importance of tree functional and phylogenetic composition on herbivore assemblage [73]. Nevertheless, there was a systematic negative trend on between tree species variation across caterpillar traits and also a weakened effect of N on body weight towards higher richness levels. However, no strong trends of tree richness were observed for within-tree species caterpillar trait diversity (FDis). In a separate study from the same field site [74], higher caterpillar species co-occurrences between tree species with higher nutritional quality were found. Here, we found particularly strong negative effects of tree richness on caterpillar beta diversity among tree species, which likely explains the accompanied reduced trait variation and the interactive effect of tree richness with leaf traits. The increased caterpillar species-sharing between tree species can also explain the increased caterpillar richness for each tree species (i.e., at the tree species level) in higher tree richness, in combination with plot-level increases, shown in a previous study for the field site [58]. These results differ from what has been observed at wider spatial scales, where it has been shown that the increase in herbivore species richness across latitudinal gradients can be a direct cumulative effect of increasing plant species richness with no plant species-level increase [15]. Studies on trait variation between separate field sites, and thus presumably different herbivore communities, have also shown increases along increasing plant richness [75–77]. Thus, our results suggest that the increasing variation of host plants is not necessarily accompanied by increasing trait variation of herbivores at fine spatial scales within the herbivore community if it leads to more mixing of the fauna and highlights the need to take into account the spatial scale in trait studies.

For our fine spatial-scale approach, the decrease in beta diversity at higher tree richness can be seen as support for the Resource Concentration Hypothesis [6], stating that higher plant richness favors generalists. However, direct effects on our site-specific generalism measure were weak, despite an earlier study in the same field site showing positive effects of tree richness on generalist abundances at the sapling stage [78]. Effects of tree richness on generalism became more evident with leaf trait interactions, specifically in relation to leaf Mg content, where the overall effect of Mg on generalism was positive and further promoted in lower tree richness levels. This nutrition–tree richness connection demonstrates that the level of herbivore generalism a tree species experiences is a combination of the trait variation in the tree neighborhood and a tree species' nutritional quality, with the latter appearing to be relatively more important. The caterpillar species-sharing between tree species can be a result of more widely spread oviposition, increased movement of caterpillars within vegetation, or a mixture of both. As caterpillar chemoreception capabilities are limited [79] and movement in vegetation is essentially non-targeted, generalists, with their lower nutrient use efficiency [24], are more likely to benefit from dietary mixing opportunities in the immediate surrounding vegetation. It should be noted, however, that the high number of species found only on single tree species in our study are unlikely to represent only strictly monophagous species, which can be rare even in diverse tropical insect communities [80,81]. Nonetheless, as the local plant community determines the possible diet breadth for herbivores, looking at the diet breadth within the plant community makes a realistic estimate of herbivore–plant interactions at fine spatial scales [82]. Such a community perspective allows looking into habitat selection through nutritional differences represented by the dominant plant species of a local community.

Whether higher plant richness increases predation pressure (Enemies Hypothesis [6]) has been debated due to confounding plant structural, predator, and parasite intra-guild interactions [83,84]. We did not observe directional effects of tree richness on defensive traits but found a negative trend in trait variation. As nutritional content was observed to have a strong effect on defensive traits, the lack of directional effects of tree richness does not necessarily mean a lack of top-down pressure but a possible interference effect on optimal defense strategies in highly variable environments. Notably, generalist species have been shown to be less well-defended than specialists [85].

Overall, how herbivorous insects are affected by tree richness has focused more on the important role of plant defenses [86] than on nutritional content. Our study suggests that tree richness not only has bottom-up effects on herbivorous insects through nutrition, but may also subsequently alter the top-down effects they experience. In this sense, tree richness, plant defenses, and nutritional quality should be viewed together in future studies of herbivore community assembly.

4.2. Nutritional and Seasonal Effects on Caterpillar Traits

Unexpectedly, our results showed overall higher effects of leaf Mg on caterpillar abundance and trait composition than leaf N content. Some studies have demonstrated the importance of micronutrients such as Mg [45,46] on herbivore insects, but most of the research with caterpillar dietary requirements has focused on the balance between protein and carbohydrate intake (e.g., [23–25]). However, if generalists possess overall lower nutrient use efficiencies, as shown in an example case for N [24], and also indicated by slower growth rates compared to specialists in a multi-species experiment [16], it would be a valid strategy to also favor other essential high nutrient concentrations and balance the overall intake [14]. This interpretation would correspond to the expectations of the Optimal Foraging Hypothesis [12,13].

Nutritional effects did not remain stable over the seasons. Even though a reduction in leaf quality towards later seasons is expected to be common among plant species [4,38,41], using season alone as a proxy for leaf quality poses some problems due to differences in the base level of the leaf nutritional content between tree species. Other factors, such as predation pressure, can also vary between seasons [53,87], obscuring the mechanisms through which the seasonal progression affects the caterpillar community. Increased body size of caterpillars in later seasons has been attributed in some studies to reduced predation and overwintering preparation [62,87], but with simultaneously increased leaf age leading to higher dispersal, presumably due to escape from poor quality hosts, and earlier populations also having higher fecundity [62]. In addition, smaller herbivorous insects may prefer younger leaves [4,40], and caterpillar generalism has been shown to be higher in spring [58,88]. The higher body weights we observed in spring question the uniformity of these responses. However, assuming smaller insects prefer younger leaves because of higher nutritional content, our results—with lower body weights in spring with increasing Mg content and higher N content in monocultures—fit well in the framework. The tree richness-dependent effect of N content may demonstrate the easier finding of host plants by smaller, high nitrogen content-favoring species. Alternatively, or in addition, the negative N–body size relationship may be explained by a higher proportion of earlier instars that benefit from higher N content [9,25].

In our study, hair coverage was connected to lower nutritional content, similar to aposematism, promoting the interpretation that lower nutrient content leads to slower growth rates and a higher need for defenses [4,48]. Interestingly, hair coverage was higher in spring as opposed to aposematism, even though the two traits were correlated, suggesting otherwise a defensive trait syndrome. A possible explanation for the disparity of hair coverage and aposematism in regard to season comes from the effect of predation by birds. Aposematic coloration is expected to be of higher importance outside the fledgling season [53], and hairiness could be an alternative defensive measure in spring by not suffering from increased conspicuousness.

Additionally, beta diversity and variation of generalism and aposematism between tree species increased towards autumn. This, along with generalism being more common in spring and aposematism in autumn, shows the species pool was more strongly separated along these traits when the differences between tree species in leaf nutritional content are expected to be highest. Similarly, within-tree species FDis was also negatively affected by nutritional content (Mg) in spring and summer, demonstrating the unifying effect of nutritional content on the caterpillar species pool. In addition, Mg also increased abundance despite reducing species richness. Predation can shape the caterpillar community in low nutrient content, favoring more specialized species if they are better defended [85], but competitive exclusion can also be strong between herbivore species [89,90], and the observed pattern might suggest that generalists have competitive advantages in high nutrient environments.

The observed trends with respect to increasing C content were bi-directional, with, on the one hand, higher aposematism (overall, but especially promoted in autumn) and lower generalism in autumn, which can be expected by higher structural carbohydrate and tannin concentrations on caterpillar growth [17]. However, on the other hand, hair coverage, generalism, and caterpillar abundance were promoted by high C content, with the latter two in earlier seasons, which can be expected by carbohydrates being essential nutrients in the caterpillar diet [22,31]. In addition, older instars can shift their preference from a protein-rich to a carbohydrate-rich diet [9,25]. However, where we observed negative effects of nutritional content on body weight by N and Mg, we did not observe any positive relationship of C. Instead, head capsule width was negatively influenced by C content, which is according to the expectation of smaller individuals eating selectively from tougher leaf tissue [36]. However, the effect of N and Mg was similarly negative on head capsule width, even after accounting for the effect of body weight and thus the promotion of larger amounts of early instars, which obscures what role the C content and nutrition in general play in determining the head size of caterpillars. Moreover, tougher food content has, in other cases, been connected to increased head sizes [33], and it may be that the head size–C content relationship is dependent on the instar stage, as most caterpillars in this study were very small and presumably early instars. Our results also showed that besides leaf nutritional content influencing the head capsule width, as seen also with (Mg) on relative head capsule width, smaller caterpillars had relatively larger heads, suggesting a hypoallometric relationship of head and body size. The expected geometric growth rate of head size along Dyar's rule has been shown to weaken during the development of the caterpillar and respond to growth-related factors [61,91,92]. Increasing body weight could then be expected to increase the between-tree species variation of relative head capsule width because of nutritional effects, which, however, was not observed in this study. More light on the nutritional content–head size relationship would be gained by the inclusion of mandible structures that affect the feeding mode and diet choice [33–36], but which was out of scope in this study. Overall, the seasonal interaction of carbon content is important to take into account with studies focusing on the bottom-up effects of leaf quality on herbivore traits, but further benefits would be gained by also separating the different sources of carbon within the leaves.

4.3. Inter- vs. Intra-Specific Trait Variation in Caterpillars

As we analyzed the caterpillar fauna time point specifically, the results are influenced, besides inter-specific variation, by intra-specific variability due to caterpillar trait ontogenetic change. The inter-specific variation was shown to be clearly higher than the intra-specific variation for all traits except relative head capsule width. However, this comparison does not capture all of the ontogenetic effects, as many of the caterpillars were caught only at a certain life stage. Indication of ontogenetic changes was seen with aposematism, as it was more common in larger caterpillars, supporting the expectation of their higher visibility due to body size itself and the accompanied higher mobility [51,52]. Additionally, Mg content promoted smaller relative head sizes in addition to higher abundances, which hints toward higher proportions of early instars on these trees. In conclusion, inter-specific variation, nevertheless, appeared to be a stronger determinant than intra-specific variation of the observed trait distributions across caterpillar taxa already before intra-specific averaging of the traits.

4.4. Methodological Considerations

Some method-related correlations unavoidably arose in our experimental design of manipulated tree richness. However, these effects were, in most cases, weaker than those of tree richness, leaf traits, and caterpillar body weight. The models that include leaf traits also had clearly better AIC values compared to random variable- and covariate-only models. In addition, sensitivity comparison revealed that the used presence-only analysis structure balances the strong abundance differences between caterpillar species, though the trends became somewhat weaker with the loss of the most common species. It is not surprising that the number of tree replicates had a strong effect on caterpillar species richness. This demonstrates, in part, the role of asymmetrical self-thinning caused by tree species competition with high planting densities (representing the natural development of the stands [54]). Self-thinning of long-lived plants in arthropod studies can then influence arthropod species richness, which reflects on their trait distributions, as was seen with caterpillar species richness having effects of varying strength on caterpillar traits in this study. The positive effect of caterpillar species richness on variation of abundance is caused by the highly skewed relationship of these variables, as an increase in overall caterpillar abundance resulted largely from more species being found. We accounted for these confounding effects with the stepwise averaged presence-only approach and use of covariates to ensure reliable estimates. Averaging leaf traits per tree species per richness level also accounts for the potential effect tree richness can have on herbivores by inducing changes in leaf traits [64]. As our study approach is time point-specific, especially in spring, the differences in the timing of budburst between tree species may lead to differences in observed caterpillar body sizes. However, no effect of season on body size variation between tree species was observed, and body sizes were altogether higher in spring than in later seasons, indicating that the leaf phenological effect was likely weak. The larval stage used in this study offers benefits over the adult stage for studies of nutritional effects, as nutrient intake is essentially directed to growth without the interference of reproductive input. However, as the developmental stage, growth rate differences, and species size distributions can induce overlapping effects, the use of immature insects in trait research with naturally assembled communities needs further development of the theoretical background.

5. Conclusions

Studies investigating bottom-up effects on multiple caterpillar traits at the community level have been sparse (but see [16]) despite the ecological importance of these interactions. Our study demonstrates that the effects of tree richness, season, and leaf traits predictably influence the species diversity and trait composition of immature herbivorous insects in naturally assembled herbivore communities. The influence of plant richness on herbivore traits was shown to influence the species pool already at a fine spatial scale and to differ from the effects observed at wider scales. The study also demonstrates that the effects of nutritional bottom-up effects require still further investigation on plant–herbivore interactions, especially for nutrients other than nitrogen. Testing the functional bottom-up relationships of plant–herbivore interactions across host plant richness levels is highly important, given the strong impact they have on ecosystem functions [93]. This will further advance the general knowledge of biodiversity–ecosystem functioning relationships [94,95].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/insects13121100/s1, Figure S1: Variable correlations; Figure S2: Relative head capsule width sensitivity analysis; Table S1: Sampling details per tree species; Table S2: Lepidoptera samples per family; Table S3: Caterpillar generalism; Table S4: Sensitivity analysis; Table S5: Caterpillar trait intra- versus inter-specific variation.

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Data Availability Statement: Caterpillar trait data: available in a publicly accessible repository that does not issue DOIs. These data can be found here: [https://data.botanik.uni-halle.de/bef-china/datasets/657] (accessed on 29 November 2022). Leaf trait data: restrictions apply to the availability of these data. Data were obtained from Andréa Davrinche and Sylvia Haider and are available from the authors at [https://data.botanik.uni-halle.de/bef-china/datasets/648] (accessed on 29 November 2022) with their permission.

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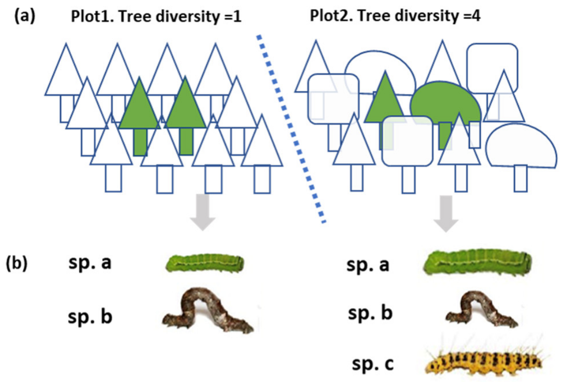
Appendix A



(c) **Caterpillar traits**

Caterpillar species	Tree species	Tree richness	Season	Body weight mg	Generalism	...
lep.sp.a	tree.sp1	1	Summer	18	16	
lep.sp.b	tree.sp1	1	Summer	65.8	5	
lep.sp.b	tree.sp1	1	Autumn	37.3	16	
lep.sp.a	tree.sp2	1	Summer	10	16	
lep.sp.b	tree.sp2	1	Summer	50.5	5	
lep.sp.a	tree.sp2	4	Autumn	15	16	
lep.sp.c	tree.sp2	4	Autumn	0.3	2	

(d) **Caterpillar trait averages**

Tree species	Tree richness	Season	Body weight mg	Generalism	...	FDis
tree.sp1	1	Summer	50.9	10.5		1.9
tree.sp1	1	Autumn	37.3	16		0
tree.sp2	1	Summer	30.25	10.5		1.8
tree.sp2	4	Autumn	7.65	9		1.6

Figure A1. Depiction of the general framework of this study: (**a**) monoculture shown on the left and 4-species mixture on the right; (**b**) caterpillars collected from these tree richness levels during two seasons; (**c**) caterpillar trait averages per caterpillar species per tree species per tree richness per season; (**d**) caterpillar trait averages across caterpillar species per tree species per tree richness per season, as used in subsequent analyses. Averaging of caterpillar values per caterpillar species first per tree individuals not demonstrated for brevity. FDis values were estimated between all traits using caterpillar species averages for each tree species per tree richness level per season.

Table A1. Summary of linear model testing for changes in caterpillar trait standard deviations (SD) between tree species. All factors are scaled by subtracting the mean and dividing by standard deviation. All variables except tree replicates, sampling season, and tree richness are log + 1 transformed. Body weight values are also cube root transformed. Standardized parameter estimates (with standard errors, t, and *p*-values) are shown for explanatory variables. *p*-values in bold mean $p \leq 0.05$, *p*-values of italic mean $p \leq 0.1$.

	Caterpillar Species Richness SD			**Abundance SD**		
	Est ± SE	*t*	*p*	*Est ± SE*	*t*	*p*
(Intercept)	0.996 ± 0.089	11.141	**<0.001**	1.459 ± 0.097	15.026	**<0.001**
Tree replicates	0.006 ± 0.130	0.047	0.963	-	-	**-**
Caterpillar species richness	-	-	-	0.451 ± 0.115	3.937	**0.002**
Sampling season	−0.017 ± 0.093	−0.184	0.857	−0.117 ± 0.105	−1.110	0.291
Tree richness	−0.047 ± 0.130	−0.363	0.724	−0.004 ± 0.110	−0.036	0.972
	Caterpillar FDis SD			**Caterpillar generalism SD**		
	Est ± SE	*t*	*p*	*Est ± SE*	*t*	*p*
(Intercept)	0.662 ± 0.031	21.122	**<0.001**	1.41 ± 0.042	33.862	**<0.001**
Caterpillar species richness	−0.132 ± 0.037	−3.575	**0.004**	−0.078 ± 0.049	−1.580	0.142
Sampling season	0.019 ± 0.034	0.550	0.594	0.126 ± 0.045	2.772	**0.018**
Tree species richness	−0.075 ± 0.036	−2.115	*0.058*	0.030 ± 0.048	0.631	0.541
	Caterpillar body weight SD			**Caterpillar head capsule width SD**		
	Est ± SE	*t*	*p*	*Est ± SE*	*t*	*p*
(Intercept)	0.550 ± 0.042	13.063	**<0.001**	0.322 ± 0.020	15.998	**<0.001**
Caterpillar species richness	−0.129 ± 0.050	−2.587	**0.025**	−0.096 ± 0.024	−4.039	**0.002**
Sampling season	0.016 ± 0.046	0.351	0.733	−0.028 ± 0.022	−1.291	0.223
Tree species richness	−0.092 ± 0.048	−1.930	*0.080*	−0.067 ± 0.023	−2.934	**0.014**
	Caterpillar relative head capsule width SD					
	Est ± SE	*t*	*p*			
(Intercept)	0.096 ± 0.011	8.763	**<0.001**			
Caterpillar species richness	−0.016 ± 0.016	−1.007	0.337			
Caterpillar body weight	0.004 ± 0.015	0.254	0.805			
Sampling season	<0.001 ± 0.012	0.007	0.995			
Tree species richness	0.002 ± 0.014	0.169	0.869			
	Caterpillar hair coverage SD			**Caterpillar aposematism SD**		
	Est ± SE	*t*	*p*	*Est ± SE*	*t*	*p*
(Intercept)	0.615 ± 0.023	26.604	**<0.001**	0.192 ± 0.011	17.872	**<0.001**
Caterpillar species richness	−0.132 ± 0.027	−4.825	**0.001**	−0.066 ± 0.013	−5.177	**<0.001**
Sampling season	−0.006 ± 0.025	−0.221	0.829	0.067 ± 0.012	5.737	**<0.001**
Tree species richness	−0.057 ± 0.026	−2.161	*0.054*	−0.026 ± 0.012	−2.159	*0.054*

Table A2. Summary of linear model testing of changes in beta diversity estimates between tree species. Analysis run similarly for overall beta diversity and its two components. All factors are scaled by subtracting the mean and dividing by standard deviation. Response factors and number of sampled plots are log + 1 transformed. Standardized parameter estimates (with standard errors, t, and p-values) are shown for explanatory variables. p-values in bold mean $p \leq 0.05$, p-values of italic mean $p \leq 0.1$.

	Caterpillar Species Turnover			**Caterpillar Species Nestedness**		
	Est ± *SE*	*t*	*p*	*Est* ± *SE*	*t*	*p*
(Intercept)	0.627 ± 0.005	126.823	**<0.001**	0.043 ± 0.005	9.471	**<0.001**
Number of sampled plots	−0.012 ± 0.007	−1.769	0.105	0.007 ± 0.006	1.165	0.269
Sampling season	0.016 ± 0.005	3.183	**0.009**	−0.009 ± 0.005	−1.863	*0.089*
Tree species richness	−0.023 ± 0.007	−3.340	**0.007**	0.012 ± 0.006	1.827	*0.095*
	Caterpillar beta diversity					
	Est ± *SE*	*t*	*p*			
(Intercept)	0.651 ± 0.003	225.127	**<0.001**			
Number of sampled plots	−0.008 ± 0.004	−1.983	*0.073*			
Sampling season	0.011 ± 0.003	3.776	**0.003**			
Tree species richness	−0.016 ± 0.004	−4.029	**0.002**			

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Supplement 1

Leaf trait measurements and selection for analysis

Leaf samples were collected between August and October 2018, and comprised only fully developed, non-senescent leaves free of damage from herbivores, pathogens or mechanical stress. Leaves were sampled from all 16 tree species in all richness levels (monocultures, 2-, 4-, 8-, 16- and 24-species mixtures), including several tree replicates each and several leaf samples from each tree's crown. In total, this amounted to more than 2 000 leaf samples (see also, [54]). Because of this high number of samples, leaf traits were not measured directly, but 'predicted' via reflectance spectroscopy. For this purpose, a so called 'calibration set' was collected, composed of ten samples per species (10 to 25 leaves each) across all richness levels, randomly positioned within the crown of several randomly selected trees for each species.

For all leaves (predicted samples as well as calibration samples), reflectance spectra from fresh leaf samples with an ASD FieldSpec® 4 Wide Resolution Spectroradiometer (Malvern Panalytical Ltd., Malvern, United Kingdom) across 250 to 2500 nm was measured. The equipment was optimized regularly with a calibration panel (Spectralon®, Labsphere, Durham, New Hampshire, USA).
Only the calibration leaves were processed for direct trait measurements: saturated fresh leaves were weighed for each sample, scanned and weighed again after 72 hours drying at 80 °C. Image leaf area was analyzed (WinFOLIA software, Regent Instruments, Quebec, Canada) and specific leaf area (leaf area / leaf dry mass) as well as leaf dry matter content (leaf dry mass / leaf fresh mass) were calculated [62]. Dried calibration leaves were then ground to fine powder from which 200 mg were processed by a nitric acid digestion. Magnesium, calcium and potassium contents were analyzed from the filtrate via atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany), and phosphorus content with a spectrophotometric assay using an acid molybdate technique. For carbon and nitrogen content, 5 mg of leaf powder were analyzed with an elemental analyzer (Vario EL Cube, Elementar, Langenselbold, Germany).

Finally, spectra of the calibration samples were analyzed with the Unscrambler X software (version 10.1, CAMO Analytics, Oslo, Norway). Individual pre-treatments per leaf trait were applied to the spectral data to reveal relevant parts of the spectra and to reduce noise. For each trait, the pre-treated spectral data were used to fit a Partial Least Square regression model (PLS). In the last step, these PLS models were used to predict the true samples' trait values based on their reflectance spectra. The predicted trait values were averaged per species per tree richness level.

Table S1. Sampling details per tree species. Amount of sampled trees per species for each richness level per season, and the respective caterpillar species richness and abundance.

Tree species	Season	Tree richness	Tree replicates	Caterpillar richness	Caterpillar abundance
Castanea henryi	Autumn	1	5	4	8
Castanea henryi	Autumn	2	8	2	3
Castanea henryi	Autumn	4	6	3	4
Castanea henryi	Autumn	8	7	0	0
Castanea henryi	Autumn	16	5	3	3
Castanea henryi	Spring	1	6	4	4
Castanea henryi	Spring	2	8	0	0
Castanea henryi	Spring	4	6	0	0
Castanea henryi	Spring	8	4	1	1
Castanea henryi	Spring	16	5	1	1
Castanea henryi	Summer	1	5	7	10
Castanea henryi	Summer	2	9	5	6
Castanea henryi	Summer	4	6	3	5
Castanea henryi	Summer	8	5	6	8
Castanea henryi	Summer	16	5	10	16
Castanopsis eyrei	Autumn	1	4	1	1
Castanopsis eyrei	Autumn	2	1	1	1
Castanopsis eyrei	Autumn	4	1	0	0
Castanopsis eyrei	Autumn	8	4	3	4
Castanopsis eyrei	Autumn	16	2	0	0
Castanopsis eyrei	Spring	1	4	0	0
Castanopsis eyrei	Spring	2	1	1	1
Castanopsis eyrei	Spring	4	1	0	0
Castanopsis eyrei	Spring	8	4	4	4
Castanopsis eyrei	Spring	16	2	0	0
Castanopsis eyrei	Summer	1	4	3	3
Castanopsis eyrei	Summer	2	1	2	3
Castanopsis eyrei	Summer	4	1	1	1
Castanopsis eyrei	Summer	8	4	5	8
Castanopsis eyrei	Summer	16	2	7	15
Castanopsis sclerophylla	Autumn	1	8	5	5
Castanopsis sclerophylla	Autumn	2	9	1	1
Castanopsis sclerophylla	Autumn	4	5	2	2
Castanopsis sclerophylla	Autumn	8	5	1	1
Castanopsis sclerophylla	Autumn	16	5	0	0
Castanopsis sclerophylla	Spring	1	8	2	2
Castanopsis sclerophylla	Spring	2	9	3	3
Castanopsis sclerophylla	Spring	4	5	2	2
Castanopsis sclerophylla	Spring	8	5	2	2
Castanopsis sclerophylla	Spring	16	5	3	4

Castanopsis sclerophylla	Summer	1	8	6	12
Castanopsis sclerophylla	Summer	2	9	10	13
Castanopsis sclerophylla	Summer	4	5	10	12
Castanopsis sclerophylla	Summer	8	5	9	9
Castanopsis sclerophylla	Summer	16	5	4	5
Choerospondias axillaris	Autumn	1	6	1	1
Choerospondias axillaris	Autumn	2	10	4	5
Choerospondias axillaris	Autumn	4	5	3	10
Choerospondias axillaris	Autumn	8	5	0	0
Choerospondias axillaris	Autumn	16	5	1	2
Choerospondias axillaris	Spring	1	2	1	1
Choerospondias axillaris	Spring	2	9	3	3
Choerospondias axillaris	Spring	4	5	0	0
Choerospondias axillaris	Spring	8	2	0	0
Choerospondias axillaris	Spring	16	5	0	0
Choerospondias axillaris	Summer	1	6	1	1
Choerospondias axillaris	Summer	2	10	4	5
Choerospondias axillaris	Summer	4	4	1	3
Choerospondias axillaris	Summer	8	5	1	1
Choerospondias axillaris	Summer	16	5	4	5
Cyclobalanopsis myrsinifolia	Autumn	1	8	3	3
Cyclobalanopsis myrsinifolia	Autumn	2	9	3	4
Cyclobalanopsis myrsinifolia	Autumn	4	5	2	2
Cyclobalanopsis myrsinifolia	Autumn	8	8	0	0
Cyclobalanopsis myrsinifolia	Autumn	16	5	1	1
Cyclobalanopsis myrsinifolia	Spring	1	10	8	10
Cyclobalanopsis myrsinifolia	Spring	2	9	3	3
Cyclobalanopsis myrsinifolia	Spring	4	4	3	4
Cyclobalanopsis myrsinifolia	Spring	8	8	5	8
Cyclobalanopsis myrsinifolia	Spring	16	5	0	0
Cyclobalanopsis myrsinifolia	Summer	1	8	11	47
Cyclobalanopsis myrsinifolia	Summer	2	9	12	36
Cyclobalanopsis myrsinifolia	Summer	4	5	3	4
Cyclobalanopsis myrsinifolia	Summer	8	8	14	21
Cyclobalanopsis myrsinifolia	Summer	16	5	4	5
Koelreuteria bipinnata	Autumn	1	6	2	4
Koelreuteria bipinnata	Autumn	2	12	4	7
Koelreuteria bipinnata	Autumn	4	8	2	2
Koelreuteria bipinnata	Autumn	8	5	2	2
Koelreuteria bipinnata	Autumn	16	4	0	0
Koelreuteria bipinnata	Spring	1	6	0	0
Koelreuteria bipinnata	Spring	2	10	4	6
Koelreuteria bipinnata	Spring	4	8	1	1
Koelreuteria bipinnata	Spring	8	5	0	0

Koelreuteria bipinnata	Spring	16	4	0	0
Koelreuteria bipinnata	Summer	1	6	4	4
Koelreuteria bipinnata	Summer	2	13	12	29
Koelreuteria bipinnata	Summer	4	8	4	5
Koelreuteria bipinnata	Summer	8	5	2	2
Koelreuteria bipinnata	Summer	16	4	0	0
Liquidambar formosana	Autumn	1	6	2	2
Liquidambar formosana	Autumn	2	9	3	3
Liquidambar formosana	Autumn	4	5	2	2
Liquidambar formosana	Autumn	8	4	2	2
Liquidambar formosana	Autumn	16	6	5	5
Liquidambar formosana	Spring	1	6	2	2
Liquidambar formosana	Spring	2	9	1	2
Liquidambar formosana	Spring	4	5	1	10
Liquidambar formosana	Spring	8	4	3	3
Liquidambar formosana	Spring	16	6	0	0
Liquidambar formosana	Summer	1	6	5	9
Liquidambar formosana	Summer	2	9	6	11
Liquidambar formosana	Summer	4	5	3	7
Liquidambar formosana	Summer	8	4	5	8
Liquidambar formosana	Summer	16	7	8	12
Lithocarpus glaber	Autumn	1	6	0	0
Lithocarpus glaber	Autumn	2	10	3	3
Lithocarpus glaber	Autumn	4	10	2	2
Lithocarpus glaber	Autumn	8	5	1	1
Lithocarpus glaber	Autumn	16	5	3	3
Lithocarpus glaber	Spring	1	6	2	2
Lithocarpus glaber	Spring	2	10	2	2
Lithocarpus glaber	Spring	4	9	2	2
Lithocarpus glaber	Spring	8	5	1	1
Lithocarpus glaber	Spring	16	5	0	0
Lithocarpus glaber	Summer	1	6	5	6
Lithocarpus glaber	Summer	2	11	10	25
Lithocarpus glaber	Summer	4	10	12	29
Lithocarpus glaber	Summer	8	5	6	7
Lithocarpus glaber	Summer	16	5	8	10
Nyssa sinensis	Autumn	1	6	0	0
Nyssa sinensis	Autumn	2	10	0	0
Nyssa sinensis	Autumn	4	4	0	0
Nyssa sinensis	Autumn	8	4	0	0
Nyssa sinensis	Autumn	16	5	3	4
Nyssa sinensis	Spring	1	6	1	1
Nyssa sinensis	Spring	2	9	4	5
Nyssa sinensis	Spring	4	4	0	0

Nyssa sinensis	Spring	8	5	0	0
Nyssa sinensis	Spring	16	5	0	0
Nyssa sinensis	Summer	1	6	4	6
Nyssa sinensis	Summer	2	9	3	4
Nyssa sinensis	Summer	4	4	2	4
Nyssa sinensis	Summer	8	5	7	12
Nyssa sinensis	Summer	16	5	5	8
Quercus fabri	Autumn	1	6	3	5
Quercus fabri	Autumn	2	9	2	3
Quercus fabri	Autumn	4	4	2	3
Quercus fabri	Autumn	8	4	0	0
Quercus fabri	Autumn	16	3	0	0
Quercus fabri	Spring	1	6	1	1
Quercus fabri	Spring	2	9	2	2
Quercus fabri	Spring	4	5	3	3
Quercus fabri	Spring	8	4	1	1
Quercus fabri	Spring	16	3	1	1
Quercus fabri	Summer	1	6	3	4
Quercus fabri	Summer	2	9	4	5
Quercus fabri	Summer	4	5	7	22
Quercus fabri	Summer	8	4	5	5
Quercus fabri	Summer	16	3	6	9
Quercus glauca	Autumn	1	8	3	5
Quercus glauca	Autumn	2	9	7	11
Quercus glauca	Autumn	4	5	3	4
Quercus glauca	Autumn	8	5	3	7
Quercus glauca	Autumn	16	4	0	0
Quercus glauca	Spring	1	6	0	0
Quercus glauca	Spring	2	9	5	5
Quercus glauca	Spring	4	5	3	3
Quercus glauca	Spring	8	5	2	2
Quercus glauca	Spring	16	4	3	3
Quercus glauca	Summer	1	8	7	15
Quercus glauca	Summer	2	9	9	19
Quercus glauca	Summer	4	5	5	9
Quercus glauca	Summer	8	5	5	9
Quercus glauca	Summer	16	3	4	5
Quercus serrata	Autumn	1	6	3	3
Quercus serrata	Autumn	2	9	1	1
Quercus serrata	Autumn	4	5	4	4
Quercus serrata	Autumn	8	5	1	1
Quercus serrata	Autumn	16	4	2	2
Quercus serrata	Spring	1	6	3	3
Quercus serrata	Spring	2	9	4	5

Quercus serrata	Spring	4	5	0	0
Quercus serrata	Spring	8	5	2	2
Quercus serrata	Spring	16	5	3	3
Quercus serrata	Summer	1	6	3	4
Quercus serrata	Summer	2	9	5	7
Quercus serrata	Summer	4	5	3	8
Quercus serrata	Summer	8	5	4	4
Quercus serrata	Summer	16	5	8	12
Rhus chinensis	Autumn	1	4	0	0
Rhus chinensis	Autumn	4	3	1	1
Rhus chinensis	Autumn	8	2	1	1
Rhus chinensis	Spring	1	4	0	0
Rhus chinensis	Spring	4	4	0	0
Rhus chinensis	Spring	8	2	0	0
Rhus chinensis	Spring	16	1	0	0
Rhus chinensis	Summer	1	4	1	1
Rhus chinensis	Summer	4	4	3	6
Rhus chinensis	Summer	8	2	1	2
Rhus chinensis	Summer	16	1	3	5
Sapindus mukorossi	Autumn	1	6	1	1
Triadica sebifera	Autumn	1	6	0	0
Triadica sebifera	Autumn	2	9	1	1
Triadica sebifera	Autumn	4	5	4	4
Triadica sebifera	Autumn	8	3	2	2
Triadica sebifera	Autumn	16	5	1	1
Triadica sebifera	Spring	1	6	2	2
Triadica sebifera	Spring	2	7	5	6
Triadica sebifera	Spring	4	5	1	1
Triadica sebifera	Spring	8	2	0	0
Triadica sebifera	Spring	16	5	0	0
Triadica sebifera	Summer	1	6	5	7
Triadica sebifera	Summer	2	8	5	5
Triadica sebifera	Summer	4	5	1	1
Triadica sebifera	Summer	8	2	1	1
Triadica sebifera	Summer	16	5	5	8
Sapindus mukorossi	Autumn	2	9	3	3
Sapindus mukorossi	Autumn	4	5	1	1
Sapindus mukorossi	Autumn	8	8	0	0
Sapindus mukorossi	Autumn	16	6	1	2
Sapindus mukorossi	Spring	1	6	1	1
Sapindus mukorossi	Spring	2	9	3	4
Sapindus mukorossi	Spring	4	5	0	0
Sapindus mukorossi	Spring	8	5	1	1
Sapindus mukorossi	Spring	16	6	3	4

Sapindus mukorossi	Summer	1	6	3	4
Sapindus mukorossi	Summer	2	9	6	6
Sapindus mukorossi	Summer	4	5	3	5
Sapindus mukorossi	Summer	8	5	3	3
Sapindus mukorossi	Summer	16	6	2	2
Schima superba	Autumn	1	16	1	1
Schima superba	Autumn	4	7	3	5
Schima superba	Autumn	8	6	2	2
Schima superba	Autumn	16	4	0	0
Schima superba	Spring	1	16	3	3
Schima superba	Spring	4	7	1	1
Schima superba	Spring	8	6	3	3
Schima superba	Spring	16	4	0	0
Schima superba	Summer	1	16	6	13
Schima superba	Summer	4	7	5	12
Schima superba	Summer	8	6	11	15
Schima superba	Summer	16	4	6	8

Table S2. Lepidoptera samples per family. Lepidoptera species composition and abundance at the rank of family, across all tree species, richness levels, and seasons.

Family	Richness	Abundance
Erebidae	48	309
Geometridae	33	573
Notodontidae	11	22
Tortricidae	7	9
Noctuidae	6	7
Nolidae	3	4
Sphingidae	2	33
Pyralidae	2	10
Psychidae	2	4
Drepanidae	2	2
Gelechiidae	2	2
Limacodidae	2	2
Lasiocampidae	1	10
Unassigned Lepidoptera	25	33

Table S3. Caterpillar generalism. Number of caterpillar species per each potential generalism class, i.e. how many caterpillar species were found from certain amount of tree species.

Generalism	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of caterpillar species	92	20	5	2	5	4	4	2	3	1	1	1	0	2	2	1

Table S4. Sensitivity analysis. Summary results of linear mixed-effects models after fixed factor reduction using backward selection with criterion P < 0.05 for the averaged caterpillar traits per tree species per richness level per season, after removing 11 most common species that were found from over half of the tree species in the study. All factors are scaled by subtracting the mean and dividing by standard deviation. Body weight values are also cube root transformed. All variables except number of tree replicates, sampling season and tree richness are log + 1 transformed. Standardized parameter estimates (with standard errors, t and p values) are shown for the variables retained in the minimal models. P-values in bold mean P ≤ 0.05.

	Caterpillar species richness			**Caterpillar abundance**		
	Est±SE	*t*	*P*	*Est±SE*	*t*	*P*
(Intercept)	1.051± 0.035	29.765	**<0.001**	1.158± 0.023	49.701	**<0.001**
Tree replicates	0.079± 0.030	2.611	**0.010**	-	-	-
Caterpillar species richness	-	-	-	0.411±0.018	23.324	**<0.001**
Sampling **s**eason	-	-	-	0.015±0.017	0.850	0.397
Leaf C content	-	-	-	-0.009±0.022	-0.413	0.684
Season: leaf C content	-	-	-	0.067± 0.018	3.795	**<0.001**
	Caterpillar FDis			**Caterpillar generalism**		
	Est±SE	*t*	*P*	*Est±SE*	*t*	*P*
(Intercept)	0.543±0.025	21.320	**<0.001**	1.458±0.032	44.994	**<0.001**
Caterpillar species richness	0.381±0.025	15.020	**<0.001**	-	-	**-**
Caterpillar body weight	-	-	**-**	-0.100±0.034	-2.967	**0.003**
Sampling **s**eason	-	-	-	-0.200±0.034	-5.909	**<0.001**
Tree species richness	-	-	-	0.017±0.033	0.526	0.600
Leaf Mg content	-	-	-	0.012±0.033	0.361	0.718
Tree richness: Mg	-	-	-	-0.102±0.033	-3.075	**0.002**
	Caterpillar body weight			**Caterpillar head capsule width**		
	Est±SE	*t*	*P*	*Est±SE*	*t*	*P*
(Intercept)	1.052±0.029	36.015	**<0.001**	0.711±0.008	86.239	**<0.001**
Caterpillar body weight	-	-	-	0.253±0.008	30.554	**<0.001**
Sampling **s**eason	-0.097±0.029	-3.319	**0.001**	-	-	-
Leaf Mg content	-	-	-	-0.022±0.008	-2.641	**0.009**
	Caterpillar relative head capsule width					
	Est±SE	*t*	*P*			
(Intercept)	0.455±0.006	72.178	**<0.001**			
Caterpillar body weight	-0.035±0.006	-5.426	**<0.001**			
Tree richness	-0.001±0.006	-0.177	0.860			

Leaf C content	-0.017±0.008	-2.207	**0.029**			
Leaf Mg content	-0.019±0.008	-2.398	**0.018**			
Tree richness: Mg	-0.014±0.006	-2.103	**0.037**			
	Caterpillar hair coverage			**Caterpillar aposematism**		
	Est±SE	*t*	*P*	*Est±SE*	*t*	*P*
(Intercept)	0.656±0.040	16.332	**<0.001**	0.171±0.017	9.897	**<0.001**
Caterpillar body weight	-	-	**-**	0.059±0.018	3.320	**0.001**
Aposematism	0.191±0.042	4.509	**<0.001**	-	-	-
Hair coverage	-	-	-	0.075±0.017	4.323	**<0.001**
Sampling **s**eason	-0.144±0.041	-3.489	**<0.001**	0.074±0.018	4.085	**<0.001**
Leaf C content	-0.098±0.046	-2.142	**0.034**	0.058±0.017	3.343	**0.004**
Leaf N content	-0.137±0.045	-3.062	**0.003**	-	-	-
Season: C	-	-	-	0.035±0.017	2.032	**0.044**

Table S5. Caterpillar trait intra- versus interspecific variation. Intraspecific variation was estimated as the average of standard deviations (SD) of each species that had more than one individual. The interspecific variation was estimated as standard deviation between caterpillar trait averages of each caterpillar species across all sampling units.

Trait variation (SD)	*Body weight (mg CBRT)*	*Head capsule width (mm)*	*Relative head capsule width*	*Hair coverage*	*Aposematism*
Intraspecific	0.74	0.36	0.14	0	0
Interspecific	1.71	0.78	0.15	1.33	0.42

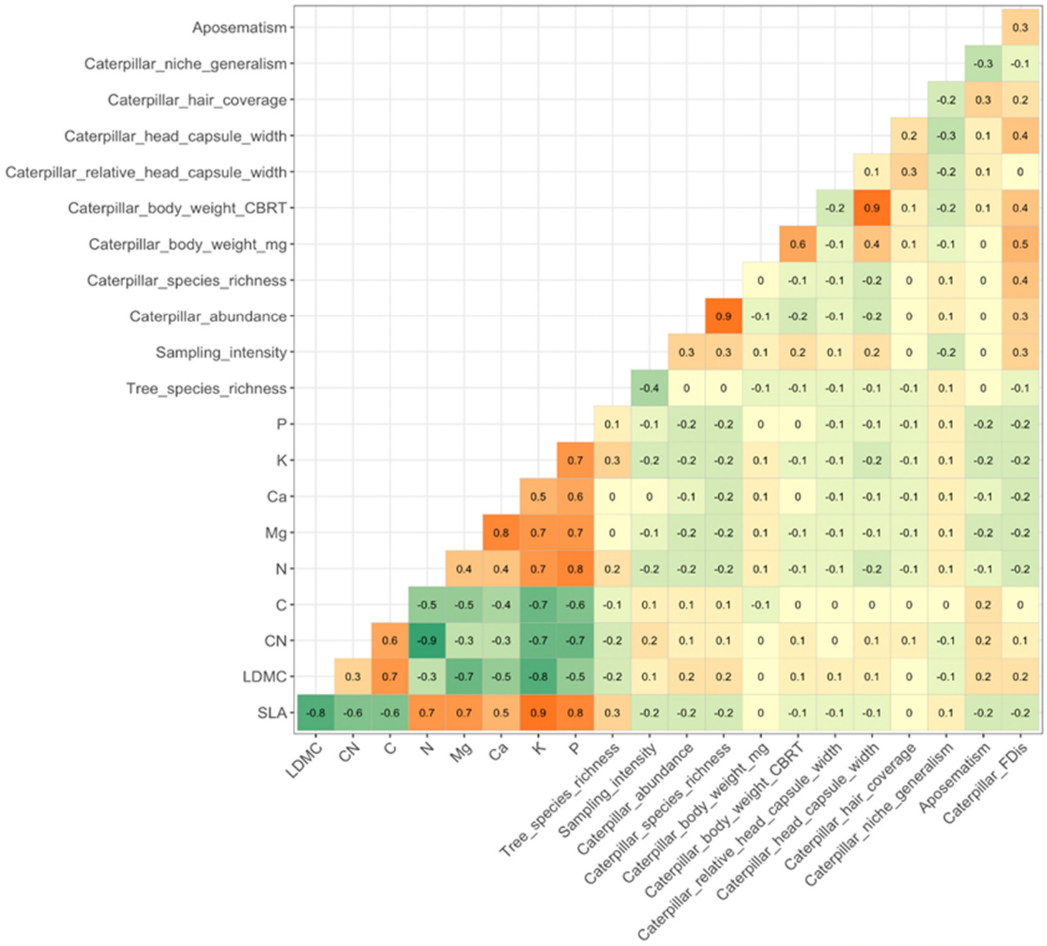

Figure S1. Variable correlations. Relationships among all potential and used response- and predictor variables for the analyses. Values are Pearson's correlation coefficients r. Leaf trait values are averaged per tree species per tree richness level, and caterpillar traits per tree species per tree richness level per season.

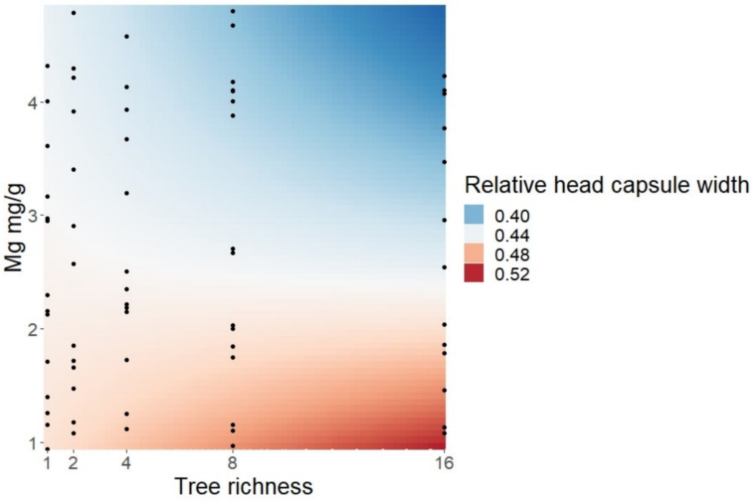

Figure S2. Relative head capsule width sensitivity analysis. Relationship of relative head capsule width to interaction of Mg (mg/g) content and tree richness. Color gradient represents estimated change in response values, and point clouds show observed values. Relative head capsule width and Mg content values are log + 1 transformed.

CHAPTER 3

Predation pressure by arthropods, birds, and rodents is interactively shaped by tree species richness, vegetation structure, and season

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Predation pressure by arthropods, birds, and rodents is interactively shaped by tree species richness, vegetation structure, and season

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Tree species richness, forest structure, and seasonal fluctuations between rainy and dry seasons can strongly affect trophic interactions in forest ecosystems, but the inter- and scale dependence of these variables remains unclear. Using artificial caterpillars (~18,000 replicates), we analyzed predation pressure by arthropods, birds, and rodents along a tree species richness gradient across seasons in a subtropical tree diversity experiment (BEF-China). The aim of the study was to test if forest structure, in addition to tree species richness, has an effect on predation pressure and to further specify which structural variables are important in driving predation. We assessed the effects of tree species richness and forest structure at the plot and local neighborhood levels. We also included fine-scale placement covariates, plot size, and topographical covariates of the study site. Forest structure and tree species richness independently and interactively affected predation pressure. The spatial scale was an important determinant for tree species richness and structural effects, extending from within plot scales to the overall heterogeneity of the plots' surrounding environment. For example, the effect of branch density in the local neighborhood depended on both surrounding tree species richness and plot-level vegetation density. Similarly, visibility-enhancing factors increased attacks by arthropods (lack of branches in close surroundings) and by birds (open area), depending on the surrounding vegetation. A comparison of structural measures showed that predation pressure can be addressed in much greater detail with multiple specific structural features than with overall forest complexity. Seasonal change also affected predation pressure, with foliage being a stronger attractant in spring, but also by presumable topography-driven study plot differences in sun exposure and humidity between rainy and dry seasons. Our study demonstrates that predation pressure is not simply a function of tree species richness or structure but is shaped by the interplay of structural elements, spatial scale, and seasonal dynamics along gradients of tree species richness and forest structure. The structural and seasonal effects are important to take into account when addressing how current and future biodiversity loss may change top-down control of herbivory and overall ecosystem functioning.

KEYWORDS

artificial caterpillar, forest structure, scale-dependence, season, top-down control, topography, tree species richness, vegetation density

1 Introduction

Globally declining biodiversity is altering ecosystem functions (Hooper et al., 2012), with a loss of plant diversity leading to declining herbivore and predator populations and altered trophic structures (Haddad et al., 2009; Wan et al., 2020). Higher plant species richness can lead to higher predator abundances and top-down suppression of arthropod herbivory, as demonstrated in agroecosystems and grasslands (Andow, 1991; Siemann et al., 1998; Barnes et al., 2020; but see, e.g., Koricheva et al., 2000; Harmon et al., 2003). This can be due to increased habitat amounts and complexity providing alternate food sources and a more stable prey supply over time, as posited by the "Enemies hypothesis" (Root, 1973). Relationships between plant species richness and higher trophic levels are generally less well explored in forests, with more evidence for the increase of predator abundance than predator activity (Stemmelen et al., 2022). This leaves the general role of tree species richness on actual predation pressure unresolved (Staab and Schuldt, 2020).

Although some studies have shown a positive effect of tree species richness on predation rates by arthropods (Leles et al., 2017) and birds (Muiruri et al., 2016; Nell et al., 2018), others have demonstrated that forest structure is a more important determinant, for example, for bird abundance and richness (Khanaposhtani et al., 2012; Mag and Ódor, 2015). Similar to the effects of increasing plant species richness, predation can increase with increasing vegetation complexity, as also shown in grasslands, through increased niche space, alternate and more abundant food sources, microclimate amelioration, and reduced intra-guild interactions among predators (Flaherty, 1969; Finke and Denno, 2002; Langellotto and Denno, 2004). However, negative effects of habitat complexity on predator and parasite efficiency can arise as well, for example via increased refuge availability for prey in more complex vegetation (Andow and Prokrym, 1990; Hawkins et al., 1993; Clark and Messina, 1998). Studies on the effect of vegetation complexity and density on predators in forests have shown, for example, positive effects on bird abundance and diversity (MacArthur and MacArthur, 1961; Khanaposhtani et al., 2012), spider abundances (Halaj et al., 1998; Halaj et al., 2000), and predation by arthropods (Schwab et al., 2021), but also negative effects on predation by birds and ants (Šipoš and Kindlmann, 2013). Notably, however, comparisons between studies of vegetation complexity tend to be difficult because of differences in the complexity measures (McCoy and Bell, 1991; Loke and Chisholm, 2022). Structural features might play a particularly important role in forest ecosystems because of the wide range of microhabitats in canopies (Wardhaugh et al., 2014), with highly promoted arthropod abundance, vegetation biomass, and structural complexity as compared to herbaceous/grassland vegetation (Lawton, 1983). The structural variation in forests can already differ within and between monocultures due to tree size, density, and species, but is generally higher in tree species mixtures because of interspecific differences in tree crown forms and diversity-driven plasticity of tree crowns (Pretzsch, 2014; Ali, 2019; Kunz et al., 2019).

The effects of plant species richness and vegetation structure on predator abundance are highly scale-dependent (Root, 1973; Russell, 1989; Staab and Schuldt, 2020), which may explain some of the variability in earlier results. Scale dependence has also been shown for the predation activity of birds (Muiruri et al., 2016) and arthropods (Schwab et al., 2021). In forests, besides the size of a plot, area effects already play an important role through tree sizes and vegetation density, as those form the plant surface area which, in turn, determines the predator–prey interaction zone (e.g., Erwin, 1983; Nakamura et al., 2017). A larger area can support greater numbers of species and higher abundances through species–area relationships brought about by an increase in resources, greater habitat variability within a larger area, and a lower likelihood of local extinctions due to larger population sizes (e.g., Connor and McCoy, 2001). Furthermore, small-scale habitat variation can then influence predation through selection of the hunting grounds based on cues from the vegetation (e.g., volatile compounds) (Heinrich and Collins, 1983; Mäntylä et al., 2008; Sam et al., 2015; see also review in Turlings and Erb, 2018) and increased visibility (Tschanz et al., 2005). The effects of vegetation structure on predation rates, in turn, have been found to be dependent on predator and prey densities (Riihimäki et al., 2006; Scheinin et al., 2012). Predators may aggregate at the highest prey densities (Hassell and May, 1974; Kareiva and Odell, 1987), and the movement of predators between habitats of varying prey densities can promote and stabilize predator populations and prevent prey resource depletion where prey densities are high but increase depletion where they are low (Holt, 1985; Pulliam, 1988; Polis et al., 1996). Thus, very low or high predator and prey abundances can make the effect of structural habitat components negligible (McCoy and Bell, 1991). The source–sink interactions between "component communities" (Root, 1973), which the structurally different patches can be seen as, are expected to become stronger the larger the predator population in the source (Pulliam, 1988), the greater the dispersal ability of the predators, and the closer the source and sink patches are to each other (Bianchi et al., 2010). Movement between patches is suggested to be the reason why the positive effects of vegetation diversity observed at small scales are negligible when they occur at larger scales (Bommarco and Banks, 2003). This negative scale dependence of plant species richness has been observed, for example, for predation by birds in forests (Muiruri et al., 2016). However, it remains largely unexplored in most studies of tree diversity–predation relationships.

A given habitat can also vary seasonally in being a source or sink for predators and prey (Pulliam, 1988). Prey abundance and predator activity are highest in early to mid-summer in temperate forests (e.g., Remmel et al., 2009). In the tropics, arthropod abundances are highest in the rainy season, or somewhat after with a delay due to development time, correlating with the flush of new leaves (Janzen, 1973; Wolda, 1978; Richards and Coley, 2007; Valtonen et al., 2013). As the foliage-eating prey are impacted by seasonal food availability (Wolda, 1978), the associated predators need to time their activity according to prey abundance (Janzen, 1973; Polis et al., 1996; Molleman et al., 2016), and as such, predation rates have been observed to peak during these periods (Richards and Windsor, 2007; Molleman et al., 2016). Caterpillar abundance was also observed to be highest in the late rainy season in temperate but seasonally rainy sub-tropical forests (in the same field site and year of the current study) (Anttonen et al., 2022). However, organisms at higher trophic levels are expected to be more susceptible to environmental conditions and able to respond to them based on higher mobility (Menge and Sutherland, 1987), and abiotic conditions can break down the positive correlation between predator and prey abundances (Richards and Windsor, 2007). The dry season can promote arthropod abundances in more humid habitats and cause mobile arthropods to shift from open sites to forests (Janzen, 1973; Richards and Windsor, 2007), where higher canopy cover, and also structurally more complex stands, have lower solar radiation, lower temperatures, and less variation in abiotic conditions (e.g., Breshears, 2006; Ehbrecht et al., 2017).

When looking into the small-scale dynamics of predation pressure, predator abundance and species richness are not necessarily the most accurate predictors due to the source–sink interactions of habitats and small-scale predator efficiency determinants, making direct measurements of predation rates necessary. Artificial caterpillars have proved an effective method for testing predation rates in various types of forests (e.g., Posa et al., 2007; Muiruri et al., 2016; Roslin et al., 2017), allowing reliable assignment of predation to broad taxonomic groups (Low et al., 2014). The method, however, does not necessarily cover the whole extent of predator taxa in the habitats due to a lack of prey movement and olfactory signals (Lövei and Ferrante, 2017; Zvereva and Kozlov, 2023). This approach, nevertheless, allows for efficient comparisons of how predation pressure is shaped by dynamics between patches of different quality, by scale dependence of tree species richness and forest structure, and by seasonal variation in abiotic conditions.

In this study, we tested how tree species richness at different spatial scales (local neighborhood vs. plot), forest structure, and season jointly affect predation pressure on artificial caterpillars in a forest biodiversity–ecosystem functioning experiment in subtropical China (BEF-China; Bruelheide et al., 2014). In this experiment, tree species richness per plot (~26 m × 26 m) was manipulated over a gradient from monoculture to 24-species mixtures. Forest structure was quantified using different approaches: measurements of basal area (BA) of focal and neighborhood trees, tree mortality-based estimates of open area, and terrestrial laser scanning (TLS). Because tree species richness is often expected to influence predation through changes in forest structure, we analyzed the data with and without TLS-derived variables. Additionally, we compared how well predation pressure is explained by the separate measures of tree species richness and forest structural variables to measures of overall vegetation complexity. Moreover, predation pressure may respond to very fine-scale features of vegetation and visibility as well as to larger-scale variables that define the area around the plot. For this reason, we included covariates of fine-scale surroundings around the artificial caterpillar (presence of leaves and branches), of topography (elevation, slope angle, and solar irradiance), and of plot grouping (as a proxy for environmental heterogeneity in the surrounding plots).

We hypothesized that: (1) increasing tree species richness and denser (and more complex) vegetation both increase attacks through a presumed increase in predator abundance and species richness; (2) predation pressure in small-scale habitats varies depending on the large-scale structure, such as visibility promoting attacks in overall denser vegetation. Also, a higher amount of branches at the immediate neighborhood scale is expected to increase attacks through predator aggregation within larger-scale areas where overall predator and prey densities are presumably lowest; (3) predation pressure is highest in the late rainy season and is promoted by new foliage in spring. Season was expected to interact further with vegetation structure and topography, with predation pressure shifting to more humid habitats during the dry season, such as those with a more closed canopy and topographically lower solar irradiance plots. Testing how the interplay between scales of forest structural variables within close neighborhoods affects predation pressure and how these variables are influenced by plant richness will aid in producing a more mechanistic view of the top-down regulation of arthropod herbivory.

2 Materials and methods

2.1 Study area and design

The experiment was conducted in the world's largest biodiversity–ecosystem functioning experiment (BEF-China) in sub-tropical China (Jiangxi province, 117° 54′ E, 29° 07′ N) (Bruelheide et al., 2014). The annual precipitation in the area is 1,821 mm, and the mean annual temperature is 16.7°C (Yang et al., 2013). The experimental site ("site A" of the BEF-China experiment) was planted in 2009 in a mountainous area, ranging from 105 m to 275 m above sea level (Yang et al., 2013), with an average slope of 27.5° (Bruelheide et al., 2014). The mountain slopes encircle a narrow wetland valley, where the lowest elevation plots are situated. The field site is 14.8 ha in size and consists of 268 plots placed in random order, of which 65 were used in this experiment. Each plot is 25.8 m × 25.8 m in size, which equals the Chinese traditional area unit of 1 mu. Each tree species combination is represented by five plots, of which four are grouped into one continuous unit, so-called "super-plots" (see Bruelheide et al., 2014). The tree replicates used in this study were divided between the 1 mu and 4 mu plots. See Supplementary Figure S1 for a map and an example picture of BEF-China site A and plot setup, and Bruelheide et al. (2014) and Huang et al. (2018) for further details.

Trees within the plots were planted in 20 rows and 20 columns with a 1.29 m distance from each other, in equal amounts per species, and placed in a random design. The tree planting setup followed a "broken stick" design, which halves the tree species richness between levels while keeping the composition otherwise constant, with tree species richness levels of 1, 2, 4, 8, 16, and 24 (Bruelheide et al., 2014). The 24-species mixture is an extra mixture on top of the richness gradient and was included to increase the number and spatial spread of the highest-richness tree replicates. The 24- and 16-species mixtures were combined into a single high species richness level in the analyses and renamed as a 16-species mixture. We used all tree species per plot for predation estimation up to the 16 species mixtures. Additionally, some *Castanopsis eyrei* Champ. Individuals were recognized to belong to *Castanopsis fargesii* Franch., increasing the total number of tree species in the experiment to 17. All tree species used in the experiment are listed in Supplementary Table S1.

We analyzed the data based on individual trees, but the focal trees within each tree species richness level were selected as mono- and heterospecific tree species pairs. This design was used to follow the set-up of Trogisch et al. (2021) in order to match the predation estimation with high accuracy with the TLS data examining the structural traits of the trees, for which the paired design was also used (Hildebrand et al., 2021) (see Section 2.3). In the paired design, the trees were selected from the plots at random, but with the requirement that they have either a mono- or heterospecific pair. Both trees were then used for predation estimation. All possible tree species pair combinations were used up to four-species mixtures, and these combinations were then replicated at higher richness levels. Additionally, only tree species pairs with nonoverlapping neighborhoods were selected. The paired design was accounted for with a random effects structure in the models (see Section 2.4).

Predation was estimated in four campaigns: autumn 2018 (August–September), spring (March–April), mid-summer (June), and late summer (August) 2019. The autumn 2018 campaign was set as the last season in analyses due to the campaign being conducted later in autumn than in 2019 (the campaign started on 26 August 2018 vs. 8 August 2019), with leaf senescence starting in the first trees in 2018 but not in 2019. The 2019 spring campaign began for most trees just prior to bud burst and ended when the trees were nearly in full leaf. Spring and mid-summer campaigns were conducted during the rainy season, and late summer and autumn campaigns in the dry season.

The number of tree replicates was 375 in spring, 383 in mid-summer, 380 in late summer, and 384 in autumn, with almost all tree individuals remaining the same between sampling campaigns. The number of trees sampled in total across all 17 species was 96, 113, 50, 74, and 62 for richness levels 1, 2, 4, 8, and 16, respectively, varying between one and 10 (mean = 4.3, SD = 2.4) replicates per species per richness level per campaign. The differences in tree replicate numbers are caused by the experimental design of Trogisch et al. (2021), which focuses on tree species pair interactions and promotes tree species replicate numbers in monocultures (six replicates per species) and two-species mixtures (nine replicates per species) over higher tree species richness levels (five replicates per species), and by variability in self-thinning between tree species in different richness levels. The plot-level tree species richness used in the analyses was based on the planting design but corrected for *Schima superba* Gardner & Champ.- *Rhus chinensis* Mill. two-species combinations, where no individuals of *R. chinensis* were alive and were therefore treated as monocultures. Additionally, the tree species richness was estimated for each tree neighborhood based on the eight closest potential neighbors.

2.2 Predation estimation

Production, placement, and checking of artificial caterpillars followed the general recommendations by Howe et al. (2009) and Low et al. (2014). The artificial caterpillars were made of green nontoxic and odorless modeling clay (Staedtler® Noris Club® Plasticine green), formed around an iron string, and placed by wrapping the string around branches (Supplementary Figures S2, S3). Caterpillars were ~5 cm long and ~0.5 cm wide, with small variations due to manual production. The artificial caterpillar size was within the range of real caterpillars observed at the field site. Six caterpillars were placed per tree in two groups of three caterpillars each. Caterpillars within one group were placed horizontally no more than 50 cm apart from the central caterpillar of the group, with as little vertical difference as possible. The two caterpillar groups were placed at different height levels as long as the tree height allowed, with an average lower group height of 1.4 m (SD = 0.61) and a higher group height of 2.8 m (SD = 0.85). The height of the caterpillar group was recorded with half a meter accuracy, and this distance from the ground was included in the analyses to account for potentially different movement modes between predator groups. The caterpillars were placed primarily within 20 cm of leaves on branches. If branches with leaves were not within reach, the caterpillar was placed on a leafless branch or, if no branches were within reach, on the trunk of the tree, with a preference for leaves in close proximity (tiny branches). Thus, *placement on the trunk* indicates increased visibility of the caterpillars due to the absence of branches on focal trees in close proximity to the caterpillars. The location (branch or trunk) and *presence of leaves* were marked down for each caterpillar.

Each campaign consisted of three rounds, namely placing caterpillars and checking two times. Damaged caterpillars after the first round were either replaced or fixed for the second round. Rainy weather caused delays to the checking schedule due to hazardous conditions, and water droplets on the caterpillars, making small bite marks difficult to detect. Caterpillar placement between consecutive days was divided into different parts of the field site, which ensured that no area with respect to topography was systematically checked later in the season or accumulated disproportionate rain delays. In the case of rain delays, checking was intensified and divided between the delayed and the original schedule caterpillars. In a few cases, a certain tree was accidentally ignored during the intended checking date, leading to increased checking intervals. The average checking period was 8.4 (SD = 1.1), 9.1 (SD = 1.8), 7 (SD = 0.1), and 7.8 (SD = 0.9) days in spring, mid-summer, late summer, and autumn, respectively. The exact length of the checking period for each caterpillar was included in the statistical analyses.

The attack marks were identified to the following broad taxonomic categories: arthropod (Supplementary Figure S2A, C), bird (Supplementary Figures S3A–D), mammal (Supplementary Figures S3E, F) (Low et al., 2014), and snail (Supplementary Figure S2B) (M. Volf, personal communication). The mammal category was subdivided into rodent (Supplementary Figure S3E) and insectivore (likely a bat) (Supplementary Figure S3F) categories. Arthropod attacks were subdivided into two categories by visual observation of clearly distinguishable types of damage. Piercing mandible marks of varying width were considered to have been made by predators (Supplementary Figure S2A). Possible sting marks by Hymenoptera (Low et al., 2014) or Heteroptera were challenging to reliably separate from piercing mandible marks and were, therefore, included in the arthropod predator category. Shallow scraping damage was recognized to be made by grasshoppers in the Caelifera suborder (Supplementary Figure S2C) by frequent observations of them being in contact with the caterpillars and leaving similar damage on thicker tree leaves (Supplementary Figure S2D). This damage could lead to nearly the whole caterpillar being eaten and plasticine frass pellets being excreted on the spot. Obscure bite marks were checked with ×10 and ×20 field magnifiers or photographed for later assessment. Due to checking bite marks in the field, very small arthropod bite marks requiring microscopic examination were likely not noticed (Howe et al., 2009). All caterpillars were checked by the same person, and attacks were recorded as presence–absence.

In total, we placed 20,508 artificial caterpillars. Caterpillars with unrecognizable attack marks (12), being damaged by leaves, etc., or falling from the tree (488) were removed from the data. Furthermore, 2,292 caterpillar checks were removed because of missing structural trait measurements, making the final amount used in analyses 17,728 caterpillars (note that exclusions slightly overlap). Additionally, from the caterpillars kept in the data, attacks by bats were not analyzed because of only a few observations (5). Also, attacks by grasshoppers, despite their commonness (see Section 3), and snails (19 observations), were not analyzed as they represent herbivory.

2.3 Vegetation structure and topography

We aimed to test how forest structure affects predation probability in the immediate neighborhood and at the plot level, and we used several measures to describe the forest surroundings around the artificial caterpillars. The diameter at breast height was measured for the *focal trees* and the eight potential trees in the immediate *neighborhood* and transformed to BA. Although the *neighborhood BA* was estimated only from the immediate neighborhood of the focal trees, it is expected to reflect conditions of the overall plot because of the observed uniformity in low tree species richness plots and the correlation of neighborhood tree species richness on plot tree productivity at high richness levels (Fichtner et al., 2017). Based on BA, 25% of the trees reached >10 m in height at the time of the experiment (Schnabel et al., 2021). Few trees were smaller than 1.3 m, and the DBH was marked down to 0.5 cm for these trees. The *open area* in the neighborhood represents gaps in the canopy and was estimated by summing up the ground surface areas left open by dead trees around a focal tree. The area assigned to each dead tree was calculated on the basis of the systematic planting pattern and covers ~1.66 m^2. Continuous open areas (i.e., ≥ 2 dead trees next to each other) were weighed higher to account for space filling by foliage from neighboring trees, which was achieved by dividing the total open area by the number of gaps left by dead trees.

Further information on vegetation structure was derived from terrestrial laser scanning (TLS) data of the local neighborhood of each focal tree and the overall plot, conducted in February–April 2019 (Hildebrand et al., 2021). At both spatial scales, we aimed to distinguish the effects of the density of vegetation elements and their vertical distribution by using a set of clearly distinguishable structural measures. Neighborhood branch density was estimated as the number of branch-occupied voxels (defining an observed point in three-dimensional space) with a 5 cm edge per 50 cm vertical layer in a 3 m radius for each caterpillar placement height (*voxels per layer*). Neighborhood canopy packing was estimated as the *vertical Gini* index of the canopy voxel vertical distribution in a 3 m radius, where lower values indicate a more equal distribution (Ehbrecht et al., 2017) of biomass and thus a less densely packed canopy. At the plot level, the density of vegetation elements was addressed using the mean fractal dimension (*MeanFrac*) index (Ehbrecht et al., 2017) as a proxy. MeanFrac is a scale-independent measure that increases with a higher perimeter-area ratio, defined to measure structural complexity, and it roughly responds to the space-filling capacity of an object independently of area (Loke and Chisholm, 2022) and, thus, to the density of vegetation elements (Ehbrecht et al., 2017; Zemp et al., 2019). As a scale-independent measure, stands with a high density of branches from small trees can gain the same or higher MeanFrac values than stands with large trees and a higher amount of open space (Ehbrecht et al., 2017; Zemp et al., 2019), which ensures that when using MeanFrac as a proxy for vegetation density, it is not driven directly by biomass. The canopy vertical stratification of the plot was quantified using the effective number of layers (*ENL*) index (Ehbrecht et al., 2016). For calculating ENL, the voxel point cloud was subdivided into 25 cm slices, the proportion of filled voxels in each slice was quantified, and the inverse Simpson Index was calculated between these layers. ENL values increase with increasing tree height and a more even vertical distribution of space occupation. Thus, the lowest ENL values occurred in the small amounts of plots with very small trees with practically no canopy layer, but the variation of ENL highly increased when trees were larger (Supplementary Figure S4).

Additionally, in comparison to using MeanFrac and ENL separately, we reduced the plot-level structural variables to a single measure of stand structural complexity index (*SSCI*), which is MeanFrac scaled by ENL (Ehbrecht et al., 2017). For clarity between measures, we refer to MeanFrac as vegetation density and SSCI as canopy complexity. MeanFrac, ENL, and SSCI were aligned relative to the slope angle (see Perles-Garcia et al., 2021). Forest structure can vary based on tree species richness (Williams et al., 2017; Kunz et al., 2019), including canopy vertical stratification, as shown at the BEF-China field site (Perles-Garcia et al., 2021). However, the correlations between tree species richness and structural variables in our study were low enough to allow them to be used in the same GLME models due to the high number of tree species with a wide range in crown forms, growth, and mortality rates. We further reduced tree species richness and all plot and neighborhood-level structural variables, i.e., neighborhood tree species richness, focal BA, neighborhood BA, open area in the neighborhood, voxels per layer, vertical Gini, MeanFrac, and ENL with principal components analysis (all variables scaled) for a measure of overall forest complexity using the function "princomp" in the package "vegan" (Oksanen et al., 2022). The scores of the first three principal components (PC), which together explained ~64% cumulative variance (Supplementary Table S2A), were selected for further analysis. The highest loadings on PC1 were ENL and neighborhood BA, but all other variables also contributed (Supplementary Table S2B). The highest loadings on PC2 were voxels per layer, MeanFrac, and vertical Gini, and on PC3 focal BA, but also with further smaller contributions by other variables.

Plot replicates were divided between 1 mu and 4 mu plots. The smaller plots had a more variable plot neighborhood, as all their eight surrounding plots had a different tree species composition compared to the focal plot, while tree species composition in a 1 mu super-plot was the same as in three of the neighboring plots. Thus, increasing *plot size* (1 mu vs. 4 mu) can be considered a proxy for a lower variation in tree species diversity and vegetation structure in the more distant neighborhood. Topographical variables, *elevation* (measured by hypsometer and interpolation from a map using GIS), *slope angle* (GIS), and *solar irradiance* (GIS, MWh/m^2) (Bruelheide et al., 2013), were also included to account for the differences in the environmental conditions caused by plot placement along slope positions. Slope angle also influences canopy vertical structure, which is not completely addressed by ENL, as the canopy follows a vertical gradient along the slope irrespective of the stratification along the trunks (Lang et al., 2010).

2.4 Statistical analysis

Arthropod predator, bird, and rodent attacks were analyzed using generalized linear mixed-effects models (glmmTMB) (Brooks et al., 2017) (see Supplementary Material 2 for the analysis code). The response variable of being attacked was analyzed as binary using Bernoulli distribution with complementary log-log transformation (link function "cloglog") in R v 4.2.2 environment (R Core Team, 2022). Random factors used in the models were focal tree species identity and focal trees nested within the plot. Tree species pair identity nested within the plot was tested in comparison to the focal tree, with the models compared by their AIC values.

Before including fixed factors, low collinearity between them was ensured by estimating their internal Spearman correlations (all variables: $r < 0.7$; see Supplementary Figure S5). In addition, variance inflation was estimated for all fixed factors and their interactions (only variables with vif < 5 were included in the models) with package "performance" (Lüdecke et al., 2021). Further model validations using predicted and observed estimates and residuals were done using the "DHARMa" package (Hartig, 2022). In order to focus on the most important estimates, interactions of fixed factors, but not the covariates, were reduced based on model AIC using the function "drop1". Fixed factors in all models were season (as an ordinal variable representing shift from early to late growing season and transition from rainy to dry season), tree species richness, neighborhood- and focal-tree BA, open area in the neighborhood, plot size, plot topography, covariates describing the immediate placement conditions, and checking schedule-related covariates: checking round and the number of days the caterpillar was positioned on the tree (delays caused by rainy days). Focal and neighborhood BA were square root-transformed for increased linearity in all models. The presence of leaves, placement on a branch or trunk, and checking round were included in the models as factorials, and all other variables were scaled by subtracting the mean and dividing by the standard deviation. The effect of tree species richness was tested by comparing the AIC values of two different models, one using plot-level richness and the other using the richness of the eight closest potential neighbors. The relationship of tree species richness with structural metrics was further tested by comparing models that either included only tree species richness or additionally included the TLS-derived structural variables. Furthermore, two different models were compared that used either SSCI or MeanFrac and ENL. Finally, due to moderate collinearity between tree species richness and ENL (Spearman $r = 0.47$ and 0.45 with plot and neighborhood tree species richness, respectively) and between voxels per layer and MeanFrac (Spearman $r = 0.6$), neighborhood tree species richness and MeanFrac were removed from the reduced arthropod predator model using TLS-derived structural variables in order to see if this has strong effects on the respective moderately collinear covariates.

Furthermore, several interactions between explanatory variables were tested. After ensuring low vif values, for arthropod predator models, these were as follows:

- Interactions of tree species richness with focal and neighborhood tree sizes, voxels per layer, vertical Gini, and MeanFrac.
- Interactions of plot, neighborhood, and fine-scale placement variables. Interactions of voxels per layer and vertical Gini were included with MeanFrac, and interactions of the presence of leaves were included with voxels per layer and ENL but not with MeanFrac due to high vif values. The interaction of MeanFrac and ENL was included with focal and neighborhood tree sizes. The effect that placement on the trunk may have on visibility due to the absence of branches in close proximity to the artificial caterpillar was further tested with interaction with focal and neighborhood tree sizes, all TLS-derived plot- and neighborhood structural variables (that describe the canopy structure surrounding the patches of increased visibility), open area in the neighborhood, and placement height. The interaction of open area in the neighborhood was further included with all plot and neighborhood TLS-derived structural variables, neighborhood tree size, and placement height.
- In the comparative model using SSCI, the same interactions were included as with MeanFrac and ENL except for interactions of vertical Gini and placement on branch or trunk with SSCI and voxels per layer with the presence of leaves, due to increased vif values.
- The interactions of plot size with tree species richness, neighborhood BA, and TLS-derived plot-level structural variables were included. The plot size–tree species richness relationship was also included with neighborhood tree species richness, as it was highly correlated with the plot-level tree species richness (Spearman $r = 0.86$).
- Seasonal differences in attack probability were tested with tree species richness, all TLS-derived plot and neighborhood structural variables, the presence of leaves, all topographical variables, and checking round and number of days on the tree.

Due to the low number of attacks, bird and rodent models were analyzed with simplified models in order to avoid overfitting and to keep the results generalizable. All the same interactions with season and plot size were used as with arthropod predators, except in the bird model, where the interaction of season and presence of leaves was dropped due to high vif values. Otherwise, interactions were limited to testing the effects of plot-level vegetation density (MeanFrac) and canopy complexity (SSCI). These included tree species richness, focal and neighborhood tree sizes, voxels per layer, vertical Gini, open area in the neighborhood, placement height, presence of leaves, and placement on branch or trunk, except for bird models where the interaction of placement on branch or trunk with SSCI was dropped due to a high vif value.

In the models with neighborhood tree species richness and forest structure reduced to principal components, interactions with PC1, PC2, and PC3 were included with each other, plot size, and season for all predator groups. Additionally, for arthropod predators, interactions of PC1, PC2, and PC3 were included with placement on the branch or trunk, and PC1 and PC3 with the presence of leaves, but not PC2, in order to reduce vif values. Interactions between checking round, days on the tree, and topographical variables were included with season for all predator groups, similar to other models.

3 Results

Overall, attacks by arthropods were much more frequent than those by any vertebrate predator. Predatory arthropod attack rates per season were 5.2% in spring, 19.8% in mid-summer, 2.4% in late summer, and 9.6% in autumn. Bird and rodent attacks were systematically low. Bird attacks increased toward the later seasons, with per-season values of 0.2% in spring, 0.7% in mid-summer, 1.8% in late summer, and 1.6% in autumn. Rodent attacks decreased toward the later seasons, with per-season values of 0.9% in spring, 1.0% in mid-summer, 0.6% in late summer, and 0.2% in autumn. Additionally, grasshopper attack rates per season were 2.0% in spring, 5.6% in mid-summer, 51.4% in late summer, and 17.6% in autumn.

The following are the results of models including neighborhood tree species richness and TLS-derived variables as fixed factors and using focal tree individuals as random factors (Table 1) for each predator group (see Section 3.5 for comparison to alternative analyses).

3.1 Plot size

Neighborhood tree species richness did not show a direct significant relationship with any of the predator groups (after including TLS-derived variables), but arthropod predator attacks increased in larger plots with high tree species richness (Figure 1A; Table 1). In contrast, arthropod predator attacks were promoted at low vertical stratification (ENL) (Figure 1B) in 1 mu plots, and a similar, although nonsignificant ($0.1 < p > 0.05$) relationship was observed with vegetation density (MeanFrac) (Figure 1C). Larger plot sizes had a negative effect on rodent attacks, and attack probability was higher in smaller plots of low vegetation density (Figure 1D).

3.2 Forest structure

Neighborhood tree species richness showed a positive effect on arthropod predator attacks in more densely branched neighborhoods (voxels per layer) (Figure 2A; Table 1). In addition, more densely branched neighborhoods also had a positive effect on arthropod predator attacks at low plot-level vegetation density and a negative effect at high vegetation density (Figure 2B). For bird attacks, no significant direct influence was observed with plot vegetation density and open area in the neighborhood, but the attacks were promoted when there was more open area in the

TABLE 1 Summary of generalized linear mixed effects model results for arthropod predator, bird, and rodent attacks, using neighborhood tree species richness and TLS-derived structural variables (for the model without TLS variables, see Supplementary Table S3); MeanFrac and ENL are used separately in the models instead of SSCI (for the model including SSCI, see Supplementary Table S4).

	Arthropod predator attacks (AIC = 10,161.0)			Bird attacks (AIC = 1,971.3)			Rodent attacks (AIC = 1,328.6)		
	Estimate ± Std. error	*z*	Pr (>|*z*|)	Estimate ± Std. error	*z*	Pr (>|*z*|)	Estimate ± Std. error	*z*	Pr (>|*z*|)
Intercept	−2.49 ± 0.08	−29.5	**<0.001**	−5.38 ± 0.24	−22.3	**<0.001**	−5.89 ± 0.31	−19.1	**<0.001**
Tree richness	0.08 ± 0.05	1.7	*0.083*	−0.23 ± 0.17	−1.4	0.171	−0.19 ± 0.18	−1.1	0.278
Plot size	−0.06 ± 0.04	−1.6	0.118	0.03 ± 0.10	0.3	0.769	−0.48 ± 0.15	−3.1	**0.002**
Plot size: tree richness	0.10 ± 0.04	2.3	**0.023**	0.19 ± 0.11	1.7	*0.091*	–	–	–
ENL	0.12 ± 0.07	1.8	*0.076*	−0.50 ± 0.16	−3.1	**0.002**	−0.12 ± 0.21	−0.6	0.558
Plot size: ENL	−0.11 ± 0.05	−2.1	**0.032**	–	–	–	–	–	–
MeanFrac	0.04 ± 0.05	0.8	0.442	0.15 ± 0.13	1.2	0.224	0.07 ± 0.21	0.3	0.733
Plot size: MeanFrac	−0.08 ± 0.05	−1.8	*0.075*	–	–	–	0.38 ± 0.16	2.4	**0.017**
Leaves present	0.30 ± 0.07	4.2	**<0.001**	0.09 ± 0.20	0.4	0.663	−0.03 ± 0.24	−0.1	0.893
Leaves present: ENL	−0.18 ± 0.07	−2.7	**0.007**	NA	NA	NA	NA	NA	NA
Open area	0.01 ± 0.04	0.3	0.746	0.01 ± 0.10	0.1	0.891	0.15 ± 0.12	1.2	0.220
MeanFrac: open area	–	–	–	0.25 ± 0.11	2.3	**0.024**	–	–	–
Voxels per layer	0.07 ± 0.04	1.7	*0.087*	0.01 ± 0.12	0.1	0.935	0.23 ± 0.17	1.4	0.176
Tree richness: voxels per layer	0.11 ± 0.04	2.8	**0.005**	NA	NA	NA	NA	NA	NA
MeanFrac: voxels per layer	−0.11 ± 0.04	−2.5	**0.011**	–	–	–	–	–	–
Placement height	0.16 ± 0.03	5.4	**<0.001**	0.08 ± 0.09	0.9	0.353	−0.64 ± 0.13	−5.0	**<0.001**
Placement on trunk	−0.02 ± 0.10	−0.2	0.841	−0.49 ± 0.34	−1.5	0.145	0.10 ± 0.33	0.3	0.771
Placement on trunk: placement height	0.13 ± 0.08	1.7	*0.084*	NA	NA	NA	NA	NA	NA
Neighborhood BA	−0.05 ± 0.05	−1.0	0.312	−0.10 ± 0.13	−0.8	0.451	−0.14 ± 0.16	−0.9	0.367
Placement on trunk: neighborhood BA	−0.25 ± 0.09	−2.7	**0.007**	NA	NA	NA	NA	NA	NA
Focal tree BA	0.08 ± 0.04	2.0	**0.045**	0.09 ± 0.11	0.8	0.403	0.10 ± 0.13	0.8	0.452
Vertical Gini	0.10 ± 0.04	2.4	**0.016**	0.15 ± 0.10	1.5	0.130	−0.09 ± 0.13	−0.7	0.494
Season	0.30 ± 0.05	5.6	**<0.001**	0.76 ± 0.11	6.6	**<0.001**	−0.29 ± 0.11	−2.5	**0.012**
Checking round	−0.16 ± 0.06	−2.9	**0.004**	−0.37 ± 0.15	−2.5	**0.012**	−0.53 ± 0.19	−2.8	**0.006**
Season: checking round	−0.35 ± 0.05	−6.5	**<0.001**	–	–	–	–	–	–
Days on tree	0.55 ± 0.03	20.1	**<0.001**	−0.08 ± 0.09	−0.9	0.347	0.13 ± 0.09	1.4	0.162
Season: days on tree	0.53 ± 0.04	13.8	**<0.001**	–	–	–	–	–	–
Season: tree richness	−0.05 ± 0.03	−1.7	*0.083*	0.22 ± 0.13	1.7	*0.091*	–	–	–
Season: ENL	−0.09 ± 0.03	−2.9	**0.004**	0.31 ± 0.11	2.8	**0.005**	–	–	–
Season: meanFrac	−0.06 ± 0.03	−1.8	*0.079*	–	–	–	−0.31 ± 0.12	−2.7	**0.007**
Season: voxels per layer	0.06 ± 0.03	2.0	**0.045**	–	–	–	–	–	–
Season: leaves present	−0.20 ± 0.06	−3.7	**<0.001**	NA	NA	NA	–	–	–
Slope angle	−0.08 ± 0.05	−1.6	0.105	0.11 ± 0.15	0.8	0.448	0.15 ± 0.20	0.7	0.463
Season: slope angle	–	–	–	−0.21 ± 0.10	−2.0	**0.047**	−0.38 ± 0.14	−2.8	**0.005**

(Continued)

TABLE 1 Continued

	Arthropod predator attacks (AIC = 10,161.0)			Bird attacks (AIC = 1,971.3)			Rodent attacks (AIC = 1,328.6)		
	Estimate ± Std. error	*z*	Pr (>|*z*|)	Estimate ± Std. error	*z*	Pr (>|*z*|)	Estimate ± Std. error	*z*	Pr (>|*z*|)
Elevation	−0.07 ± 0.05	−1.5	0.124	−0.21 ± 0.12	−1.7	*0.085*	−0.20 ± 0.17	−1.2	0.247
Season: elevation	−0.10 ± 0.03	−3.6	**<0.001**	–	–	–	–	–	–
Solar irradiance	−0.01 ± 0.05	−0.1	0.908	−0.07 ± 0.12	−0.6	0.559	−0.02 ± 0.18	−0.1	0.919
Season: solar irradiance	−0.12 ± 0.03	−4.2	**<0.001**	−0.24 ± 0.09	−2.7	**0.006**	−0.30 ± 0.12	−2.5	**0.013**

Standardized parameter estimates (with standard errors, z, and *p*-values) are shown for explanatory variables. AIC values are given for comparison to alternative models not using TLS data or using SSCI. Values in bold signify $p \leq 0.05$ and in italics $p \leq 0.1$. "–" means that the variable in question was not retained in the best AIC-based model for that predator group, and "NA" means the variable was not included in the model. The number of artificial caterpillars for which predation was estimated as 17,728 for all predator groups.

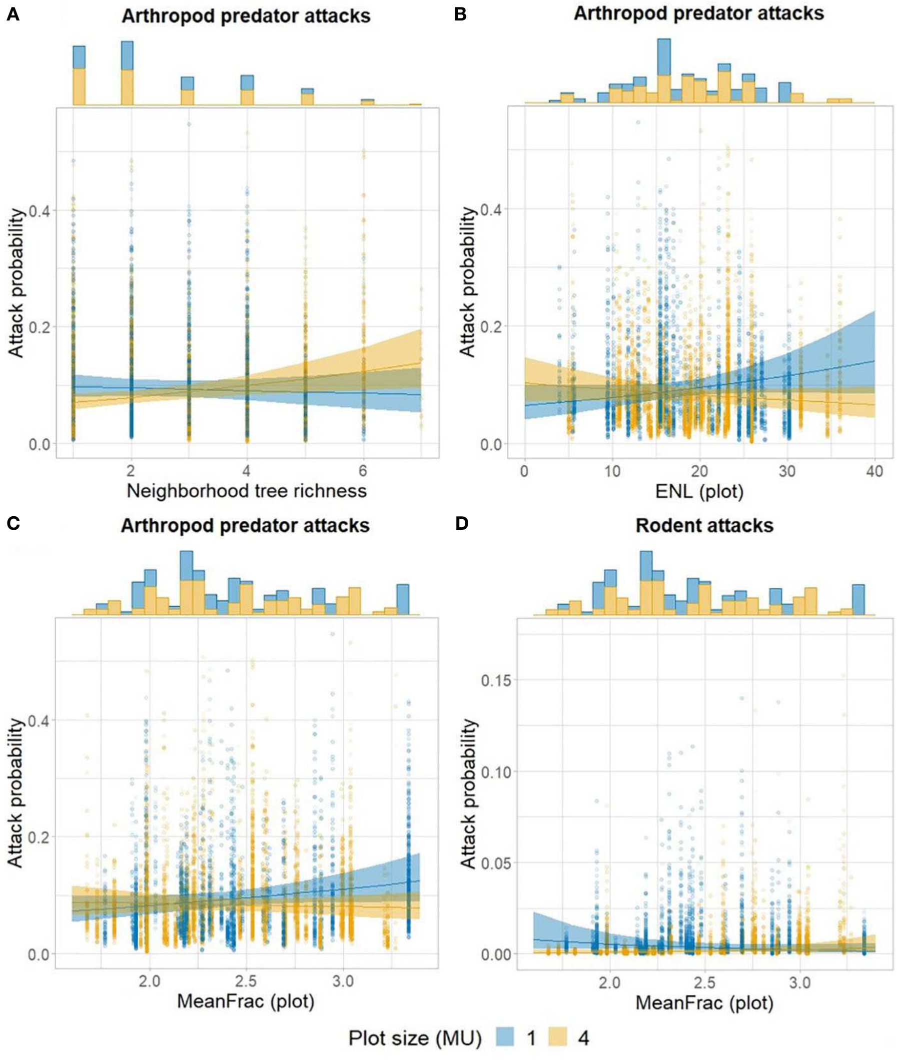

FIGURE 1
Attack probability as a function of plot size (1 vs. 4 mu) and **(A)** neighborhood tree species richness, **(B)** ENL, or **(C, D)** MeanFrac. In **(D)**, 7 data points between *y*-axis values 0.175 and 0.33 were removed for visual purposes from the point column with the highest values. Points show fitted values, shaded areas the 95% confidence intervals, and histograms the amount of observed data points per *x*-axis levels.

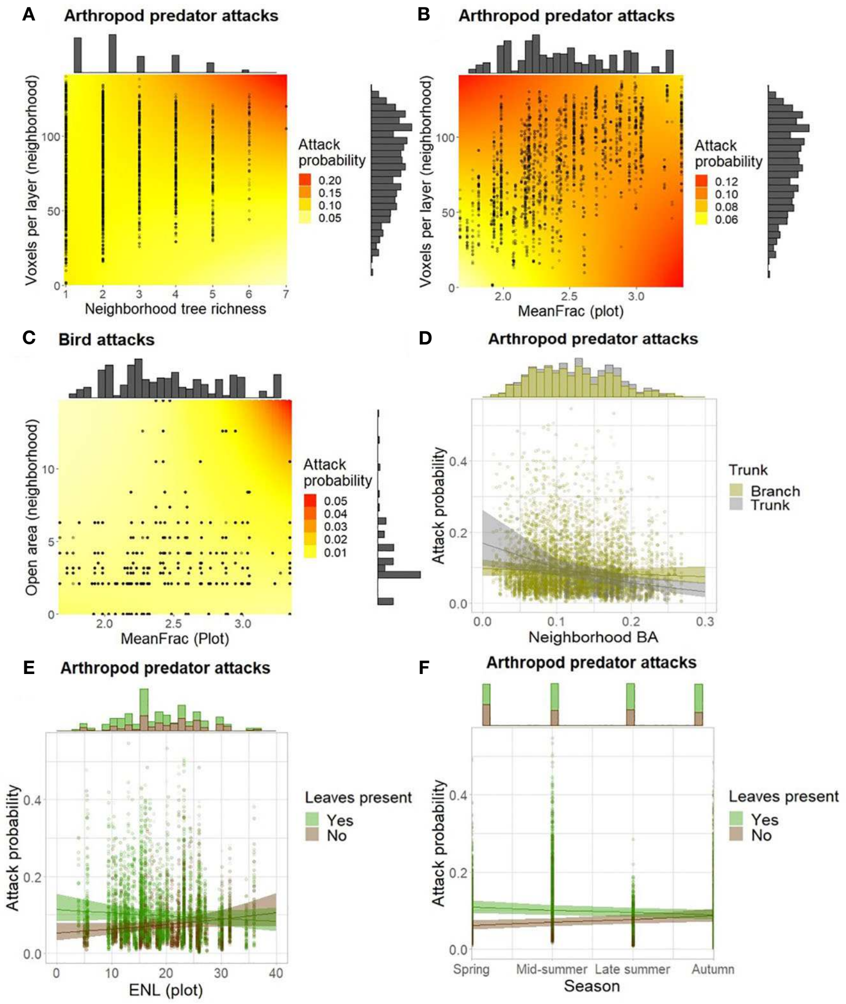

FIGURE 2
Attack probability as a function of **(A)** voxels per layer and neighborhood tree species; **(B)** voxels per layer and MeanFrac; **(C)** MeanFrac and open area in the neighborhood; **(D)** placement on trunk or branch and neighborhood BA; and the presence of leaves in close proximity of caterpillars and **(E)** ENL or **(F)** season. In **(A–C)**, colors represent the estimated change in attack probability and colors represent the estimated change in attack probability and points the observed values. In plots **(D, F)**, points show fitted values and shaded areas the 95% confidence intervals. Histograms show the amount of observed data points per axis level.

high vegetation density neighborhoods (Figure 2C). Arthropod predator attacks were more common on larger trees (focal tree BA), and additionally, attacks were more likely when there were no branches close to the caterpillars (placement on trunk instead of branch) and the surrounding neighborhood trees were smaller, but less likely when the neighborhood trees were large (Figure 2D). Higher placement heights had a positive effect on arthropod predator attacks, whereas rodent attacks were more frequent with lower placement heights. A canopy with fewer vertical layers promoted bird attacks at the plot level. The more frequent arthropod predator attacks when leaves were present in the immediate surroundings were also further promoted in less vertically stratified plots (Figure 2E). Additionally, a more densely packed canopy at the neighborhood level (vertical Gini) had a positive effect on arthropod predator attacks.

3.3 Seasonal effects

Arthropod predator and rodent attacks were highest in spring, whereas bird attacks increased toward autumn. Arthropod predator attacks were promoted in spring when leaves were present in the immediate surroundings of the caterpillars (Figure 2). Higher canopy vertical stratification had a positive effect on arthropod predator attacks in spring, but the relationship turned negative in autumn (Figure 3A). Bird attacks were instead highest at less vertically stratified plots except in autumn, when they were systematically high across the ENL value range (Figure 3B). A lower amount of branches in the local neighborhood had a negative effect on arthropod predator attacks toward autumn (Figure 3C). Rodent attacks were promoted in denser vegetation plots in spring (Figure 3D), and a similar but nonsignificant ($0.1 < p > 0.05$)

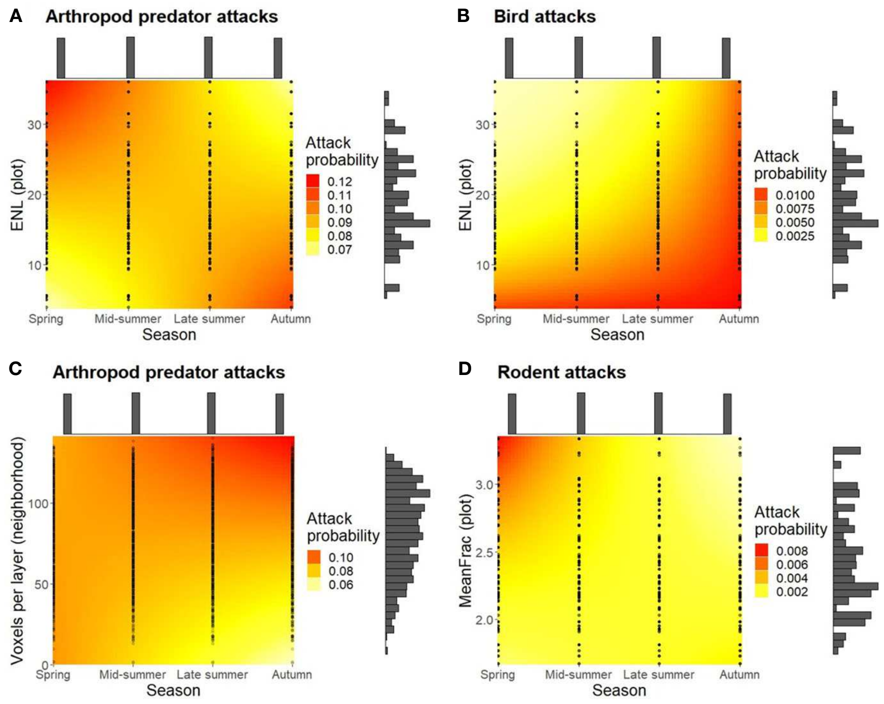

FIGURE 3
Attack probability as a function of season and **(A, B)** ENL, **(C)** voxels per layer, or **(D)** MeanFrac. Colors represent the estimated change in attack probability, points the observed values, and histograms the amount of observed data points per axis level.

positive trend with vegetation density was observed with arthropod predators (Figure 2F).

Plots with lower solar irradiance had a higher attack probability with all predator groups in the dry season toward autumn (Figures 4A–C), but high solar irradiance had an equally high effect on rodent attacks, with a positive trend also for arthropod predator attacks in spring. Similarly, plots at low elevation promoted arthropod predator attacks in the dry season, with a weaker positive trend in high elevation plots observed in spring (Figure 4D). In addition, lower slope angles promoted bird attacks in autumn (Figure 4E) and higher slope angles promoted rodent attacks in spring (Figure 4F).

3.4 Checking schedule

Attacks were less frequent with all predator groups in the second checking round, but this effect varied seasonally for arthropod predators, with a positive effect of the later checking round in spring turning negative toward autumn (Supplementary Figure S9A). The delays caused by rainy days led to a significant increase in attacks by arthropod predators but not by birds and rodents. However, this increase was strong only during the dry season (Supplementary Figure S9B).

3.5 Model comparisons

Comparison of models with tree species richness at the neighborhood level instead of the plot level revealed that neighborhood tree species richness led to clearly improved models for arthropod predators and birds ($\Delta AIC > 2$), but for rodents the improvement was small ($\Delta AIC = 1.1$). Models without terrestrial laser scanning (TLS)-derived structural variables (Table 1) showed higher estimates of neighborhood tree species richness and neighborhood BA (Table 1; Supplementary Table S3), whereas in the models with TLS-derived variables, the ENL showed similar relationships with stronger estimates (see Supplementary Figure S6 for seasonal neighborhood tree species richness relationship for arthropod predators). Removing tree species richness from the arthropod predator model using TLS-derived structural variables showed a sign of missing covariates, with the interaction of plot size with ENL becoming weak (results not shown). Thus, because of the moderate collinearity of ENL with neighborhood tree species richness (Spearman $r = 0.45$; Supplementary Figure S5), which varied in strength between tree species (Supplementary Figure S7) and neighborhood BA (Spearman $r = 0.54$), the results of these variables need to be interpreted in comparison to each other. Instead, removing MeanFrac from the arthropod predator TLS model had fairly small effects on the estimates of voxels per layer despite their moderately high collinearity (Spearman $r = 0.60$), with the direct effect of voxels per layer becoming significantly positive and the interaction of voxels per layer with season becoming weaker (results not shown), due to the lack of the wider-scale vegetation density covariate with an opposite seasonal trend. The inclusion of TLS variables affected also estimates of slope angle due to slope angle and ENL demonstrating different aspects of canopy vertical

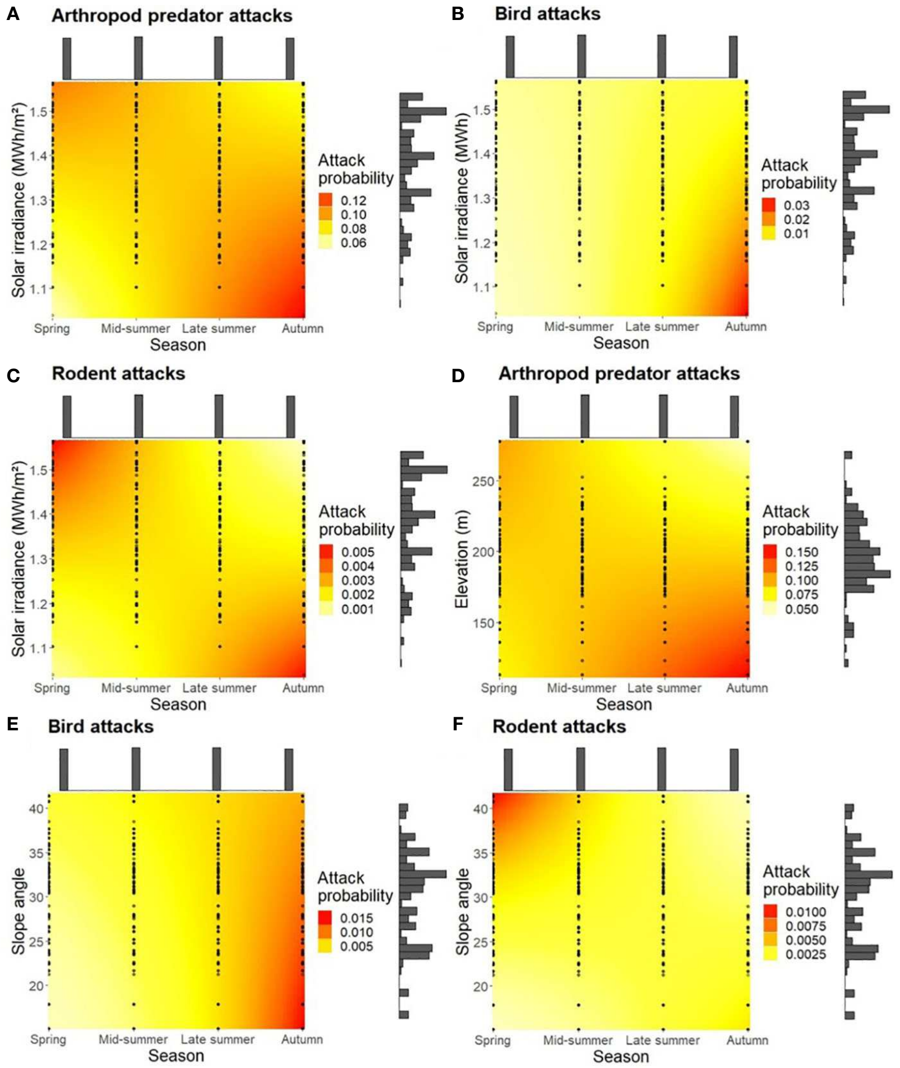

FIGURE 4
Attack probability as a function of season and **(A–C)** solar irradiance, **(D)** elevation, or **(E, F)** slope angle. Colors represent the estimated change in attack probability, points the observed values, and histograms the amount of observed data points per axis level.

structure, with only low collinearity between them (Spearman $r = 0.17$). Using the focal tree as a random factor instead of tree species pair identity also improved the arthropod predator and bird models (ΔAIC > 2; results not shown), but in the case of rodents, the improvement was fairly small (ΔAIC = 1).

Simplifying the plot-level forest structure to SSCI (Supplementary Table S4) instead of using MeanFrac and ENL (Table 1) separately led to reduced information value (ΔAIC > 2; see Table 1 and Supplementary Table S4 for the exact AIC scores) of arthropod predator and bird models, as estimates of SSCI and its interactions were weaker than with MeanFrac and ENL. However, in the case of rodents, where otherwise only MeanFrac from the structural measurements showed a strong relationship with the likelihood of a caterpillar being attacked, the change in AIC was marginally in favor of SSCI (ΔAIC = 0.3).

Simplifying tree species richness and forest structure to PC scores offered a robust outlook on the effects of forest overall complexity on predation, with none of the PCs explaining predation directly for arthropod predators, but PC1 having a negative effect on predation by birds and rodents, and PC3 having a nonsignificant ($0.1 < p > 0.05$) negative trend on birds (Supplementary Table S5). The PC1, whose loadings were affected by multiple variables but most strongly by neighborhood BA and ENL, and focal BA-driven PC3 interacted with the season in the case of arthropod predators and birds, and vegetation density measure-driven PC2 in the case of rodents. The PC1 and PC2 also had significant interaction in the case of arthropod predators. The PC-based analysis offered clearly poorer information value compared to using structural measures separately for arthropod predators and rodents (ΔAIC > 2; see Table 1 and Supplementary Table S5 for the exact AIC scores), whereas the difference was marginal for birds (ΔAIC = 0.1). Notably, interactions with plot size and very fine-scale variables of attraction and visibility (presence of leaves and branches) in PC-based models were weak and not retained in the reduced models, in contrast to models using structural measures separately.

4 Discussion

Our results demonstrate that predation by arthropods and vertebrates is influenced interactively by tree species richness and various forest structural features at different spatial scales, from the plot level to the immediate vicinity of the artificial caterpillars. In addition, forest structure and topography affected the predation pressure seasonally. Furthermore, using separate measures of forest structure instead of overall measures of complexity provided higher information value in the GLME models. Particularly, the specific spatial-scale relatedness of variables became obscured with complexity measures. Our results, thus, emphasize that predation pressure is not a simple one-factorial function of tree species richness or any specific forest structural metric and that understanding the regulation of top-down control in forests requires closer attention to scale dependency and seasonal dynamics.

Predation by arthropods was higher than by vertebrates, as often shown in studies with the same methods (e.g., Sam et al., 2015; Leles et al., 2017; Roslin et al., 2017; but see Poch and Simonetti, 2013; Yang et al., 2018). Yet, we restrict the comparisons here to only among predator groups, as the likelihood of attacking artificial caterpillars might vary between predator taxa (Zvereva and Kozlov, 2023). Birds are well known to be important predators of caterpillars, and rodents have been reported as an important predator group of arthropods in agroecosystems (Tschumi et al., 2018) and have also been observed to attack artificial caterpillars placed on trees (e.g., Posa et al., 2007). However, it needs to be noted that the estimated attack probabilities of rodents and birds were low in our study due to overall infrequent attacks, and therefore, interpretations should only be made with caution. As we lack predator abundance or behavior-related data from the field site during the time of the experiment, we discuss here the potential mechanisms explaining the relationships between tree species richness and forest structure with predation pressure in light of other studies focusing on these relationships. The main focus is on the effects through expected changes in predator abundance, movement between patches, and close-scale visibility and attraction determinants.

4.1 Tree species richness

Our results provided partial support for the expectation of increased predation at higher tree species richness, based on the expected increase in predator abundances as posited by the "Enemies hypothesis" (Root, 1973), but this support was dependent on predator group, spatial scale, and season. The relationship was generally positive and similar to earlier studies about arthropod predator abundances (Andow, 1991; Haddad et al., 2009), predation rates (Leles et al., 2017), and attacks by birds (Muiruri et al., 2016). However, after the inclusion of forest structural metrics, the positive effect of tree species richness was replaced altogether by structural effects for birds and remained only in larger plots and in more densely branched neighborhoods for arthropods, showing that the tree species richness effect is partially driven by accompanying changes in forest structure. The effect of higher tree species richness on predator population sizes is likely stronger in larger areas due to species–area relationships. However, different tree species can host differing predator fauna compositions (as shown for spiders, Zhang et al., 2018), and, for example, differences in leaf structure can influence predation rates (Carter et al., 1984; Grevstad and Klepetka, 1992; Coll and Ridgway, 1995; Clark and Messina, 1998). In turn, higher branch/foliage density has been shown to increase prey and arthropod predator (spider) abundances (Halaj et al., 1998; Halaj et al., 2000). Thus, denser mixtures of foliage from different neighboring tree species may locally increase predation pressure through predator richness and abundance, especially for the tree species where the efficiency of predators is otherwise lowest. The direct effect of plant species richness may, thus, be more evident in agroecosystems and grasslands than in forests (Russell, 1989; Wan et al., 2020) due to plants of different species being systematically in closer contact with each other when they are smaller.

4.2 Forest structure

Besides tree species richness, forest structure is an important component affecting predator–prey interactions as it shapes the physical environment that animals encounter. Our results showed that predation pressure responded to vegetation structure between spatial scales, as demonstrated in previous studies of predation by arthropods (Schwab et al., 2021). The positive effects of a more vertically stratified canopy (ENL) and vegetation density (MeanFrac) on predation by arthropods were restricted to smaller plots. Even if the higher canopy vertical stratification and vegetation density would promote arthropod predation, the higher tree species and structural variability in the plot surroundings may have overruled this effect. More variable plot neighborhoods also increased rodent attacks, but in contrast to arthropods, rodent attacks were promoted in smaller low vegetation density plots. The different responses to plot size–forest structural relationships likely demonstrate habitat size restrictions between the predator groups, as rodent abundances have been shown to respond to habitat characteristics at various spatial scales, but in areas mostly much larger compared to our study plots (Bowman et al., 2000; Silva et al., 2005).

In addition to the plot size-related effects, the response of predators to small-scale vegetation structure was shaped by the larger-scale neighborhood structure within the plots, as the intensity of arthropod predator attacks varied in relation to neighborhood branch density and plot-level vegetation density. The encounter and/or acceptance likelihood of less-appealing artificial prey might increase if natural prey is scarce, as search time can be expected to be inversely related to prey density (Andow and Prokrym, 1990). For example, higher predation rates on artificial caterpillars were observed in forest sites that actually had lower real lepidopteran density compared to those with higher density, a result that was attributed to the increased pressure on the available prey (Koh and Menge, 2006). It has also been demonstrated that seemingly prey-deficient sink habitats can encounter steady predation pressure from neighboring source populations, upholding larger predator abundances (Holt, 1985; Pulliam, 1988; Koricheva et al., 2000; Bommarco and Banks, 2003; Harmon et al., 2003). As arthropod attacks increased in the lower neighborhood branch density patches only in overall high vegetation density plots, there is a likely source effect from the surrounding vegetation making the more visible caterpillars subject to more frequent predator encounters in these simple structured component communities. In turn, higher predation pressure in densely branched neighborhoods when the plot-level vegetation is less dense might indicate aggregation of predators, either by higher prey density attracting or retaining predators in these patches (Hassell and May, 1974; Kareiva and Odell, 1987) or possibly by the dense patch itself appearing as a cue of prey presence within a surrounding area of lower quality.

Arthropod predation varied also in relation to the presence of leaves in the immediate surroundings of the caterpillars and canopy vertical layering at the plot level. The direct positive effect of a vertically more densely packed canopy was stronger for predation by arthropods in the local neighborhood (vertical Gini), but the positive effect of leaves in the immediate surroundings of caterpillars was promoted when the canopy was less vertically stratified at plot level. Predators can use cues of prey availability from herbivore-damaged leaves (Heinrich and Collins, 1983; Mäntylä et al., 2008; Sam et al., 2015), which naturally require leaves to be present, but the leaves themselves might work as an indicator of prey in stands with less foliage. This was further indicated by the increased effect of the presence of leaves when they were still scarce during budburst and by increased arthropod attacks at higher placement heights where the caterpillars were closer to the canopy. Potential prey outside the foliage zone might receive less attention from the predators, and conversely, when the canopy is more vertically stratified, the presence of leaves as a fine-scale cue may have weaker effects.

Potential visibility effects were observed with predation by birds, as attacks were more common in the plots with the smallest trees and the least stratified canopy. Birds are expected to prefer shade habitats (Perfecto et al., 1996), but they are highly mobile predators, and caterpillars in more visible environments may attract more attacks. In addition, larger open areas in the local neighborhood increased attacks on more densely vegetated plots. Denser vegetation in the canopy layer as well as in the understory is known to promote bird species richness, abundance, and the predation pressure they exert (MacArthur and MacArthur, 1961; Khanaposhtani et al., 2012; Mag and Ódor, 2015; Filloy et al., 2023). Instead, results have been more equivocal on the role of reduced habitat complexity and increased openness in increasing predation by birds due to easier finding of prey, ranging from positive (Šipoš and Kindlmann, 2013; Yang et al., 2018) to negative (Koh and Menge, 2006). It is thus likely, as suggested in earlier studies (Muiruri et al., 2016), that visibility is important for birds mainly in small spatial scales, with habitat selection being of higher importance.

Whereas vegetation biomass has been shown to increase predation rates in grasslands (Haddad et al., 2009; Ebeling et al., 2014), we did not observe positive effects of tree sizes besides the focal tree BA. Instead, lower neighborhood BA demonstrated possibly visibility-driven effects in the absence of branches on the focal trees. The effect of vegetation biomass on predation pressure in forests might, thus, be more variable due to the higher size and structural variation within the vegetation than what occurs in grasslands. However, some effects observed in this study may be additionally influenced by canopy structure-driven differences in understory vegetation, which varied to a large extent in the study plots and was clearly higher when the trees were small or had large open areas around them. For example, open areas have been observed to attract predators, presumably through higher herb/sapling and resulting higher herbivore densities (Richards and Windsor, 2007). Rodent attacks were also more common at lower placement heights, and rodent abundances are known to be increased by denser understory vegetation (Silva and Prince, 2008; Fischer and Schröder, 2014). The effects of understory were, however, not possible to quantify in our study.

4.3 Seasonal variation along forest structure and topography

Our results showed that predation pressure is not static in relation to forest structure and topography but has a seasonal dynamic across predator groups. New foliage can increase predation through the promotion of herbivore prey abundance (Richards and Coley, 2007), and the positive effect of canopy vertical stratification on predation by arthropods and more densely vegetated plots on rodents in spring is likely due to high foliage resource abundance for herbivores. However, besides the effects of foliage, our results suggest a shift in predation pressure based on abiotic effects between rainy and dry seasons. Plots with less sunny conditions (solar irradiation) had higher predation pressure in the dry season, and an additional similar shift was seen with arthropod predators along the elevational gradient toward the more humid lowland plots. Predation has been shown to decrease with increasing elevation, attributed to lower temperatures (Preszler and Boecklen, 1996; Roslin et al., 2017), but as the differences in elevation within the BEF-China sites were only small, the effects of higher elevation are more likely to indicate seasonal differences in exposure to wind and sun. Increased checking intervals due to rain also had hardly any effect on arthropod predation during the rainy season but instead promoted arthropod attacks during the dry season.

Arthropod predators and rodents additionally appeared to favor more sun-exposed plots in spring, likely due to earlier leaf production and increased herbivore prey abundance but also possibly due to benefitting from higher temperatures themselves during the cooler weather period. Topography affected predation only a little during the mid-summer rainy period, possibly due to lower difference in foliage abundance and altogether higher temperatures with presumably lower variation in humidity than during the dry season. In addition, altogether higher prey and predator densities may also reduce the effect between habitats of varying quality (McCoy and Bell, 1991), and caterpillar abundances were observed to be highest in the mid-summer rainy season in the BEF-China field site in the study year (Anttonen et al., 2022), when the arthropod predator attack intensity was also highest. Predation pressure following prey abundance also likely explains the observed higher arthropod predator attacks in the second checking round in spring and the first round in autumn. Arthropod predation pressure further increased in autumn in more densely branched neighborhoods, likely due to more shadowy microhabitats and/or aggregation on the most promising patches of prey in the season when prey abundance is lower. Bird attacks also increased toward late summer, when the predation pressure by naïve fledglings is highest (Remmel et al., 2009; Zvereva and Kozlov, 2023), but the attacks were nearly equally high even after the fledgling season in autumn, likely because of increased abundance and species richness caused by migratory birds (Van Bael et al., 2008). During this period, the preference for the plots with the smallest trees and canopy with the least vertical layers became absent, potentially due to the combined effect of reduced prey but increased bird abundance, forcing birds to search for prey across the available habitats.

The seasonal effect of canopy vertical stratification on predators may have also depended on canopy-driven microclimatic effects, besides differences in foliage abundance. ENL values decrease when the plot has a vertically more uniform canopy cover, which can drastically decrease light availability and temperature (Breshears, 2006), leading to more humid conditions. In addition to the positive effect that higher canopy vertical stratification had in spring, arthropod predator attacks also increased during the dry season in less- stratified canopy plots. Instead, no seasonal effect of BA was seen with arthropods even in the non-TLS model, demonstrating that the observed seasonal ENL–predation relationship is not driven simply by tree size differences. In addition, predation pressure by birds and rodents responded seasonally to canopy vertical structure through slope angle in a similar manner as arthropods to ENL. Altogether, the observed seasonal effects indicate that besides predation pressure following seasonal shifts in prey abundance, the predator's avoidance of more sun-exposed areas during the dry season and a combination of young leaves (Richards and Coley, 2007), foliage abundance, and microclimatic effects in spring are important determinants shaping the predator's response to its environment. However, specific studies on how tree phenology and seasonal fluctuations in abiotic conditions affect predation pressure would be needed, as studies on the topic are scarce (but see Richards and Coley, 2007; Molleman et al., 2016). This is especially the case for temperate, but seasonally rainy, sub-tropical forests.

4.4 Methodological considerations

Our study showed that forest structure captures a considerable proportion of the variation in predation pressure, which otherwise could be partly explained by tree species richness. Effects of forest structure have been addressed in studies of bird and arthropod predators using a variety of measures (e.g., MacArthur and MacArthur, 1961; Halaj et al., 1998; Khanaposhtani et al., 2012; Šipoš and Kindlmann, 2013; Poch and Simonetti, 2013), often related to vegetation "complexity". The strong inconsistency between studies in terms of the value measured and the terminology used (McCoy and Bell, 1991; Tews et al., 2004; Loke and Chisholm, 2022) makes comparisons between them difficult, as there are several indices for measuring forest structure, including with TLS alone (McElhinny et al., 2005; Reich et al., 2021; Loke and Chisholm, 2022). Our results demonstrated that when using measures of overall forest complexity with principal components instead of different spatial scale-specific measures or one measure of plot-level complexity (SSCI) instead of vertical structure (ENL) or vegetation density (MeanFrac) separately, not only is the overall information value of the GLME models reduced, but also the interaction of different structural elements between spatial scales becomes challenging to define. TLS is a powerful method for measuring forest structure, making possible the estimation of multiple structural features (Calders et al., 2020) that can be further combined with other specific measures of small- and large-scale environments. However, further work is needed to clarify how the different structural variables relate to predation and animal behavior in general in different forest ecosystems.

Some specific notions of factors having an effect on the overall attack rate should be taken into consideration for future studies. The fairly long checking period in our study likely dampens the differences in predation between habitats to some extent, but this also demonstrates robustness in the results and buffers against sporadic effects caused by weather conditions. In addition, predators may learn the positions of the nonpalatable artificial caterpillars (Mäntylä et al., 2008), including eusocial insects, which likely explains the overall lower attack frequency during the second checking round of each season. Thus, longer-term experiments with artificial caterpillars would benefit from regular changes of the caterpillar's positions. Grasshoppers have been observed to attack artificial baits in other ecosystems (Gordon and Kerr, 2022), and the sudden decline in predation by arthropods in late summer may be due in part to the masking effects of high grasshopper-induced damages. Thus, regular observations of the fauna in contact with the artificial caterpillars are advisable. Very fine-scale determinants of visibility and potential attraction to predators are important to take into account in studies of the wider forest's structural effects, or vice versa, as their effects are not stable but interactive with each other. The effect of structural variables may also change seasonally, requiring close consideration of their role in study designs.

5 Conclusions

Our study highlights that not just tree species richness or structural complexity per se determines predation pressure in forests. Instead, scale dependence, the interplay of tree species richness and structural variables, and seasonal fluctuations in abiotic conditions and tree phenology all play a role in shaping the predation pressure on herbivores. These relationships, rarely addressed in previous studies, might explain some of the inconsistencies found in preceding analyses of tree diversity–predator relationships (Staab and Schuldt, 2020; Stemmelen et al., 2022). However, what effects predator and prey abundances, movement between habitats, and fine-scale predator efficiency determinants have on predation pressure, and how these relate to predators of varying mobility and habitat range, is still a question requiring more attention. Addressing these topics in forest ecosystems and BEF-research will aid in predicting how biodiversity loss will shape the top-down control of herbivores, with important consequences for ecosystem functioning. Overall, our results highlight the need to build a more dynamic framework for assessing predation pressure in forests.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

Conceptualization: PA, AS, and C-DZ. Methodology: PA, AS, MP-G, MK, GvO, C-DZ, HB, and K-PM. Validation: PA. Formal analysis: PA and AS. Investigation: PA, MP-G, and YL. Writing – original draft preparation: PA. Writing – review and editing: PA, AS, MP-G, MK, GvO, HB, YL, C-DZ, and K-PM. Visualization: PA. Supervision: AS and C-DZ. Project administration: AS, C-DZ, HB, and K-PM. Funding acquisition: HB, K-PM, AS, and C-DZ. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1199670/full#supplementary-material

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Supplementary Material 1

Predation pressure by arthropods, birds and rodents is interactively shaped by tree species richness, vegetation structure and season

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1 Supplementary tables

Table S1. Tree species used in the experiment. Some tree species synonym names have been updated as compared to Huang et al. (2018), where also C. fargesii is not listed for the study plots.

Family	Species	Author
Fagaceae	Castanea henryi	Rehd. & Wils.
Fagaceae	Castanopsis eyrei	(Champion ex Bentham) Tutcher
Fagaceae	Castanopsis fargesii	Franch.
Fagaceae	Castanopsis sclerophylla	(Lindley & Paxton) Schottky
Anacardiaceae	Choerospondias axillaris	(Roxb.) Burtt et Hill
Fagaceae	Cyclobalanopsis glauca	(Thunberg) Oersted
Fagaceae	Cyclobalanopsis myrsinifolia	(Blume) Oersted
Sapindaceae	Koelreuteria bipinnata	Franch.
Altingiaceae	Liquidambar formosana	Hance
Fagaceae	Lithocarpus glaber	(Thunb.) Nakai
Nyssaceae	Nyssa sinensis	Oliver
Fagaceae	Quercus fabri	Hance
Fagaceae	Quercus serrata	Murray
Anacardiaceae	Rhus chinensis	Mill.
Sapindaceae	Sapindus saponaria	L.
Euphorbiaceae	Triadica sebifera	L.
Theaceae	Schima superba	Gardner & Champ.

Table S2. (a) Importance of principal components with standard deviations, proportion of variance and cumulative proportion. (b) Loading scores of each variable on principal components.

(a) Importance of components:

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8
Standard deviation	1.54	1.27	1.05	0.99	0.82	0.72	0.64	0.58
Proportion of Variance	0.30	0.20	0.14	0.12	0.08	0.06	0.05	0.04
Cumulative Proportion	0.30	0.50	0.64	0.76	0.84	0.91	0.96	1.00

(b) Loadings:

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8
Tree richness	0.32	0.22	0.47	0.50	0.34	0.30	0.32	0.26
Focal BA	0.21		-0.76		0.59		0.11	
Neighborhood BA	0.50	0.12		-0.17	-0.20	-0.70	0.40	0.11
Open area	-0.24		-0.35	0.77	-0.42	-0.19		0.10
Vertical Gini	-0.30	-0.46	0.24	0.21	0.52	-0.56	-0.15	
Voxels per layer	-0.18	0.67		-0.11		-0.21	-0.49	0.47
ENL	0.53			0.29			-0.58	-0.53
MeanFrac	-0.38	0.52			0.19	-0.14	0.35	-0.64

Table S3. Summary of generalized linear mixed effect model results for arthropod predator, bird and rodent attacks without TLS derived structural variables (for the models including TLS variables see Table 1). Standardized parameter estimates (with standard errors, z and p values) are shown for explanatory variables. AIC values are given for comparison to alternative models using TLS data. Values in bold signify p ≤ 0.05, and in italics p ≤ 0.1. Hyphen '-' means that the factor in question was not retained in the best AIC based model for that predator group, and 'NA' means the factor was not included in the model. Random factors in models were tree species, and tree individual nested within plot. Number of artificial caterpillars for which predation was estimated is 17 728 for all predator groups.

	Arthropod predator attacks (AIC = 10178.2)			Bird attacks (AIC = 1981.8)			Rodent attacks (AIC = 1337.7)		
	Estimate ± Std. Error	z	Pr(>|z|)	Estimate ± Std. Error	z	Pr(>|z|)	Estimate ± Std. Error	z	Pr(>|z|)
Intercept	-2.51±0.08	-30.5	**<0.001**	-5.27±0.23	-22.7	**<0.001**	-5.8±0.31	-18.6	**<0.001**
Tree richness	0.09±0.04	2.1	**0.033**	-0.49±0.15	-3.2	**0.001**	-0.26±0.16	-1.7	*0.092*
Plot size	-0.07±0.04	-1.6	0.113	-0.02±0.10	-0.2	0.880	-0.33±0.14	-2.4	**0.018**
Tree richness:Plot size	0.08±0.04	2.0	**0.042**	0.2±0.11	1.7	*0.085*	-	-	-
Open area	<0.01±0.04	<0.1	0.972	0.11±0.10	1.2	0.240	0.16±0.12	1.3	0.190
Leaves present	0.29±0.07	4.1	**<0.001**	0.13±0.20	0.6	0.529	-0.08±0.25	-0.3	0.748
Placement height	0.19±0.03	6.3	**<0.001**	0.06±0.08	0.7	0.513	-0.66±0.13	-5.1	**<0.001**
Placement on trunk	-0.06±0.10	-0.6	0.528	-0.56±0.33	-1.7	*0.089*	-0.15±0.33	-0.5	0.651
Placement on trunk: Placement height	0.13±0.08	1.7	*0.081*	NA	NA	NA	NA	NA	NA
Neighborhood BA	-0.11±0.04	-2.5	**0.013**	-0.28±0.12	-2.4	**0.018**	-0.12±0.15	-0.8	0.396
Placement on trunk: Neighborhood BA	-0.22±0.09	-2.3	**0.020**	NA	NA	NA	NA	NA	NA
Focal tree BA	0.07±0.04	1.7	*0.091*	-0.02±0.11	-0.1	0.885	0.08±0.13	0.6	0.543
Season	0.28±0.05	5.3	**<0.001**	0.66±0.10	6.3	**<0.001**	-0.36±0.11	-3.2	**0.001**
Checking round	-0.15±0.05	-2.7	**0.007**	-0.38±0.15	-2.6	**0.010**	-0.53±0.19	-2.8	**0.006**
Season:Checking round	-0.34±0.05	-6.3	**<0.001**	-	-	-	-	-	-
Days on tree	0.55±0.03	20.1	**<0.001**	-0.06±0.09	-0.7	0.482	0.14±0.09	1.5	0.125
Season:Days on tree	0.53±0.04	13.9	**<0.001**	-	-	-	-	-	-
Season:Tree richness	-0.09±0.03	-3.6	**<0.001**	0.38±0.12	3.3	**0.001**	-	-	-
Season:Leaves present	-0.18±0.05	-3.3	**0.001**	NA	NA	NA	-	-	-
Slope angle	-0.14±0.05	-2.6	**0.009**	-0.1±0.14	-0.7	0.461	0.08±0.19	0.4	0.659
Season:Slope angle	-	-	-	-0.11±0.10	-1.1	0.278	-0.32±0.13	-2.4	**0.015**
Elevation	-0.05±0.05	-1.0	0.302	-0.1±0.12	-0.9	0.371	-0.05±0.15	-0.3	0.742
Season:Elevation	-0.09±0.03	-3.2	**0.001**	-	-	-	-	-	-
Solar irradiance	-0.03±0.05	-0.6	0.564	-0.15±0.12	-1.2	0.228	-0.10±0.16	-0.6	0.548
Season:Solar irradiance	-0.09±0.03	-3.5	**<0.001**	-0.16±0.08	-1.8	*0.065*	-0.29±0.12	-2.5	**0.012**

Table S4. Summary of generalized linear mixed effect model results for arthropod predator, bird and rodent attacks, using TLS derived SSCI-index for estimating forest structural complexity at plot level (for the model including MeanFrac and ENL see Table 1). Standardized parameter estimates (with standard errors, z and p values) are shown for explanatory variables. AIC values are given for comparison to alternative models not using TLS variables, or using MeanFrac and ENL separately instead of SSCI. Values in bold signify p ≤ 0.05, and in italics p ≤ 0.1. Hyphen ‘-‘ means that the factor in question was not retained in the best AIC based model for that predator group, and ‘NA’ means the factor was not included in the model. Random factors in models were tree species, and tree individual nested within plot. Number of artificial caterpillars for which predation was estimated is 17 728 for all predator groups.

	Arthropod predator attacks (AIC = 10168.5)			Bird attacks (AIC = 1982.9)			Rodent attacks (AIC = 1328.3)		
	Estimate ± Std. Error	z	Pr(>|z|)	Estimate ± Std. Error	z	Pr(>|z|)	Estimate ± Std. Error	z	Pr(>|z|)
Intercept	-2.48±0.08	-29.9	**<0.001**	-5.25±0.23	-22.7	**<0.001**	-5.95±0.31	-19.0	**<0.001**
Tree richness	0.07±0.04	1.7	*0.096*	-0.42±0.16	-2.7	**0.008**	-0.26±0.16	-1.6	0.101
Plot size	-0.06±0.04	-1.7	*0.084*	-0.02±0.10	-0.2	0.871	-0.41±0.14	-2.9	**0.004**
Plot size:Tree richness	0.08±0.04	1.9	*0.053*	0.22±0.12	1.9	*0.056*	-	-	-
SSCI	0.08±0.07	1.3	0.209	-0.10±0.14	-0.8	0.442	-0.11±0.19	-0.6	0.561
Plot size:SSCI	-0.07±0.04	-1.9	*0.053*	-	-	-	0.35±0.15	2.4	**0.018**
Leaves present	0.29±0.07	4.1	**<0.001**	0.11±0.20	0.5	0.588	-0.03±0.24	-0.1	0.915
Leaves present:SSCI	-0.05±0.06	-0.7	0.462	NA	NA	NA	-	-	-
Open area	<0.01±0.04	-0.1	0.950	0.12±0.09	1.3	0.201	0.11±0.12	1.0	0.342
Open area:SSCI	-	-	-	0.15±0.09	1.7	*0.097*	-	-	-
Voxels per layer	0.05±0.04	1.2	0.249	0.07±0.11	0.7	0.507	0.31±0.15	2.0	**0.047**
Tree richness:Voxels per layer	0.13±0.04	3.1	**0.002**	NA	NA	NA	NA	NA	NA
Voxels per layer:SSCI	-0.08±0.04	-1.9	*0.062*	-	-	-	-	-	-
Placement height	0.17±0.03	5.8	**<0.001**	0.06±0.09	0.6	0.516	-0.67±0.13	-5.2	**<0.001**
Placement on trunk	-0.03±0.10	-0.3	0.767	-0.61±0.34	-1.8	*0.072*	0.09±0.33	0.3	0.793
Placement on trunk: Placement height	0.14±0.08	1.8	*0.065*	NA	NA	NA	NA	NA	NA
Neighborhood BA	-0.07±0.04	-1.7	*0.094*	-0.22±0.12	-1.8	*0.075*	-0.17±0.15	-1.1	0.252
Placement on trunk: Neighborhood BA	-0.22±0.09	-2.3	**0.019**	NA	NA	NA	NA	NA	NA
Focal tree BA	0.08±0.04	1.9	*0.058*	0.03±0.11	0.3	0.768	0.08±0.13	0.6	0.532
Vertical Gini	0.10±0.04	2.5	**0.011**	0.18±0.10	1.8	*0.076*	-0.13±0.14	-1.0	0.329
Season	0.28±0.05	5.3	**<0.001**	0.65±0.10	6.2	**<0.001**	-0.37±0.11	-3.3	**0.001**
Checking round	-0.15±0.05	-2.7	**0.008**	-0.38±0.15	-2.6	**0.011**	-0.53±0.19	-2.7	**0.006**
Season:Checking round	-0.34±0.05	-6.2	**<0.001**	-	-	-	-	-	-
Days on tree	0.54±0.03	19.8	**<0.001**	-0.06±0.09	-0.6	0.528	0.13±0.09	1.4	0.165
Season:Days on tree	0.52±0.04	13.6	**<0.001**	-	-	-	-	-	-
Season:Tree richness	-0.08±0.03	-2.9	**0.003**	0.31±0.12	2.5	**0.011**	-	-	-
Season:SSCI	-0.07±0.03	-2.3	**0.023**	0.15±0.09	1.7	*0.087*	-0.29±0.11	-2.6	**0.010**
Season:Voxels per layer	0.08±0.03	2.5	**0.013**	-	-	-	-	-	-
Season:Leaves present	-0.18±0.05	-3.4	**0.001**	-	-	-	-	-	-
Slope angle	-0.09±0.05	-1.8	*0.070*	-0.04±0.14	-0.3	0.787	0.13±0.19	0.7	0.512
Season:Slope angle	-	-	-	-0.13±0.10	-1.3	0.195	-0.36±0.14	-2.6	**0.010**
Elevation	-0.06±0.04	-1.3	0.209	-0.13±0.12	-1.1	0.254	-0.15±0.16	-1.0	0.333
Season:Elevation	-0.09±0.03	-3.3	**0.001**	-	-	-	-	-	-
Solar irradiance	-0.02±0.04	-0.4	0.680	-0.13±0.12	-1.1	0.281	-0.09±0.17	-0.6	0.567
Season:Solar irradiance	-0.11±0.03	-4.1	**<0.001**	-0.18±0.08	-2.2	**0.031**	-0.32±0.12	-2.6	**0.009**

Table S5. Summary of generalized linear mixed effect model results for arthropod predator, bird and rodent attacks, using principal components (PC) of tree species richness and forest structure (for the model using tree species richness and structural metrics separately see Table 1). Standardized parameter estimates (with standard errors, z and p values) are shown for explanatory variables. AIC values are given for comparison to alternative models using tree species richness and forest structural metrics separately, not using TLS variables, or using SSCI instead of MeanFrac and ENL. Values in bold signify p ≤ 0.05, and in italics p ≤ 0.1. Hyphen ‘-‘ means that the factor in question was not retained in the best AIC based model for that predator group, and ‘NA’ means the factor was not included in the model. Random factors in models were tree species, and tree individual nested within plot. Number of artificial caterpillars for which predation was estimated is 17 728 for all predator groups.

	Arthropod predator attacks (AIC = 10187.8)			Bird attacks (AIC = 1971.2)			Rodent attacks (AIC = 1324.7)		
	Estimate ± Std. Error	z	Pr(>|z|)	Estimate ± Std. Error	z	Pr(>|z|)	Estimate ± Std. Error	z	Pr(>|z|)
Intercept	-2.50±0.09	-28.6	**<0.001**	-5.28±0.23	-22.6	**<0.001**	-5.86±0.31	-18.9	**<0.001**
Plot size	-0.07±0.05	-1.4	0.151	-0.02±0.10	-0.2	0.818	-0.41±0.15	-2.7	**0.007**
Leaves present	0.24±0.07	3.4	**0.001**	0.07±0.20	0.3	0.743	-0.03±0.24	-0.1	0.909
Placement height	0.20±0.03	7.0	**<0.001**	0.09±0.08	1.1	0.265	-0.66±0.13	-5.1	**<0.001**
Placement on trunk	-0.10±0.10	-1.0	0.311	-0.43±0.34	-1.3	0.201	0.07±0.33	0.2	0.841
PC1	-0.05±0.03	-1.5	0.134	-0.45±0.08	-5.4	**<0.001**	-0.25±0.10	-2.5	**0.013**
PC2	0.04±0.04	1.1	0.269	-0.04±0.07	-0.5	0.607	0.18±0.12	1.5	0.129
PC1:PC2	0.04±0.02	2.0	**0.050**	-	-	-	-	-	-
PC3	<0.01±0.04	0.0	0.998	-0.19±0.11	-1.8	*0.080*	-0.19±0.12	-1.6	0.121
Season	0.33±0.05	6.1	**<0.001**	0.74±0.11	6.8	**<0.001**	-0.34±0.11	-3.0	**0.003**
Checking round	-0.16±0.06	-3.0	**0.003**	-0.38±0.15	-2.6	**0.010**	-0.53±0.19	-2.8	**0.006**
Season:Checking round	-0.36±0.05	-6.6	**<0.001**	-	-	-	-	-	-
Days on tree	0.56±0.03	20.4	**<0.001**	-0.08±0.09	-0.9	0.373	0.12±0.09	1.3	0.183
Season:Days on tree	0.55±0.04	14.3	**<0.001**	-	-	-	-	-	-
Season:Leaves present	-0.26±0.06	-4.6	**<0.001**	NA	NA	NA	-	-	-
Season:PC1	-0.07±0.02	-4.0	**<0.001**	0.17±0.06	3.1	**0.002**	-	-	-
Season:PC2	-	-	-	-	-	-	-0.22±0.08	-2.6	**0.009**
Season:PC3	0.05±0.02	2.2	**0.030**	0.19±0.08	2.5	**0.013**	-	-	-
Slope	-0.13±0.06	-2.2	**0.030**	-0.07±0.13	-0.5	0.593	0.14±0.21	0.7	0.495
Season:Slope	-	-	-	-	-	-	-0.32±0.13	-2.4	**0.017**
Elevation	-0.03±0.05	-0.6	0.582	-0.13±0.11	-1.1	0.270	-0.12±0.17	-0.7	0.480
Season:Elevation	-0.12±0.03	-4.3	**<0.001**	-	-	-	-	-	-
Solar irradiance	0.01±0.05	0.2	0.818	-0.19±0.11	-1.8	*0.078*	-0.10±0.17	-0.6	0.582
Season:Solar irradiance	-0.12±0.03	-4.6	**<0.001**	-	-	-	-0.26±0.12	-2.2	**0.031**

2 Supplementary Figures

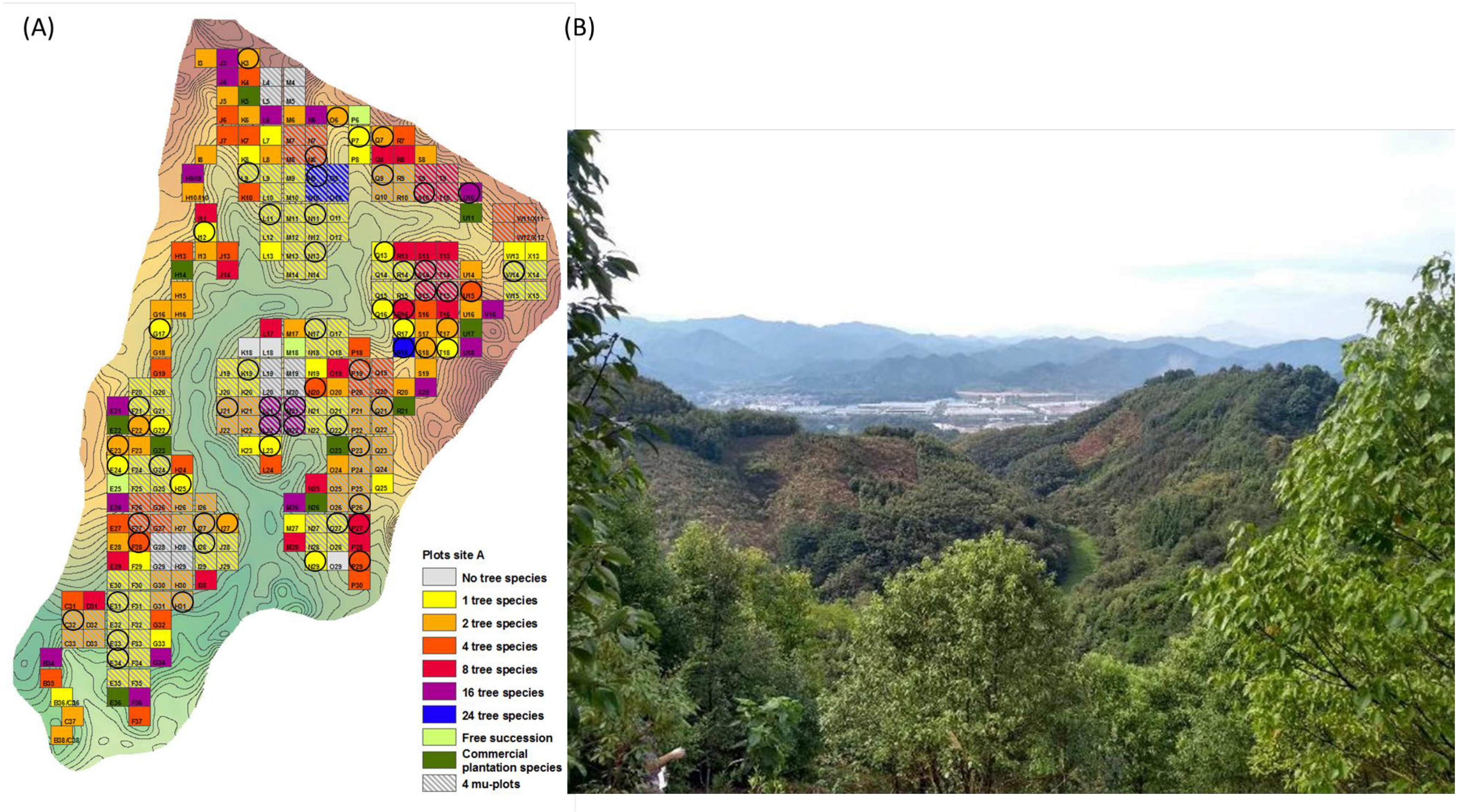


Figure S1. (A) Topography, tree species richness, and plot being 1- or 4 mu in size for BEF-China experimental field site A (modified from figure in Bruelheide et al., 2014). The plots used in this study highlighted with black circle. (B) Photograph of the field site in north to south direction. Photo credit: P. Anttonen.

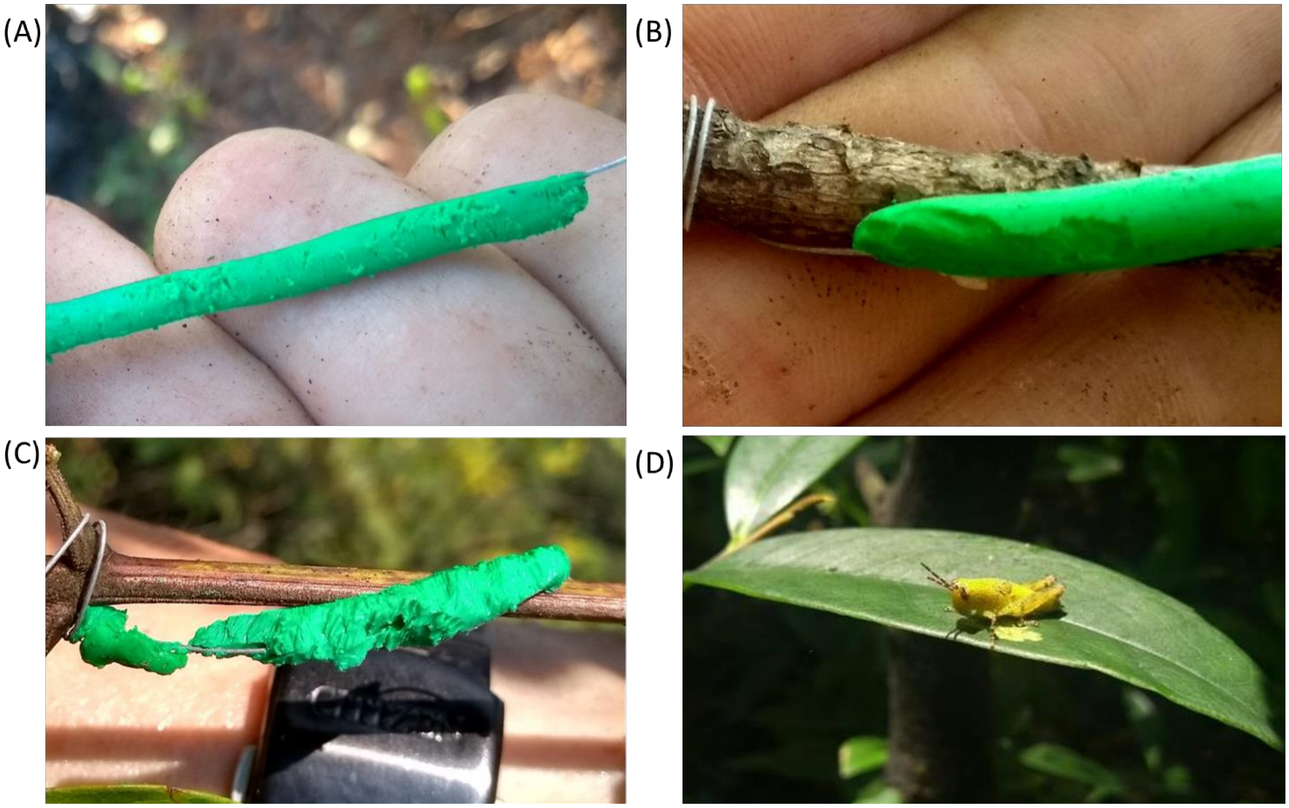


Figure S2. Invertebrate attack marks. (A) Bite marks of arthropod predators, (B) snail, or (C) grasshopper on artificial caterpillar, and (D) grasshopper bite marks on evergreen leaf.

Figure S3. Vertebrate attack marks. (A-C) Various bird attack marks, (D) mixture of bird and arthropod predator attack marks, (E) rodent teeth marks, and (F) piercing insectivore like teeth marks (likely a bat). Picture (B) shows an example of placement on trunk.

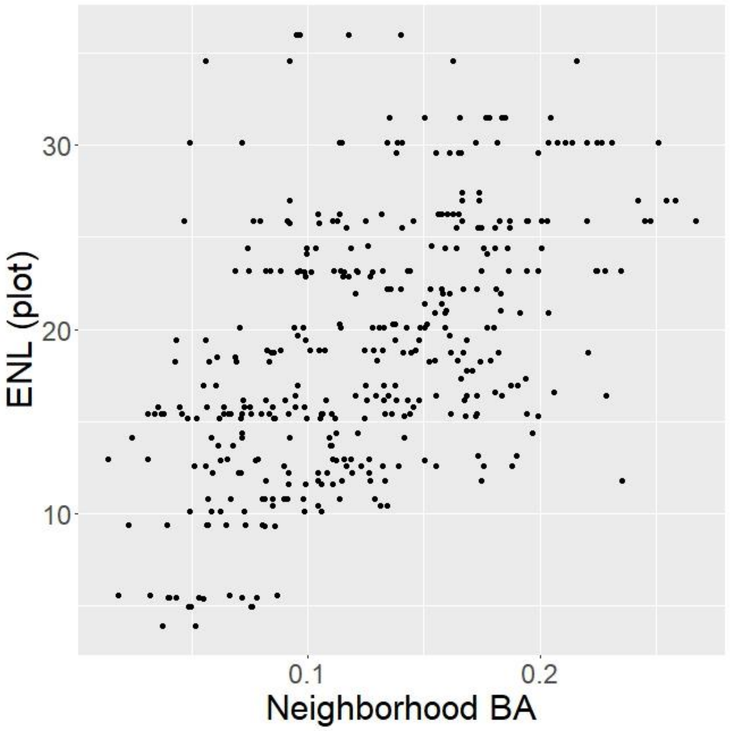
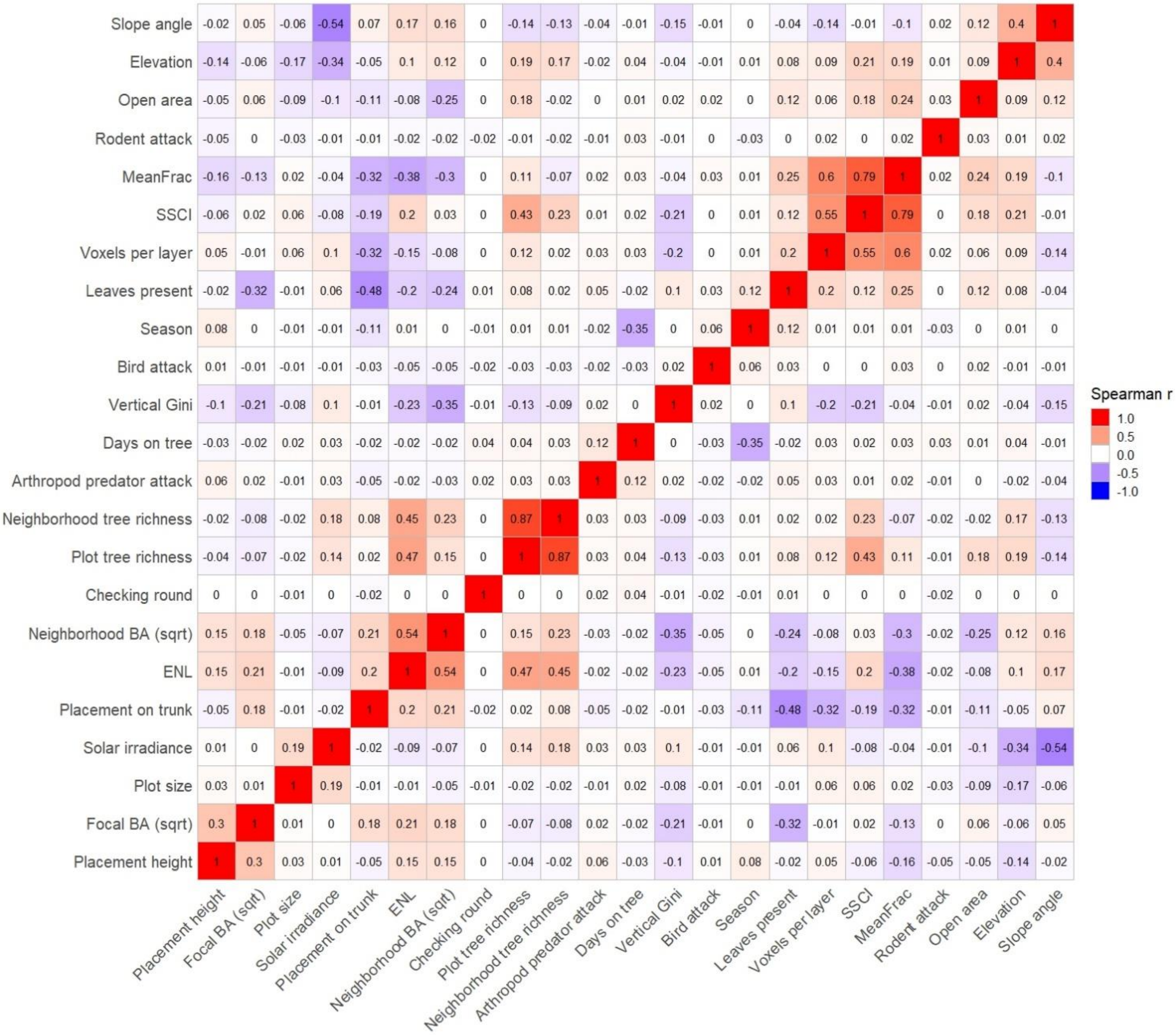


Figure S4. Relationship of ENL and neighborhood BA. Neighborhood BA values are square root transformed.



	Placement height	Focal BA (sqrt)	Plot size	Solar irradiance	Placement on trunk	ENL	Neighborhood BA (sqrt)	Checking round	Plot tree richness	Neighborhood tree richness	Arthropod predator attack	Days on tree	Vertical Gini	Bird attack	Season	Leaves present	Voxels per layer	SSCI	MeanFrac	Rodent attack	Open area	Elevation	Slope angle
Slope angle	-0.02	0.05	-0.06	-0.54	0.07	0.17	0.16	0	-0.14	-0.13	-0.04	-0.01	-0.15	-0.01	0	-0.04	-0.14	-0.01	-0.1	0.02	0.12	0.4	1
Elevation	-0.14	-0.06	-0.17	-0.34	-0.05	0.1	0.12	0	0.19	0.17	-0.02	0.04	-0.04	-0.01	0.01	0.08	0.09	0.21	0.19	0.01	0.09	1	0.4
Open area	-0.05	0.06	-0.09	-0.1	-0.11	-0.08	-0.25	0	0.18	-0.02	0	0.01	0.02	0.02	0	0.12	0.06	0.18	0.24	0.03	1	0.09	0.12
Rodent attack	-0.05	0	-0.03	-0.01	-0.01	-0.02	-0.02	-0.02	-0.01	-0.02	-0.01	0.03	-0.01	0	-0.03	0	0.02	0	0.02	1	0.03	0.01	0.02
MeanFrac	-0.16	-0.13	0.02	-0.04	-0.32	-0.38	-0.3	0	0.11	-0.07	0.02	0.03	-0.04	0.03	0.01	0.25	0.6	0.79	1	0.02	0.24	0.19	-0.1
SSCI	-0.06	0.02	0.06	-0.08	-0.19	0.2	0.03	0	0.43	0.23	0.01	0.02	-0.21	0	0.01	0.12	0.55	1	0.79	0	0.18	0.21	-0.01
Voxels per layer	0.05	-0.01	0.06	0.1	-0.32	-0.15	-0.08	0	0.12	0.02	0.03	0.03	-0.2	0	0.01	0.2	1	0.55	0.6	0.02	0.06	0.09	-0.14
Leaves present	-0.02	-0.32	-0.01	0.06	-0.48	-0.2	-0.24	0.01	0.08	0.02	0.05	-0.02	0.1	0.03	0.12	1	0.2	0.12	0.25	0	0.12	0.08	-0.04
Season	0.08	0	-0.01	-0.01	-0.11	0.01	0	-0.01	0.01	0.01	-0.02	-0.35	0	0.06	1	0.12	0.01	0.01	0.01	-0.03	0	0.01	0
Bird attack	0.01	-0.01	-0.01	-0.01	-0.03	-0.05	-0.05	-0.02	-0.03	-0.03	-0.02	-0.03	0.02	1	0.06	0.03	0	0	0.03	0	0.02	-0.01	-0.01
Vertical Gini	-0.1	-0.21	-0.08	0.1	-0.01	-0.23	-0.35	-0.01	-0.13	-0.09	0.02	0	1	0.02	0	0.1	-0.2	-0.21	-0.04	-0.01	0.02	-0.04	-0.15
Days on tree	-0.03	-0.02	0.02	0.03	-0.02	-0.02	-0.02	0.04	0.04	0.03	0.12	1	0	-0.03	-0.35	-0.02	0.03	0.02	0.03	0.03	0.01	0.04	-0.01
Arthropod predator attack	0.06	0.02	-0.01	0.03	-0.05	-0.02	-0.03	0.02	0.03	0.03	1	0.12	0.02	-0.02	-0.02	0.05	0.03	0.01	0.02	-0.01	0	-0.02	-0.04
Neighborhood tree richness	-0.02	-0.08	-0.02	0.18	0.08	0.45	0.23	0	0.87	1	0.03	0.03	-0.09	-0.03	0.01	0.02	0.02	0.23	-0.07	-0.02	-0.02	0.17	-0.13
Plot tree richness	-0.04	-0.07	-0.02	0.14	0.02	0.47	0.15	0	1	0.87	0.03	0.04	-0.13	-0.03	0.01	0.08	0.12	0.43	0.11	-0.01	0.18	0.19	-0.14
Checking round	0	0	-0.01	0	-0.02	0	0	1	0	0	0.02	0.04	-0.01	-0.02	-0.01	0.01	0	0	0	-0.02	0	0	0
Neighborhood BA (sqrt)	0.15	0.18	-0.05	-0.07	0.21	0.54	1	0	0.15	0.23	-0.03	-0.02	-0.35	-0.05	0	-0.24	-0.08	0.03	-0.3	-0.02	-0.25	0.12	0.16
ENL	0.15	0.21	-0.01	-0.09	0.2	1	0.54	0	0.47	0.45	-0.02	-0.02	-0.23	-0.05	0.01	-0.2	-0.15	0.2	-0.38	-0.02	-0.08	0.1	0.17
Placement on trunk	-0.05	0.18	-0.01	-0.02	1	0.2	0.21	-0.02	0.02	0.08	-0.05	-0.02	-0.01	-0.03	-0.11	-0.48	-0.32	-0.19	-0.32	-0.01	-0.11	-0.05	0.07
Solar irradiance	0.01	0	0.19	1	-0.02	-0.09	-0.07	0	0.14	0.18	0.03	0.03	0.1	-0.01	-0.01	0.06	0.1	-0.08	-0.04	-0.01	-0.1	-0.34	-0.54
Plot size	0.03	0.01	1	0.19	-0.01	-0.01	-0.05	-0.01	-0.02	-0.02	-0.01	0.02	-0.08	-0.01	-0.01	-0.01	0.06	0.06	0.02	-0.03	-0.09	-0.17	-0.06
Focal BA (sqrt)	0.3	1	0.01	0	0.18	0.21	0.18	0	-0.07	-0.08	0.02	-0.02	-0.21	-0.01	0	-0.32	-0.01	0.02	-0.13	0	0.06	-0.06	0.05
Placement height	1	0.3	0.03	0.01	-0.05	0.15	0.15	0	-0.04	-0.02	0.06	-0.03	-0.1	0.01	0.08	-0.02	0.05	-0.06	-0.16	-0.05	-0.05	-0.14	-0.02

Figure S5. Spearman correlation coefficients of all response and explanatory variables used in the study. Any variables with Spearman r > 0.7 were not included in the same model. Categorical variables are included to correlation test as binary.

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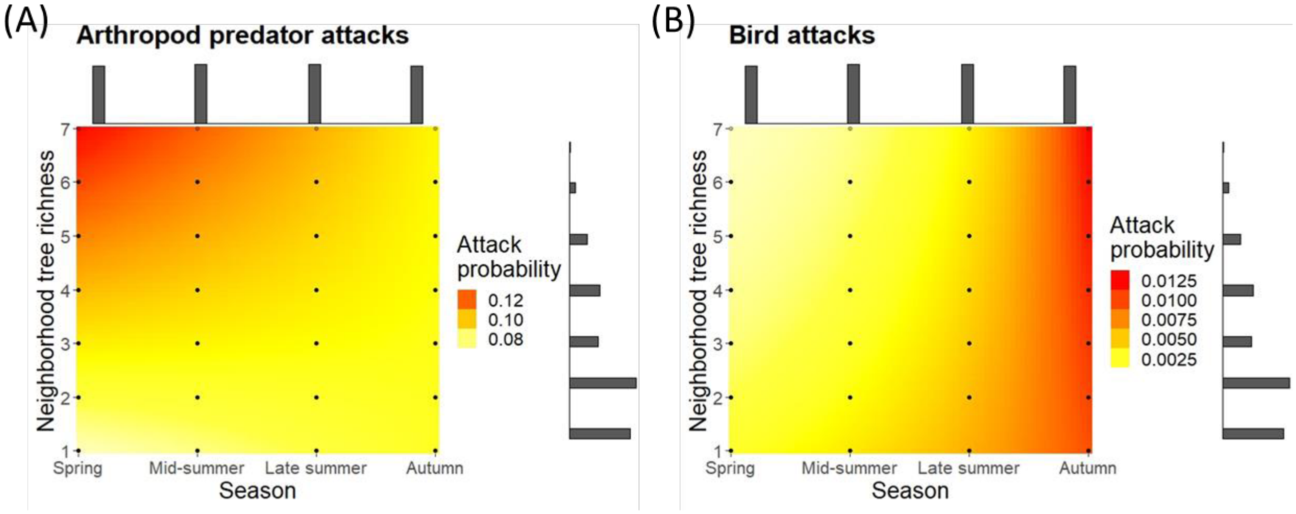

Figure S6. Attack probability as a function of season and neighborhood tree species richness from the model variant without TLS derived structural variables (A) for arthropod predators and (B) birds. Colors represent the estimated change in attack probability, points the observed values, and histograms the amount of observed data points per axis levels.

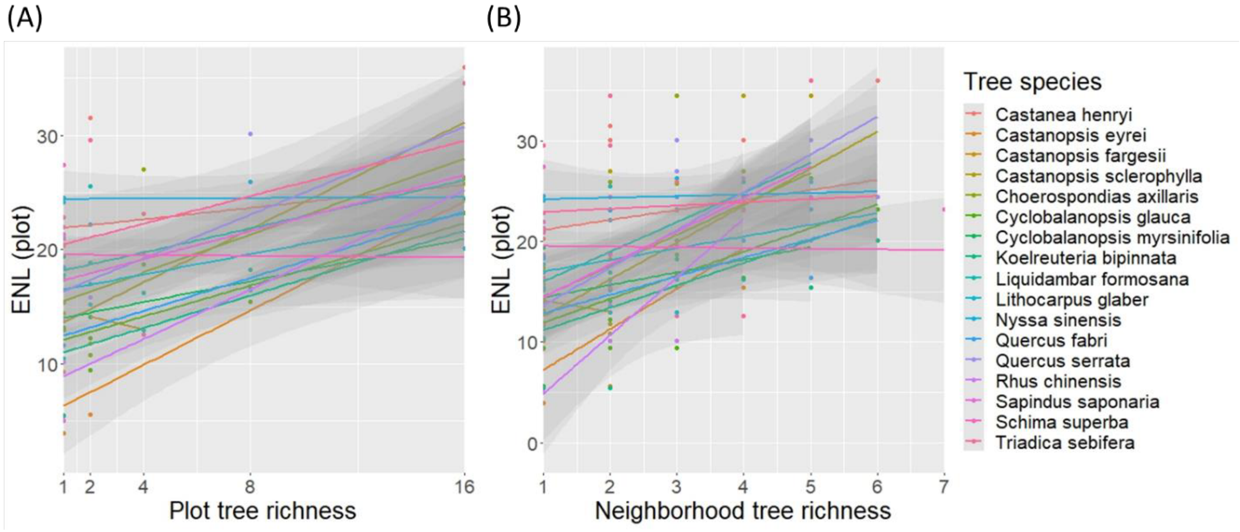

Figure S7. Relationship of ENL with tree richness at (A) plot level, and (B) neighborhood level within the framework of this study for each tree species. Shaded areas show 95 % confidence intervals.

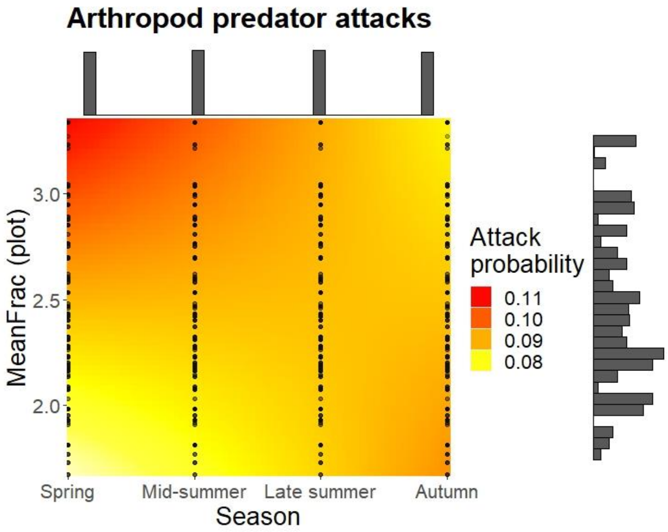

Figure S8. Attack probability as a function of season and MeanFrac for arthropod predators. Colors represent the estimated change in attack probability, points the observed values, and histograms the amount of observed data points per axis levels.

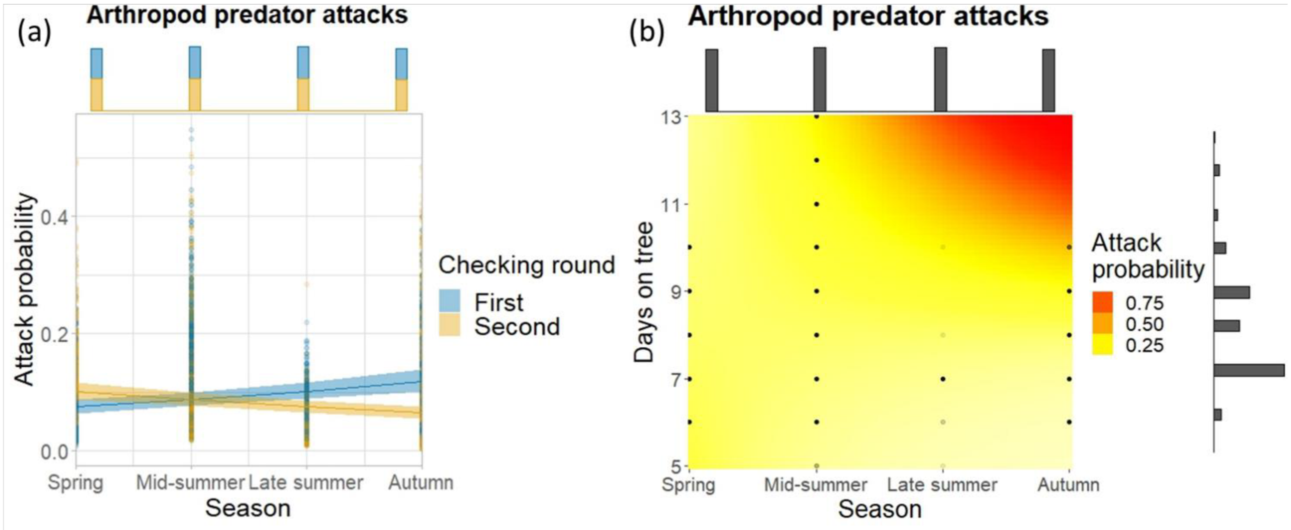

Figure S9. Attack probability as a function of season and (A) checking round, or (B) number of days the caterpillar was on the tree before checking. In figure (A) points show fitted values and shaded areas the 95 % confidence intervals. In the figure (B), colors represent the estimated change in attack probability and points the observed values. Histograms show the amount of observed data points per axis levels.

Supplementary Material 2

Analysis code

Predation pressure by arthropods, birds and rodents is interactively shaped by tree species richness, vegetation structure and season

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Online location of the supplementary material

The analysis code (75 pages) is available at:

https://www.frontiersin.org/articles/10.3389/fevo.2023.1199670/full

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CHAPTER 4

Tree species richness, leaf quality, and topography shape herbivory in a subtropical Biodiversity-Ecosystem Functioning experiment

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Tree species richness, leaf quality, and topography shape herbivory in a subtropical Biodiversity-Ecosystem Functioning experiment

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Abstract

Herbivory accumulation in forests can be shaped between environments by multiple features from tree species richness and associational neighborhood effects, to leaf traits and environmental conditions. In this study we aimed to assess herbivory in a subtropical BEF (Biodiversity-Ecosystem Functioning) experiment through a comprehensive set of variables including tree species richness, leaf traits (nitrogen, magnesium and carbon), forest structure, topography, as well as study plot spatial relationships. We further investigated how the seasonal timing of the herbivory accumulation relates to the aforementioned variables. Differences in the herbivory during a full growing season between trees increased strongly during the second half of the growing season, mainly driven likely by seasonal decline in leaf quality increasing differences between deciduous and evergreen trees. Herbivory further accumulated more on the high-leaf-quality deciduous trees along increasing tree species richness gradient, as well as on lower carbon content trees in their neighborhoods, demonstrating a resource dilution effect. Moreover, associational susceptibility led to spillover from larger neighboring trees with higher nitrogen content. Herbivory increased closer to edges when trees were more apparent and in high-tree-species-richness plots, whereas herbivory increased in central locations in low-tree-species-richness plots. The tree centrality pattern combined with the changing proportion of edge to central position trees with increasing plot size explains why herbivory was otherwise relatively higher in smaller high-tree-species-richness plots but larger in low-richness plots. Branches in lower positions generally experienced higher herbivory, likely through shading-induced increase in leaf quality, but this effect was lost in conditions indicating overall high light intensity and water limitation. Our study demonstrates that herbivory is driven by multiple simultaneously affecting, and sometimes contrasting, environmental and leaf quality determinants, and brings further light to BEF relationships in forests.

Keywords: associational susceptibility/resistance, deciduous/evergreen, herbivory, nutritional content, patch size, resource concentration/dilution, season, tree species richness

1. Introduction

Herbivory is a key ecosystem function that affects plant growth and health already at low damage levels (e.g. Zvereva et al., 2012); reviewed in Crawley, 1989). The dominant “background level” of herbivory well under defoliating damage (reviewed in Kozlov and Zvereva, 2017), can influence nutrient turnover, plant productivity and other ecosystem services (reviewed in Huntly, 1991; Maguire et al., 2015; Kozlov and Zvereva, 2017), and modify plant species community structure and diversity (reviewed in Crawley, 1989; Huntly, 1991).

Important drivers of herbivory are identified to be plant species richness (reviewed in Andow, 1991; Jactel et al., 2021) and leaf quality (reviewed in Mattson, 1980; Scriber and Slansky, 1981). High nutritional content of leaves tends to have a positive effect on herbivore abundance and herbivory, i.e. ‘Plant Vigour Hypothesis’ (Price, 1991), especially by nitrogen (N) (Coley, 1983;

Whitfeld et al., 2012; reviewed in Mattson, 1980) but also by animal micronutrients such as magnesium (Mg) (Prather et al., 2020; Zhu et al., 2021; Anttonen et al., 2022). Negative effects on herbivores can be caused by high carbon content that correlates with leaf toughness and phenolics (Feeny, 1976; Dudt and Shure, 1994), but also by nitrogen-based defensive compounds with increasing leaf nitrogen (e.g. Campbell and Vallano, 2018).

Increasing plant species richness has been shown to often decrease herbivory, but with notably many exceptions (reviewed in Andow, 1991; Jactel et al., 2021). The reduction in herbivory in plant mixtures is often attributed to the lower resource base in mixtures as compared to monocultures, i.e. 'Resource Concentration Hypothesis' (Root, 1973), through either lower host plant abundance (White, 2013; Muiruri et al., 2019) or diversity per se (Bach, 1980). Variation in the plant species composition can obscure herbivore host finding through 'associational resistance' by olfactory, visual, and/or contact cues (Tahvanainen and Root, 1972; Finch and Collier, 2000; Sholes, 2008). In addition to increase of resource base by host plant abundance, higher plant biomass can have high positive effect on herbivore species richness and abundance (Marques et al., 2000; Whitfeld et al., 2012), but the increase can be less than proportional to plant biomass (Moore and Francis, 1991; Otway et al., 2005). Herbivory can, instead, increase on more apparent host plants due to differences in chemical defenses and size compared to neighboring plants (Feeny, 1976; Floater and Zalucki, 2000; Castagneyrol et al., 2013; Damien et al., 2016), and specialist herbivores can accumulate on fewer available hosts, demonstrating 'resource dilution' (Futuyma and Wasserman, 1980; Otway et al., 2005; Plath et al., 2012; Damien et al., 2016; but see Sholes, 2008). Herbivores can further 'spill over' from the preferred host plant to the surrounding vegetation demonstrating 'associational susceptibility' (Futuyma and Wasserman, 1980; White and Whitham, 2000). Positive neighborhood effects in plant mixtures, such as spill-over, are expected to occur more with generalist herbivores due to their versatility in host use (Bernays and Minkenberg, 1997). Although increased variability of nutrients in plant mixtures can suppress herbivory populations (Wetzel et al., 2016), generalists can benefit from dietary mixing by balancing their nutritional intake (Simpson et al., 1988; Karban et al., 2010; Lefcheck et al., 2013), extending their diet to plants ill-suited as exclusive food source (Barnes, 1955), and by deferring the negative effects caused by plant secondary compounds (Bernays et al., 1994; Hägele and Rowell-Rahier, 1999; Simpson and Raubenheimer, 2001). In addition, dietary mixing can increase the overall food consumption (Unsicker et al., 2008).

Further, larger monocultures are easier found by herbivores and more likely to retain them (Bach, 1988; Finch and Collier, 2000), and larger mixtures can enhance the associational resistance (Vehviläinen et al., 2007). Surrounding non-host vegetation can, in addition, mask smaller monocultures easier due to higher perimeter/area ratio (Bach, 1988). In contrast, easier movement of herbivores between smaller plots may explain why the positive effect of monocultures has been observed to weaken with increasing plot size (Bommarco and Banks, 2003). Thus, herbivory can rely on herbivore movement (reviewed in Risch et al., 1983; Smith and McSorley, 2000) and host detection capability (Bukovinszky et al., 2005). In forests, studies of vegetation patch-size effects in continuous vegetation are scarce, as they usually focus on forest fragmentation (e.g. De Carvalho Guimarães et al., 2014; Maguire et al., 2015), thus including for example effects of changing light conditions and increases in biomass (De Carvalho Guimarães et al., 2014; Régolini et al., 2014). A wider range of habitats in plant mixtures can further lead to top-down suppression of herbivory by a more abundant and species-rich predator community, i.e. the 'Enemies Hypothesis' (Root, 1973), and cause herbivore abundances to be higher near the mixture plot edges compared to central areas (Harmon et al., 2003). However, the support for increasing top-down control of herbivory in forests has been mixed (Staab and Schuldt, 2020; Stemmelen et al., 2022), and signs of top-down control in terrestrial ecosystems have often been demonstrated to be relatively weak compared to bottom-up effects (Schmitz, 1993; Polis, 1999; Scherber et al., 2010).

Herbivore abundances are often highest in the high leaf quality early to mid-growing season (e.g. Feeny, 1976; Murakami et al., 2005; Seifert et al., 2021), as structural carbon and tannins increase and nutritional content decreases when leaves age (Feeny, 1970; Chavana-Bryant et al., 2017; Menezes et al., 2022; reviewed in Mattson, 1980; Scriber and Slansky, 1981; Hauer-Jákli and Tränkner, 2019). However, the decline in nutritional content is not equal between tree species (Coley, 1983; Chavana-Bryant et al., 2017), as mature leaves of shade-tolerant tree species tend to be tougher, with higher phenolic and lower nitrogen and water content than in pioneering tree species (Coley, 1983; Dudt and Shure, 1994), leading to slower herbivory accumulation on the mature, but not the new leaves, of shade-tolerant species (Coley, 1983). Shade leaves in lower canopy tend to suffer higher herbivory (Lowman, 1985; Zhang et al., 2022), often attributed to decrease in phenolic contents (reviewed in Coley and Barone, 1996) to which shade-in-tolerant tree species are further more susceptible to (Dudt and Shure, 1994). However, effects of light conditions can be complex, as for example nitrogen is representative of photosynthetic capacity and tends to increase in higher light conditions (Pons, 2016), but several studies have shown increase in N content in shaded conditions (Henriksson et al., 2003; Barber and Marquis, 2011b; Stoepler and Rehill, 2012), and response to combination of light-induced changes in temperature, nutritional, and defensive leaf traits can be herbivore species specific (Stamp and Osier, 1998; Lemoine et al., 2014). Herbivores may further respond to light and temperature irrespective of changes in leaf quality (Osisanya, 1970; Nichols-Orians, 1991; Stoepler and Rehill, 2012), adapt their feeding to the metabolic changes caused by the thermal habitat, or change the habitat to improve the efficiency of nutritional intake (Stamp and Osier, 1998; Coggan et al., 2011; Clissold et al., 2013), and, in general, compensate for low-quality food by increasing feeding (Lee et al., 2006; Stiling and Cornelissen, 2007; Castagneyrol et al., 2018b).

Although lower leaf water content in mature leaves, and in drought and higher light intensity conditions can decrease herbivory (Coley, 1983; Henriksson et al., 2003; Huberty and Denno, 2004), drought conditions have also been shown to increase herbivory on stressed plants in drier soils, i.e. ‘Plant Stress Hypothesis’ (White, 1974), as seen with defoliations caused by herbivore outbreaks (reviewed in Mattson and Haack, 1987; Jactel et al., 2012). Especially short-term water stress can be expected to show beneficial effects for herbivores (Mattson and Haack, 1987), as it can elevate leaf nitrogen content without causing herbivores to be water deficient (Huberty and Denno, 2004). Drier soils can further diminish the differences in herbivory between canopy vertical stratum (Shao et al., 2021). The ‘resource availability’ hypothesis (Coley et al., 1985) further predicts that in nutrient-poor soils fast-growing pioneering tree species that out-grow the herbivore damage can be more susceptible to herbivory than poor nutrient condition adapted, better defended, species (Coley, 1983; Coley et al., 1985). Notably, nutrient availability is affected by soil water availability (Lambers and Oliveira, 2019). Nutrient-poor growing conditions can further cause generalist herbivore species to narrow their host breadth to most suitable host plants (Robinson and Strauss, 2020). However, in general, the effects of plant water stress have been inconsistent for chewing insects (Huberty and Denno, 2004; Cornelissen et al., 2008). Overall, much is still not known of how patterns in herbivory are determined in herbivore-species-rich ecosystems in response to leaf traits, tree species richness, and associational neighborhood interactions.

By incorporating leaf traits, forest structure and topography in a controlled subtropical tree species richness experiment (BEF-China; Bruelheide et al. 2014), our study aims to provide mechanistic insight on local neighborhood determinants of herbivory. Herbivory was assessed in two consecutive years on the same trees at the end of the growing season, and at the end of the rainy season in mid-summer in the second study year. We expected that 1) differences in herbivory between high leaf quality deciduous and lower quality evergreen trees are promoted in the second half of the growing season, and that 2) the increase in herbivory along the tree species richness gradient observed in an earlier study in the BEF-China experiment (Schuldt et al., 2017) is driven by plot size relationships, and resource dilution of highest-leaf-quality deciduous trees and dominant family (Fagaceae). We further expected that 3) herbivory is affected by tree apparency, associational susceptibility an associational resistance between neighboring trees depending on their size and leaf quality, that 4) herbivory response to intraspecific leaf trait variation is highest in monocultures, and that 5) environmental conditions indicating increased light conditions and drier soils modify the herbivory response between deciduous and evergreen trees and intraindividual differences between branch vertical locations.

2. Material and methods

2.1. *Study design*

This study was conducted in the BEF-China experimental forest area, which is currently the largest biodiversity-ecosystem functioning experiment in the world (Bruelheide et al., 2014), located in southeast China (Jiangxi province, 117°54'E, 29°07'N). Climatically the area lies in the northern parts of the subtropical zone, and the mean annual precipitation and temperature are

1821 mm and 16.7 °C, respectively (Yang et al., 2013). The study was conducted in site A of the BEF-China experiment, which was planted in 2009 and has a size of 18.4 ha. The site is located on mountain slopes surrounding a narrow wetland valley, with elevation above sea level and slope angle varying between 115.4 m - 277.6 m and 15.12° - 41.43°, respectively, between study plots (Bruelheide et al., 2013).

The study site consists of 271 plots, of which we used 61 that form a random extinction tree species richness gradient. Plot size is 25.8 m x 25.8 m, which corresponds to Chinese traditional unit 'mu'. Trees within the plots are planted in a regular rows by columns design (20 x 20 trees) in 1.29 m distance to each other, with equal proportions of species per mixture. Each mixture is represented by five plots, of which four are placed next to each other, forming a so-called "superplot" (Bruelheide et al., 2014). Tree replicates in the study were divided between the singleton plots (1 mu) and superplots (4 mu). Location as tree centrality for each tree was counted as the distance from the plot edge toward the center of 1 mu plots, and in the case of 4 mu plots toward the "superplot" centroid.

The study followed a tree species richness gradient from monocultures to 2, 4, 8, 16 and 24 species mixtures. The 24-tree species mixture is an extra level on top of the design, used here as a combined level with the 16-tree species mixtures, in order to increase the replicate number level and spatial distribution of the study trees in the highest tree species richness level. Tree individuals were selected by random within plot, but as tree species pairs following the design of (Trogisch et al., 2021), in order to link herbivory directly to leaf trait and neighborhood structural metrics measured using this design (Davrinche & Haider, 2021; Hildebrand et al., 2021). The tree species pair design promotes replicate numbers in lowest tree species richness levels, with 6, 9, 5, 5, 5 replicates per tree species in tree species richness levels 1, 2, 4, 8 and 16, respectively. The actual amount of tree individuals per tree species per richness level varied to some degree from this setup due to self-thinning reducing availability of trees of specific tree species in different richness levels. Additional smaller differences were also caused by two species mixture of Schima superba Gardner & Champ. - Rhus chinensis Mill. where no alive individuals of R. chinensis were found, and which were relabeled as monocultures. Additionally, some individuals of Castanopsis eyrei Champ. were recognized to belong to closely related Castanopsis fargesii Franch., and were removed from the data. Finally, differences in selection of the tree individuals between the herbivory estimation, leaf trait measurements (see section 3.3) and laser scanning (see section 3.4) further reduced some individuals. The actual amount of tree individuals per tree species per richness level thus varied between 1 to 16 (mean = 4.82, SD = 2.43), with 87, 107, 50, 61 and 69 tree individuals in tree species richness levels 1, 2, 4, 8 and 16, respectively. The tree species amount is slightly higher with deciduous tree species than with evergreens, with 10 and 6 species, respectively. Most common family of trees in the experiment is Fagaceae with 8 species, of which 5 are evergreen. The only non Fagaceae evergreen is the S. superba, which belongs to Theaceae (Table S1).

2.2. *Herbivory estimation*

Herbivory was visually estimated as the proportion of herbivore damaged leaf area. Leaves that were obviously damaged by other means (e.g. ripped or scratched), or the damage was clearly due to pathogens, were excluded. Five branches were selected by random along the whole canopy vertical layering of each tree, except in small amount of cases where the top-most branches could not be reached with very tall trees. The collection height of the branch was estimated with half a meter accuracy. In order to separate branch height variation from tree size variation, relative sampling height was counted by dividing each sampling height with the highest sampling point of the respective tree. The highest branch per tree was by average 4.7m (SD = 2.1m) for deciduous and 4.2m (SD = 1.7m) for evergreen trees, and the average relative sampling height was 0.82 (SD = 0.21) for deciduous and 0.71 (SD = 0.26) for evergreen trees.

Only new leaves of the current year were estimated from evergreen species. From each branch, ten leaves starting from the tip of the branch were selected and if there were less than ten new leaves the estimation continued on a nearby branch. From compound leaves, leaflets were estimated instead of the whole leaf. The damaged leaf area was evaluated to six categories: 0%, < 5%, < 25%, < 50%, < 75% and > 75%. Estimating herbivory as proportion of leaf area eaten is a common method, but with varying damage categories between studies (e.g., Vehviläinen et al., 2007; Castagneyrol et al., 2013; Schuldt et al., 2017; see also Kozlov and Zvereva, 2017 for further details). We used robust categories with an equal distribution, but noted down the low amount of damage separately (< 5%) in order to avoid inflating the < 25% category, as many leaves had only tiny bite marks on them. However, slight increase of herbivory estimates can still occur at the low levels of estimates because of not using yet finer grain categories (Kozlov and Zvereva, 2017). These were not used for ensuring robustness of estimates conducted by multiple people. For analysis, we used the mean of each category, 0, 2.5%, 12.5%, 62.5%, and 87.5%, respectively, and averaged the damage for each branch. As reviewed by Kozlov and Zvereva (2017), the chance of underestimating damage due to completely missing leaves is very low due to their low proportion of all leaves, and the leave petiole usually being left on the branch. The types of herbivore damage observed consisted of different kinds of defoliating (chewing/skeletonizing/cutting) marks, piercing marks from sap suckers, mines, and galls. We analyzed herbivory as the overall damage across the different categories, but because the estimation is area-based it responds most strongly to the abundant defoliating damage. The chance of other than defoliating damage pushing the estimate per leaf to a higher category, other than from 0% to < 5% and in case of rarely observed very abundant piercing marks or large mines from < 5% to < 25%, is very low . Leaf damage estimation was conducted three times: in August-September 2018 (26.8.-22.9.) and 2019 (16.8.-8.9.), and June 2019 (2.6-26.6.). June 2019 campaign was conducted in the mid-summer at the late rainy season, and the two autumn campaigns after dry season near the end of the growing season. First signs of leaf senescence were observed toward the end of autumn 2018 campaign, whereas senescence had not started yet during the autumn 2019 campaign.

2.3. *Leaf traits*

Nutritional leaf trait constitution of the trees was estimated from several leaf samples per tree crown from each focal tree used in herbivory estimation. The estimation of leaf traits was conducted by reflectance spectroscopy based predictions using ASD FieldSpec® 4 Wide Resolution Spectroradiometer (Malvern Panalytical Ltd., Malvern, United Kingdom) across 250 to 2500 nm. The equipment was optimized regularly with a calibration panel (Spectralon®, Labsphere, Durham, New Hampshire, USA). The predicted nutritional content values gained through reflectance spectroscopy were calibrated by samples with direct trait measurements (see for details Davrinche and Haider, 2021).

Nutritional elemental contents estimated were carbon (C), nitrogen (N), magnesium (Mg), calcium (Ca), potassium (K) and phosphorus (P), of which C, N and Mg were selected based on internal collinearities (Pearson $r < 0.7$) and on known importance of these nutrients for insects (e.g. Mattson, 1980; Scriber and Slansky, 1981; Elser et al., 2000; Chapman, 2013; Prather et al., 2020; Zhu et al., 2021). Additionally, the inter- and intraspecific coefficient of variation (CV) was estimated for C, N and Mg. Interspecific CV was estimated between tree species leaf trait averages, and the overall intraspecific CV as the average of each tree species' intraspecific CV.

In order to separate the effects that leaf traits (N, Mg, C) have on herbivory through intraspecific- and interspecific variation, two relative measures were calculated. Intraspecific deviation was estimated by subtracting the tree species average of each leaf trait value from the tree specific values. Neighborhood deviation was estimated by first counting the average for each leaf trait of the eight potential closest neighboring trees (within the 1.29 m planting distance) using tree species averaged values, and then subtracting this from the species average of each focal tree. With samples from the 24-tree species mixtures, the extra eight species (Table S1; 12 individuals in total including two unknown tree species at the edge of a plot) otherwise not in the design lacked leaf traits, and in these cases the neighborhood average was estimated based only on the species included to the 16 species pool. For C. fargesii in the neighborhood (7 individuals in total) the species leaf trait average was obtained from the adjacent BEF-China experiment field site, site B (Bruelheide et al., 2014).

2.4. *Forest structure and topography*

We assessed multiple variables in order to characterize the structure of the forest stands at the plot level and at the level of the immediate neighborhood. Focal- and neighborhood tree sizes were estimated as diameter at breast height and transformed to basal area (BA). Few trees were smaller than 1.3 m in height and their DBH was marked down as 0.5 cm. Tree apparency was further calculated as:

$$Tree\ apparency = \frac{(Focal\ BA + Mean\ neighborhood\ BA)}{(Focal\ BA + Neighborhood\ BA)}$$

which is an adaptation of (Castagneyrol et al., 2013) due to regular tree planting distances.

Based on the mortality of the neighboring trees, the open area in neighborhood was estimated to account for the increase in light availability. Open area was counted as sum of the areas of dead tree positions around the focal tree (~1.66 m2 for each dead tree based on planting distances). Because branches of neighboring trees can grow to fill the space left by a dead tree, increased weight was given to larger continuous gaps by dividing the overall dead tree area by the number of continuous gaps (i.e. ⩾ 2 dead tree positions next to each other).

The canopy structure was addressed with TLS derived measures, measured in February-April 2019 (Hildebrand et al., 2021). Branch abundance was estimated as the number of voxels (describes an object in three dimensional space) with 5 cm edge in 50 cm vertical layer with 3 m radius around each focal tree. Vertical distribution of the voxels within the 3 m radius was estimated using Gini-index (vertical Gini). Lover vertical Gini values indicate more equal canopy distribution and less densely packed canopy. Branch abundance and vertical Gini can be both considered to correspond to light conditions surrounding the focal tree, as foliage distribution is largely governed by light foraging (Valladares and Niinemets, 2007). As the measures are taken in 3 m radius, the correlation to light conditions is robust, not taking into account competition between focal and neighboring trees. The vegetation density at plot level was estimated using mean fractal dimension MeanFrac (Ehbrecht et al., 2017) as a proxy. Fractal dimension is a measure of structural complexity, but it in general responds to the space filling capacity of an object (Loke and Chisholm, 2022). MeanFrac is scale-independent, making the values non-correlated with tree sizes in the plot. Thus, the higher values indicating higher density of vegetation elements can be gained also by small and densely branched trees, whereas large trees can, in turn, gain lower values if there is high amount of open space around them (Ehbrecht et al., 2017; Zemp et al., 2019). Five of the top-most branches in herbivory estimations were slightly higher than highest TLS layer and were corrected to match it, a difference likely caused by the difference in timing between the measures.

Topography of the plots was included in the analyses to account for microclimatic differences within the study area. Topographic factors were elevation (measured by hypsometer and interpolation from map using GIS), slope angle (GIS), the solar radiation the plot accumulates during a day (GIS, kWh/m²), and slope northness and eastness (Bruelheide et al., 2013). Because of collinearity between the topographical variables, principal component analysis was carried between them using the package "vegan" (Oksanen et al., 2022) in R statistical environment (R Core Team, 2022). The three most important PC scores explained 76.6% of total variance and were used as explanatory variables in the statistical analyses of herbivore damage (see table 1 for full PCA information). PC.1 was driven strongest by higher elevation, steeper slopes and lower overall solar irradiation but to a lesser degree also by more eastern locations. PC.2 responded most strongly to northern slope positions and lesser degree to lower overall solar irradiation. PC.3 responded strongest to more western slope positions and to a lesser degree to more southern slope locations and overall lower solar irradiation.

Table 1. Importance and loadings of principal components of topographical variables.

Importance of components:	PC.1	PC.2	PC.3	PC.4	PC.5
Standard deviation	1.405	0.989	0.938	0.824	0.700
Proportion of Variance	0.395	0.196	0.176	0.136	0.098
Cumulative Proportion	0.395	0.591	0.766	0.902	1.000

Loadings:	PC.1	PC.2	PC.3	PC.4	PC.5
Elevation	0.507			0.826	0.246
Slope	0.576	0.144	0.102	-0.124	-0.788
Solar mWh	-0.499	-0.316	-0.347	0.484	-0.544
Eastness	0.352	-0.193	-0.875	-0.228	0.144
Northness	-0.194	0.917	-0.320	0.130	

2.5. *Data analysis*

We analyzed total yearly accumulation of herbivore damage, and the accumulation by the end of rainy season in the second study year (2019). The yearly accumulation was estimated for combined dataset of the two study years, and for comparison, separately for each study year.

All analyses were conducted in R v 4.2.2 environment (R Core Team, 2022) with generalized linear mixed effects models with package 'glmmTMB' (Brooks et al., 2017). Model validation using simulated datasets (1000) was carried out with package ‘DHARMa’ (Hartig, 2022). Coley (1983) noted that herbivore damage distribution tends to be positively skewed, with small number of high values pulling the mean away from the median, and at the same time smaller than median values being rare. This was the case also in our study, though with the skewness being so sharp that the mode was still smaller than the median (Figure S1). Further, the damage proportions relate to different sized leaves between tree species, and thus, beta distribution with logit link was assumed suitable for the analysis. However, this led to systematically slightly lower DHARMa residuals than the estimates, similarly than if using linear mixed effects analysis with the traditional approach of arcsine square root transformed data (e.g. White and Whitham, 2000; Stoepler and Rehill, 2012) or the alternative logit transformation (Warton and Hui, 2011), and instead more robust to skewness gamma distribution with log link function was used in the final analyses. The response value range was scaled up in the gamma distributed models by the minimum positive value in each dataset (0.25% herbivory per branch) in order to include the low number of samples with no damage (0.002% of branches across all campaigns). Only ~1% of the 1000 simulations with DHARMa provided systematically slightly lower or higher residuals than the gamma distributed model.

Explanatory variables used in all analyses were: tree species richness, tree species status as deciduous/evergreen and family identity as Fagaceae/other, relative branch height, focal BA, neighborhood BA, open area, TLS derived variables neighborhood branch abundance, vertical Gini and vegetation density, leaf traits as Intraspecific and neighborhood deviation, tree centrality within the plot, and first three topography PC axes. Year of collection was included as a covariate in the combined autumn dataset analysis. Additional model comparisons were conducted with variable replacements. To test how herbivory responds to plot size and thus the perimeter/area ratio, the tree centrality was replaced by plot size (1 vs. 4 mu, as factorial), and to test whether tree size effects are influenced by the relative focal and neighborhood tree sizes, focal- and neighborhood BA were replaced with tree apparency. All continuous variables were scaled by subtracting the mean and dividing by standard deviation. Before running analyses, low collinearity between explanatory variables was ensured by estimating their internal Spearman correlations ($r < 0.7$), to which tree type variables were included as binary and plot size as ordinal.

Further, variance inflation was tested for all explanatory variables and their interactions (vif < 5 for all variables) using the package 'performance' (Lüdecke et al., 2021). To account for non-independence of tree individuals of a species, and branches within a tree, as well as tree replicates within a plot, random intercepts were included for tree species, and tree individual nested within plot. In the combined autumn dataset random intercepts were included per year for each variable. The effect of tree species pair design was accounted for by comparing AIC values of models using focal tree to tree species pair as a random factor, and using in the final model the one providing better AIC value.

Additionally, interactions between explanatory variables were included in the analyses. In order to evaluate how increasing tree species richness relates to other drivers of herbivory, interactions were included with 1a) tree type as deciduous/evergreen and family identity as Fagaceae for resource dilution effects, except in summer and autumn 2019 models where interaction with family identity as Fagaceae was dropped due to high vif value, 1b) tree centrality within the plot or plot size for resource concentration and edge effects, 1c) neighborhood deviations for each leaf trait for test of associative effects from nutritional perspective, 1d) intraspecific leaf trait deviations and relative branch height for testing if intraspecific and intra-individual variation has higher effect on herbivory in monocultures, and 1e) focal BA and branch abundance for small scale resource abundance differences between tree richness levels. In order to further estimate the effects of tree size, interactions of focal BA with 2a) tree centrality within the plot or plot size, and 2b) intraspecific leaf trait deviations were included. For estimating the effects of surrounding vegetation structure, interactions with neighborhood BA were included with 3a) branch abundance and 3b) neighborhood leaf trait deviations. For vertical differences in herbivory within tree individuals, interaction were included with 4a) focal BA for tree size dependent effects, 4b) neighborhood branch abundance and vertical Gini as further proxies for light conditions, and 4c) tree type as deciduous/evergreen to test whether herbivory responds to their intra-individual variation differently. Because topographical conditions can modify the light and water conditions of trees, interactions of all three topography PC axes were included with 5a) tree type as deciduous/evergreen, 5b) relative branch height, and 5c) branch abundance, and 5d) the elevation and slope steepness driven PC1 with focal BA and tree centrality within the plot in order to estimate if edge- and small scale resource concentration effects are constrained to less stressful lowland habitats. All the same interactions were included with tree apparency than with focal BA and neighborhood BA.

All models were reduced in order to obtain the most parsimonious models based on the model information value using Akaike information criterion (AIC) using function ‘drop1’. Difference of $\Delta AIC \geq 2$ was considered to indicate a substantially poorer model (Burnham and Anderson, 2002). However, the reduction with the autumn 2018 model was stopped at $\Delta AIC = 1$ due to further reduction leading to worse model reliability as indicated by simulation comparisons using DHARMa. Each initial model was compared by AIC with the alternative variables, and the same comparison was done for the reduced models.

3. Results

Variation in herbivory within each tree type was notably high across branches. Average herbivory across all branches of all trees was 7.8% (SD = 7.1) at mid-summer at the end of rainy season 2019, 12.4% (SD = 10.4) in autumn 2018, and 11.7% (SD = 9.0) in 2019. In 2018, herbivory was higher in deciduous 13.9% (SD = 11.4) than on evergreen 9.7% (SD = 7.7) trees (Figure 1). Herbivory was further slightly higher in deciduous Fagaceae 14.2% (SD = 9.1) than deciduous trees in other families 13.8% (SD = 12.4), and also higher with evergreen Fagaceae 10.4% (SD = 8.1) than the only non-Fagaceae tree species, Schima superba 6.9% (SD = 4.6).

At mid-summer 2019, herbivory was slightly lower on deciduous 7.5% (SD = 6.4) than on evergreen 8.4% (SD = 8.0) trees (Figure 1). In contrast, at autumn 2019, herbivory was higher in deciduous 12.4% (SD= 9.0) than in evergreen 10.6% (SD = 9.0) trees. At mid-summer 2019, deciduous 9.0% (SD = 8.1) and evergreen 9.1% (SD = 8.4) Fagaceae had very close to the same amount of herbivory, and deciduous trees in other families had lower herbivory 6.6% (SD = 5.2). In contrast, at autumn 2019, herbivory was clearly higher in deciduous Fagaceae 14.7% (SD = 9.5) than in evergreen Fagaceae 11.2% (SD = 9.2), in which the herbivory was very close to the same as in non-Fagaceae deciduous trees 11.2% (SD = 8.5). Herbivory was lowest in Schima superba at mid-summer and autumn 2019, 5.8% (SD = 5.4) and 8.1% (SD = 7.8), respectively.

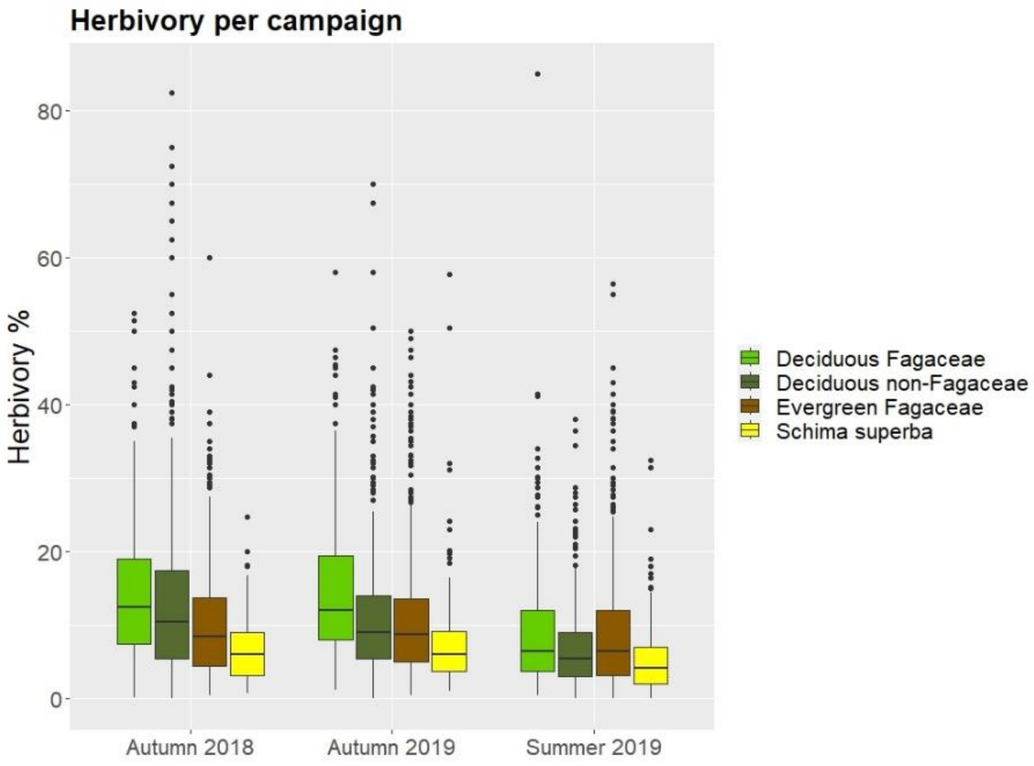

Figure 1. Herbivore damage per branch for each sampling campaign. Damage levels shown for deciduous Fagaceae and deciduous trees in other families, and for evergreen Fagaceae and the only non-Fagaceae evergreen tree species, Schima superba.

Deciduous trees had higher N and Mg, and lower C content than evergreens (Figure 2). Trees in the Fagaceae family had higher N (Figure 2a) but lower Mg (Figure 2b) content than trees in other families. Deciduous Fagaceae also had higher C content than other families, and evergreen Fagaceae had by average slightly lower carbon content than Schima superba (Figure 2c). The interspecific CV was higher than intraspecific with Mg (0.429 vs. 0.248) and C (0.022 vs. 0.014) but lower with N (0.134 vs. 0.146).

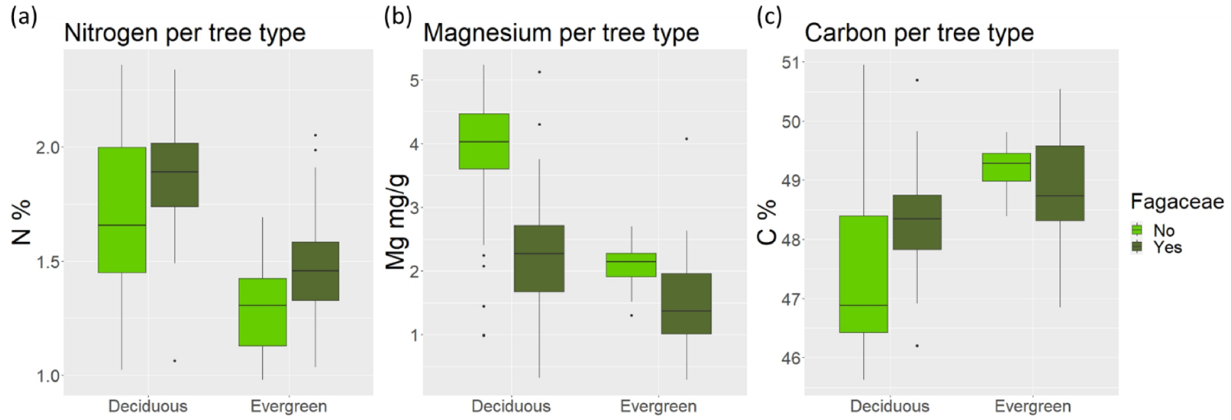

Figure 2. Tree individual averages of leaf traits per evergreen/deciduous and Fagaceae/other family trees for (a) nitrogen (N), (b) magnesium (Mg), and (c) carbon (C).

1.1. GLME estimates of herbivory damage

The best model based on AIC for overall herbivory damage using the combined autumn dataset included tree centrality instead of plot size (ΔAIC = 10) and focal and neighborhood BA instead of tree apparency (ΔAIC = 6). Focal tree as random factor instead of tree species pair led to higher information value models (ΔAIC ≥ 28.5). The best model for overall herbivory accumulation explained 41.2% percent of the overall variation, of which 10.5% by fixed factors, and from the random factors 14.8% by focal tree within plot, 10.4% by plot, and 5.5% by tree species. In the summer 2019 analysis the model explained 34.9% percent of the overall variation, of which 7.2% by fixed factors, and from the random factors 20.4% by focal tree within plot, 3.6% by plot, and 3.7% by tree species.

In the combined autumn dataset analysis tree species richness showed marginally significant overall positive relationship with herbivore damage (p = 0.078) (see Table 2 for full GLME results). Deciduous trees and tree species in the family Fagaceae accumulated more damage than evergreens and non-Fagaceae trees, and these differences further increased toward higher tree species richness levels (Figure 3a, b). Deciduous trees also accumulated slightly more damage in higher elevations (Topography PC.1) whereas evergreens suffered less damage (Figure 3c).

Table 2. Summary of generalized linear mixed effects model results of overall herbivory using combined autumn 2018 and 2019 dataset. Standardized parameter estimates (with standard errors, z and p values) are shown for explanatory variables. Values in bold signify p ≤ 0.05, and in italics p ≤ 0.1.

Overall herbivory	**Proportion of leaf damage**		
	Estimate± Std. Error	z value	Pr(>|z|)
(Intercept)	2.425±0.059	41.20	**<0.001**
Tree species richness	0.065±0.037	1.77	*0.078*
Evergreen focal tree	-0.473±0.099	-4.77	**<0.001**
Fagaceae focal tree	0.326±0.089	3.65	**<0.001**
Tree centrality	0.026±0.018	1.40	0.162
Focal BA	0.004±0.020	0.18	0.857
Neighborhood BA	0.042±0.020	2.10	**0.036**
Relative branch height	-0.023±0.011	-2.04	**0.042**
Vertical Gini	-0.022±0.019	-1.15	0.250
Branch abundance	0.009±0.016	0.56	0.577
Topography PC.1	0.016±0.023	0.68	0.496
Topography PC.2	-0.021±0.029	-0.73	0.468
Intraspecific N deviation	0.011±0.018	0.61	0.540
Intraspecific Mg deviation	0.039±0.016	2.37	**0.018**
Neighborhood C deviation	0.012±0.026	0.47	0.638
Neighborhood N deviation	-0.074±0.030	-2.45	**0.014**
Tree species richness: Evergreen focal tree	-0.135±0.042	-3.23	**0.001**
Tree species richness: Fagaceae focal tree	0.076±0.039	1.98	**0.048**
Tree species richness: Tree centrality	-0.046±0.017	-2.76	**0.006**
Tree species richness: Intraspecific N deviation	-0.075±0.018	-4.12	**<0.001**
Evergreen focal tree: Topography PC.1	-0.074±0.035	-2.11	**0.035**
Tree centrality: Focal BA	-0.048±0.018	-2.65	**0.008**
Tree centrality: Topography PC.1	-0.029±0.014	-2.07	**0.039**
Neighborhood BA: Branch abundance	0.041±0.015	2.72	**0.007**
Neighborhood BA: Neighborhood C deviation	-0.040±0.017	-2.33	**0.020**
Relative branch height: Vertical Gini	0.023±0.010	2.29	**0.022**
Relative branch height: Topography PC.1	0.033±0.008	3.92	**<0.001**
Relative branch height: Topography PC.2	-0.037±0.012	-3.03	**0.002**

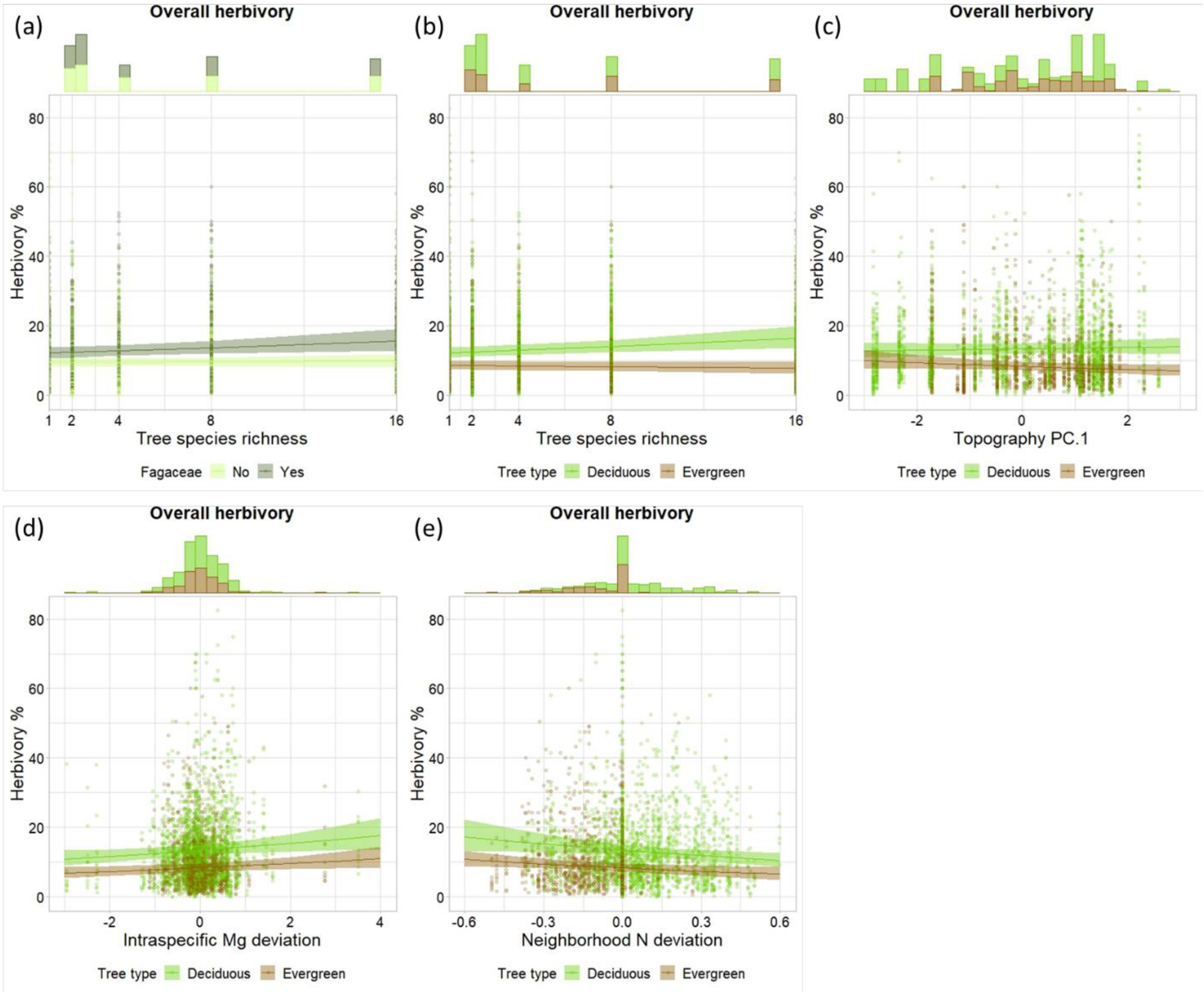

Figure 3. Herbivore damage as a function of tree species richness and focal tree (a) belonging to the family Fagaceae, or (b) being deciduous/evergreen, and of tree type as deciduous/evergreen and (c) topography PC.1, (d) intraspecific Mg deviation, and (e) neighborhood N deviation. Points represent the observed values and histograms the amount of observed data points per x-axis level.

Trees with higher intraspecific Mg content (Figure 3d) and trees surrounded by higher N content trees (Figure 3e) had systematically higher herbivory. In contrast, the effect of intraspecific N deviation depended on tree species richness level, with increased herbivore damage on high-N-content trees in low tree richness levels but decreased herbivory in high richness levels (Figure 4).

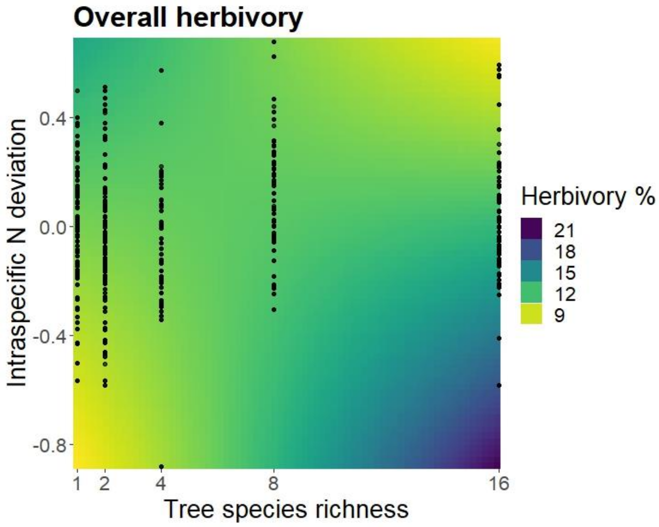

Figure 4. Herbivore damage as a function of tree species richness and intraspecific N deviation. Colors represent the estimated change in herbivory and points represent the observed values.

In contrast to the best model using tree centrality, tree richness was significantly positively related to herbivore damage in the model using plot size (estimate ± std. error = 0.142 ± 0.054, z = 2.64, p = 0.008). Trees accumulated more damage in larger monoculture plots, and in smaller highest tree species richness level plots (estimate ± std. error = -0.125 ± 0.063, z = -1.98, p = 0.048) (Figure 5a). In the model using tree centrality (Table 2), trees growing closer to the plot center accumulated more herbivore damage in low tree species richness, and trees closer to edge in highest richness levels (Figure 5b). Larger trees accumulated more damage closer to plot edges, whereas smaller trees gained slightly more damage closer to plot centers (Figure 5c). Similar relationship was seen if focal BA was replaced in the model with tree apparency (estimate ± std. error = 0.062 ± 0.019, z = -3.25, p = 0.001). Trees in central positions accumulated otherwise more damage than trees close to edges, but this effect disappeared in plots in higher elevations/steeper slopes (topography PC.1; Figure 5d).

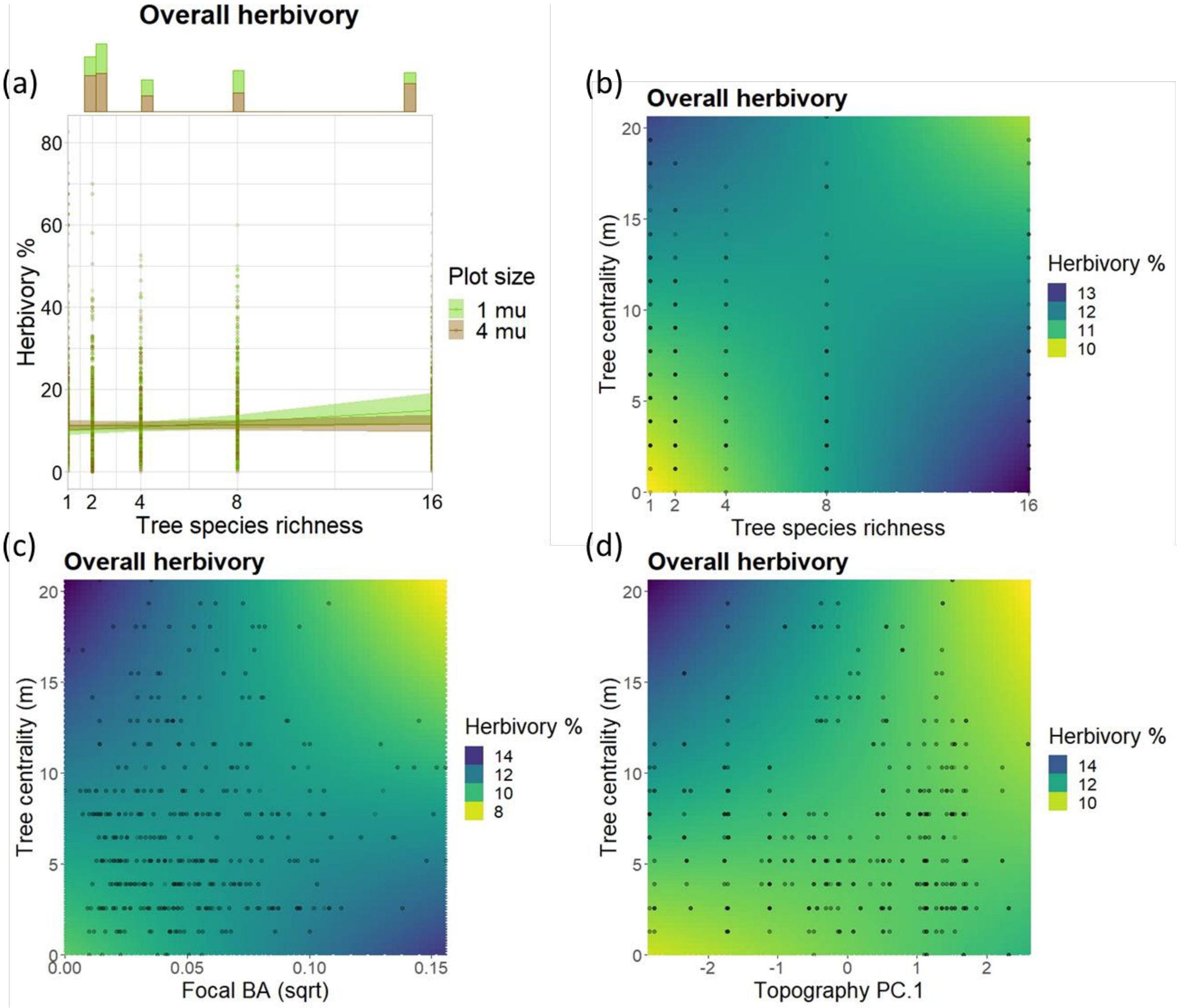

Figure 5. Herbivore damage as a function of (a) plot size and tree species richness, or tree centrality and (b) tree species richness, (c) focal BA, or (d) topography PC.1. In figure (a) shaded areas show 95% confidence intervals, points the observed values, and histograms the amount of observations per tree species richness level for each plot size. In figures (b-d) colors represent the estimated change in herbivory and points represent the observed values. Centrality values up ~13 m appear in both 1 and 4 mu plots, and higher values only in 4 mu plots.

Larger trees in the neighborhood promoted herbivore damage, and this effect was stronger in the height layers with higher branch abundance (Figure 6a), and when the neighboring trees were of higher C content than the focal tree (Figure 6b). In the alternative model with tree apparency instead of focal- and neighborhood BA, the tree apparency had marginally significant negative relationship with herbivory (estimate ± std. error = 0.033 ± 0.018, z = -1.81, p = 0.070) and similar interaction with tree centrality than focal BA (estimate ± std. error = -0.062 ± 0.019, z = -3.25, p = 0.001).

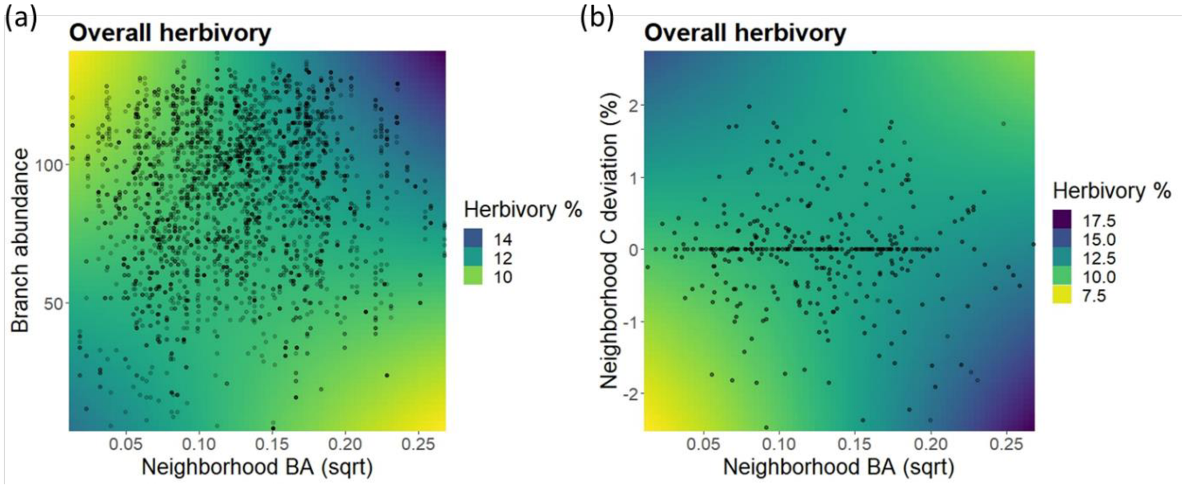

Figure 6. Herbivore damage as a function of neighborhood BA and (a) branch abundance per height layer, or (b) neighborhood C deviation. Colors represent the estimated change in herbivory and points represent the observed values.

Branches in the lower heights accumulated more herbivore damage, but this effect became absent when the branches were more unequally vertically distributed (Figure 7a). The lower branches also did not accumulate more damage when the trees were growing in high elevations/steep slopes (topography PC.1; Figure 7b) and on south facing slopes (topography PC.2; Figure 7c). In all these cases, the relationship of herbivory with branch height was further reversed to a slight degree.

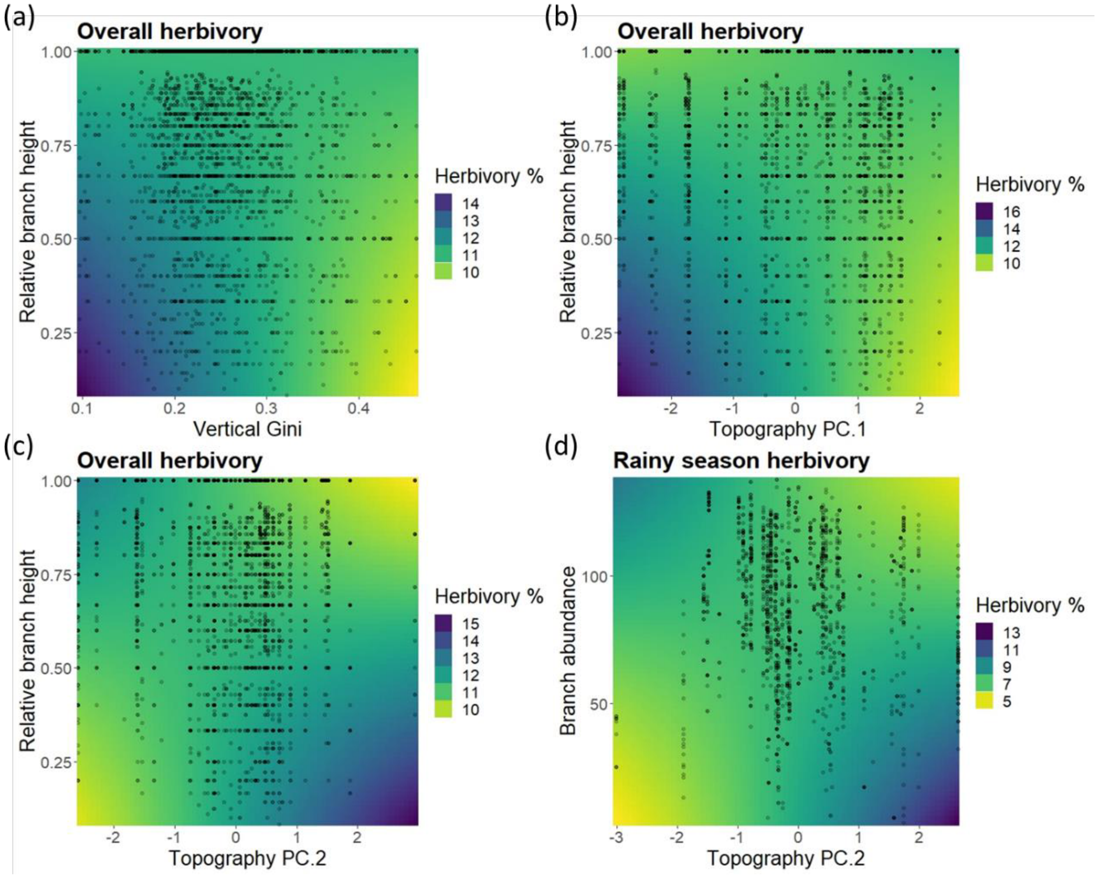

Figure 7. Herbivore damage for overall herbivory as a function of relative branch height and (a) vertical Gini, (b) topography PC.1, or (c) topography PC.2, and for end of rainy season herbivory as a function of (d) branch abundance with topography PC.2. Colors represent the estimated change in herbivory and points represent the observed values.

Several of the significant effects seen on herbivory with the combined autumn dataset were weaker and not retained in one or both of the separate autumn 2018 and 2019 dataset analyses (Table 3). However, the trends in the separate years were to the same direction than with the combined autumn dataset. Significant effects on herbivory in both separate years were: tree type as evergreen/deciduous, and interactions of tree species richness with intraspecific N deviation, relative branch height with topography PC.1, and marginally significantly neighborhood BA with neighborhood C deviation. Significant effects only in 2018 were: tree species richness, neighborhood BA, and interactions of tree species richness with tree centrality and tree type as deciduous/evergreen, neighborhood BA with branch abundance, and marginally significantly branch abundance with topography PC.2. Additionally, in 2018 but not in combined autumn dataset, topography PC.3 had marginally significant negative relationship with herbivory, and significant interaction with tree type as deciduous/evergreen showing higher herbivory with deciduous trees in the east facing slopes (Figure S2). Significant effects in 2019 were: tree type as Fagaceae, marginally significantly intraspecific Mg deviation, and interactions of tree centrality with focal BA and marginally significantly with topography PC.1, relative branch height with vertical Gini, branch abundance and topography PC.2. Additionally, in 2019 but not in combined autumn dataset, vertical Gini had marginally significant negative relationship with herbivory.

3.2. Herbivore damage at the end of the rainy season

Herbivory at the end of the rainy season as compared to end of the growing season 2019 showed in several cases different relationships with the explanatory variables (Table 3). Similar to end of the growing season, significant relationships with herbivory were seen with tree type as Fagaceae, and with interaction of relative branch height with vertical Gini. In contrast to end of the growing season, trees growing in neighborhoods with higher Mg content than in the focal tree were more vulnerable to herbivore damage, and tree type as deciduous/evergreen had significant interaction with topography PC.1 (similar to combined autumn dataset). Further, herbivory increased with higher branch abundance in the north facing slopes (topography PC.2; Figure 7d).

Table 3. Summary of generalized linear mixed effects model results of herbivory measured at the end of each study year, 2018 and 2019, and by the end of the rainy season in the mid-summer 2019. Standardized parameter estimates (with standard errors, z and p values) are shown for explanatory variables. Values in bold signify p ≤ 0.05, and in italics p ≤ 0.1. Variables not retained in the model after AIC based reduction marked as '-'.

	Autumn 2018			**Autumn 2019**			**End of rainy season 2019**		
	Estimate ± Std. Error	z value	Pr(>|z|)	Estimate ± Std. Error	z value	Pr(>|z|)	Estimate± Std. Error	z value	Pr(>|z|)
Intercept	2.539±0.087	29.36	**<0.001**	2.343±0.072	32.77	**<0.001**	1.889±0.077	24.38	**<0.001**
Tree species richness	0.161±0.055	2.94	**0.003**	0.016±0.032	0.5	0.618	-	-	-
Evergreen focal tree	-0.311±0.130	-2.39	**0.017**	-0.315±0.113	-2.8	**0.005**	-0.096±0.114	-0.85	0.397
Fagaceae focal tree	-	-	-	0.342±0.109	3.14	**0.002**	0.246±0.114	2.15	**0.032**
Tree centrality	0.023±0.026	0.89	0.373	0.026±0.023	1.12	0.262	-	-	-
Focal BA	-	-	-	-0.018±0.027	-0.69	0.492	-	-	-
Neighborhood BA	0.063±0.028	2.27	**0.023**	0.010±0.026	0.38	0.704	-	-	-
Relative branch height	-0.026±0.016	-1.6	0.111	-0.019±0.016	-1.18	0.237	0.016±0.018	0.91	0.362
Vertical Gini	-	-	-	-0.042±0.025	-1.66	*0.096*	-0.005±0.028	-0.17	0.867
Branch abundance	-0.012±0.024	-0.48	0.63	-0.002±0.021	-0.1	0.922	-0.035±0.024	-1.47	0.143
Topography PC.1	0.015±0.034	0.44	0.66	-0.017±0.022	-0.75	0.452	0.02±0.027	0.76	0.445
Topography PC.2	-0.063±0.046	-1.38	0.166	-0.010±0.031	-0.32	0.747	-0.008±0.034	-0.24	0.814
Topography PC.3	-0.105±0.055	-1.92	*0.055*	-	-	-	-	-	-
Intraspecific N deviation	0.029±0.026	1.11	0.267	0.008±0.024	0.32	0.747	-	-	-
Intraspecific Mg deviation	-	-	-	0.043±0.022	1.94	*0.053*	-	-	-
Neighborhood Mg deviation	-	-	-	-	-	-	-0.082±0.034	-2.38	**0.017**
Neighborhood C deviation	0.033±0.038	0.88	0.378	0.028±0.032	0.87	0.383	-	-	-
Tree species richness: Tree centrality	-0.078±0.023	-3.36	**0.001**	-	-	-	-	-	-
Tree species richness: Evergreen focal tree	-0.158±0.054	-2.92	**0.004**	-	-	-	-	-	-
Tree species richness: Intraspecific N deviation	-0.063±0.026	-2.4	**0.016**	-0.072±0.024	-3.02	**0.003**	-	-	-
Evergreen focal tree: Topography PC.1	-	-	-	-	-	-	-0.146±0.049	-2.99	**0.003**
Evergreen focal tree: Topography PC.3	0.123±0.062	1.99	**0.047**	-	-	-	-	-	-
Tree centrality: Focal BA	-	-	-	-0.055±0.025	-2.2	**0.028**	-	-	-
Neighborhood BA: Branch abundance	0.048±0.022	2.18	**0.029**	-	-	-	-	-	-
Neighborhood BA: Neighborhood C deviation	-0.046±0.025	-1.85	*0.065*	-0.046±0.023	-1.95	*0.051*	-	-	-
Branch abundance: Topography PC.2	-0.046±0.024	-1.87	*0.062*	-	-	-	-0.062±0.022	-2.83	**0.005**
Relative branch height: Vertical Gini	-	-	-	0.048±0.014	3.41	**0.001**	0.049±0.016	3.05	**0.002**
Relative branch height: Branch abundance	-	-	-	0.051±0.017	2.97	**0.003**	-	-	-
Relative branch height: Topography PC.1	0.039±0.012	3.29	**0.001**	0.027±0.011	2.39	**0.017**	-	-	-
Relative branch height: Topography PC.2	-	-	-	-0.058±0.017	-3.4	**0.001**	-	-	-

4. Discussion

Our study demonstrates that neighborhood interactions between trees are an important element determining herbivory in forests. However, these effects largely arise during the latter half of the growing season (dry season) when herbivory accumulation is higher on the more nutrient-rich trees, especially based on N content, demonstrating a likely importance of the seasonal decline in leaf quality on neighborhood interactions. Earlier studies of herbivory from the same field site, as well as nearby natural state forest, have shown increasing herbivory with increasing tree species richness (Schuldt et al., 2010, 2015, 2017). In this study, we demonstrated that this pattern relies on the trees' functional grouping of deciduous/evergreen species and family identity, as well as plot edge effects. Further, we demonstrate that associational neighborhood effects on herbivory depend on leaf traits as well as surrounding biomass. Overall, the results showed variety of patterns in herbivory accumulation from resource concentration, to resource dilution and tree apparency based on tree size, leaf traits, and taxonomy, to associational susceptibility and spillover. Further, the results overall supported the plant vigor hypothesis with higher herbivory on more nutrient-rich trees, but topography had a strong effect on herbivory between tree types as well as between sampling heights within a tree, indicating the importance of plant stress. As discussed below, several of the mechanisms can take place simultaneously in a heterogeneous forest.

Seasonality and tree species richness

A higher proportion of overall herbivory occurred in the first half of the growing season, correlating with peak herbivore abundances being timed on highest leaf quality season (e.g. Feeny, 1970; Murakami et al., 2005); as also observed at our study site at the same year as the current study (Anttonen et al., 2022; Wang, yet unpublished data). As leaf quality reduces along the growing season when leaves mature (Mattson, 1980; Scriber and Slansky, 1981; Chavana-Bryant et al., 2017; Hauer-Jákli and Tränkner, 2019), the early season herbivory would, thus, be expected to be highest on the tree species that have the highest C and lowest N content in the autumn. This was the case in our study, as herbivory was higher in evergreen trees in mid-summer and increased more with deciduous trees in the latter half of the growing season.

Herbivory was further higher with the Fagaceae family in mid-summer. Specialized herbivore abundance peaks are known to occur on Fagaceae in early season (Feeny, 1970; Murakami et al., 2005), and caterpillar community was found to be most abundant, specialized, and to consist in high degree of early instars in the low-Mg-content trees (essentially Fagaceae) in spring (Anttonen et al., 2022). However, herbivory also increased strongly on deciduous Fagaceae during the latter half of the growing season. This emphasizes the importance of leaf N content over C content on late season herbivory, similar to what Feeny (1970) observed for early season Fagaceae herbivory, as deciduous Fagaceae had higher C content than deciduous trees in other families but higher N content than evergreen Fagaceae.

The seasonally increasing difference in leaf quality between tree species also likely explains why the resource dilution effect (e.g. Futuyma and Wasserman, 1980; Plath et al., 2012; Régolini et al., 2014) was observed specifically in the latter half of the growing season with deciduous trees. When the overall surrounding resource base declines alongside leaf quality, the higher quality deciduous trees become more apparent in their neighborhoods. However, increase in herbivory was further observed as neighborhood level apparency with low-Mg-content tree species (essentially Fagaceae) after the first half of the growing season. Resource dilution was further observed with Fagaceae with increasing tree species richness after the latter half of the growing season, likely demonstrating a phylogenetic connection of herbivores to the dominant tree family in the experiment (Wang et al., 2020). Notably, the latter half of the growing season correlates with the dry season, and drought conditions can mediate herbivory between monocultures and tree species mixtures (Castagneyrol et al., 2018a). Plant trait variability between tree species can reduce competition of light and water (Kelty, 1989; Anderegg et al., 2018; see also review in Jose et al., 2006), increasing water use efficiency (Forrester et al., 2010) which can be especially beneficial for drought-in-tolerant species (Fichtner et al., 2020), such as deciduous trees (Kröber et al., 2014).

The higher late growing season herbivory on deciduous trees than evergreen trees can be further mediated by herbivore diet breadth. Although resource dilution effect has been usually observed with and attributed to specialist herbivores tracking their preferred host plants (e.g. Futuyma and Wasserman, 1980; Otway et al., 2005; Plath et al., 2012), generalist herbivores can prefer high nutritional content and low carbon content trees in the late growing season (Barber and Marquis, 2011a; Anttonen et al., 2022). In addition, peak abundance of commonly highly generalist grasshoppers (Chapman and Sword 1997, as cited in Sword and Dopman, 1999) occur in the late summer/autumn, and the highest diet ranges can occur on the highly mobile adults (Sword and Dopman, 1999; Unsicker et al., 2008). The grasshopper sub-order Caelifera also attacked artificial caterpillars in high frequency in a simultaneously conducted predation experiment (Anttonen et al., 2023). Generalists can be further more abundant in tree species mixtures (as observed in BEF-China experiment; Zhang et al., 2017) and benefit from dietary mixing (e.g. Singer et al., 2004; Karban et al., 2010; Lefcheck et al., 2013). Feeding on a specific host, whether nutritionally optimal or sub-optimal, can also increase when the frequency of that food source is reduced, as observed with grasshoppers (Chandra and Williams, 1983; Behmer et al., 2001), connecting the resource dilution and dietary mixing mechanisms.

The plant vigor hypothesis (Price, 1991) was supported by higher tree intraspecific Mg content, and also intraspecific N content in monocultures, promoting herbivory. Whether this effect was seasonally affected cannot be ascertained here, as the trends were weak in 2019, when the differences in mid-summer and autumn herbivory were compared. Higher intraspecific N content can be especially beneficial for specialists (Cornelissen and Stiling, 2006), and intraspecific host selection can be more efficient in monocultures due to no interference from other tree species. However, where we expected a weaker positive effect in high tree species richness than in monocultures in respect to intraspecific N content, the trend was surprisingly negative. If host finding by specialists is obscured in tree species mixtures, they might remain in poorer quality hosts and compensate by increased feeding (Lee et al., 2006; Stiling and Cornelissen, 2007; Castagneyrol et al., 2018b). Notably, in a simultaneously conducted study as the current one, the average caterpillar body size was observed to increase in high-N-content tree species only in tree species mixtures, whereas low-N-content tree species hosted larger caterpillars in low tree species richness (Anttonen et al., 2022). Additionally, higher N content may also be related to higher plant defenses (Campbell and Vallano, 2018) and generalists might avoid these plants due to higher susceptibility to plant defenses (Cornell and Hawkins, 2003; Ali and Agrawal, 2012; but see Verçosa et al., 2019).

Hambäck & Englund (2005) stressed the importance of patch geometry on determining the quantitative importance of variables affecting population sizes. Our study demonstrates that the plot edge effects and the changing perimeter/area ratio between small and large plots are important in shaping the herbivory response between monocultures and tree species mixtures. Non-host vegetation surrounding a monoculture can steer the insects to stay in it, and this effect can be stronger in smaller plots due to higher perimeter/area ratio increasing the likelihood to encounter a non-host (Bach, 1988). However, herbivores may further need a repeated positive stimuli of encountering a preferred host plant for staying in a vegetation patch (reviewed in Finch and Collier, 2000; Smith and McSorley, 2000). The steering inward of non-host vegetation around the plot, need for repeated positive stimuli, and higher resource base at central positions of monocultures due to least variable host plant composition, i.e. resource concentration (Root, 1973), can in combination explain the increased herbivory toward central positions in monocultures in this study. Increased herbivory closer to plot edges in tree species mixtures would then be a result of decreasing likelihood to be steered inward. The importance of the herbivore host plant selection in respect to plot edge was indicated further by larger - more apparent - trees closer to plot edges accumulating more herbivory, a similar effect to more apparent edge trees facing openings (Régolini et al., 2014). Although forest edges facing openings have been shown to increase herbivory in monocultures, the effect is sharply reduced when surrounded by non-host vegetation (Hauck et al., 2008; Dulaurent et al., 2012), and our study demonstrates that the herbivory response to plot edge within continuous forest vegetation is further dependent on tree species richness.

The difference in herbivory-tree centrality pattern further explains why smaller tree species mixtures had higher herbivory whereas the opposite was true for monocultures, as the smaller the plot, the higher the perimeter/area ratio and larger the proportion of trees close to the edge. The plot size-tree species richness relationship on herbivory would further remain the same if the herbivore populations between monocultures and tree species mixtures are shaped by higher predation in central locations of the mixtures (Harmon et al., 2003). Higher predation pressure has been demonstrated in tree species mixtures (Muiruri et al., 2016; Leles et al., 2017; Nell et al., 2018). However, the role of top-down control on herbivory cannot be directly assessed here.

A simultaneously conducted predation pressure study as the current study demonstrated that the predation pressure shifted toward more closed-canopy monocultures in dry season likely due to lower below canopy temperatures (Anttonen et al., 2023), but the tree species richness effects on herbivory were weak in both mid-summer and autumn 2019 estimations.

Even after including tree type and edge effects to models, a mild marginally-significant increase in herbivory was observed along increasing tree species richness gradient. Besides potential top-down effects, the trend may be affected by leaf quality. Trees growing in mixtures can have higher leaf magnesium (Forey et al., 2016) and nitrogen content (Mraja et al., 2011); Davrinche, unpublished data from BEF-China; but see mixed Moore and Francis, 1991; and negative effects Kostenko et al., 2017), and lower leaf defenses (Kostenko et al., 2017; Castagneyrol et al., 2018a; but see mixed or no effect Mraja et al., 2011; Moreira et al., 2014). However, as herbivory has also been observed to be non-related to tree species richness induced changes in leaf quality (Moreira et al., 2014; Kostenko et al., 2017), the effect of tree species richness mediated effects on herbivory is expected to be fairly weak.

Associational neighborhood effects and biomass

Whereas apparency by tree size increased herbivory at plot edges, low-C-content trees surrounded by large high-C-content neighbors demonstrated a leaf quality related apparency effect (Feeny, 1976). Herbivore movement between high and low-C-content trees can be expected to be low, as high-C-content indicates high structural carbon and tannin contents (Elser et al., 2000; Chapman, 2013), and herbivore ability to feed on tough leaves is dependent on herbivore species (reviewed in Bernays, 1998) and life stage (reviewed in Hochuli, 2001) specific feeding mode. In contrast, higher-N-content neighboring trees led to associational susceptibility and spillover to lower quality neighbors, as can be expected from high herbivore abundance hosting trees at least as long as the tree species are similar enough to allow the herbivore feeding on both (Futuyma and Wasserman, 1980; White and Whitham, 2000). Interestingly, no significant trends with leaf trait neighborhood deviations were observed in interaction with tree species richness going up from 2-species mixtures, demonstrating that the increased variability in the taxonomic composition did not have any strong effect on the observed relationships. However, the accuracy of the estimates is somewhat reduced due to using tree species averages, and especially for N content which had higher intraspecific than interspecific variation.

We further observed a biomass effect by larger neighboring trees increasing herbivory which was promoted with high branch abundance. High biomass may override further apparency effects (Moore and Francis, 1991; Damien et al., 2016) and leaf trait induced effects on herbivory (Whitfeld et al., 2012; De Carvalho Guimarães et al., 2014). However, the biomass effect may be enhanced by shading, as with larger neighborhood trees, the focal tree Mg content increased and C content decreased with the same set of tree individuals (Davrinche, data unpublished). In contrast to the positive effect of biomass and apparency based on tree size, herbivory slightly increased when neighboring trees and the branch abundance were low, demonstrating an overall resource dilution effect. However, in contrast, no effect of vegetation density per se was observed, indicating that herbivory responds to overall biomass but not the space filling of vegetation.

Topography and branch vertical distribution

The additional difference in herbivory between evergreen and deciduous trees along the topography PC.1 (essentially higher elevations and steeper slopes) is along the expectations of the ‘resource availability’ hypothesis of herbivory being more severe on fast growing and less defended tree species in poorer soil nutrient conditions (Coley et al., 1985). Thus, in contrast to higher nutritional contents of deciduous trees supporting plant vigor hypothesis, the topographical effect appears to support the ‘plant stress hypothesis’ (White, 1974), assuming that the deciduous trees are more susceptible to water stress (Kröber et al., 2014). Though we did not have direct measures of soil nutrient nor water content available in this study, water availability can be expected to decrease with increasing elevation and slope angle, and further affect the nutrient uptake (Lambers and Oliveira, 2019). Notably, the higher herbivory on deciduous trees also occurred already in the first half of the growing season when there was otherwise no difference to evergreens. However, instead of increased plant stress on deciduous trees, systematic decrease in leaf quality across tree species may have led to generalists favoring the highest-leaf-quality tree species (Robinson and Strauss, 2020), demonstrating rather a topography driven resource dilution effect. Therefore determining the driving force of tree type-topography relationship would require further study of the herbivore composition differences in respect to topography. Predation pressure was further relaxed during dry season in high elevation and steep slope conditions (Anttonen et al., 2023), which may have affected the overall lack of negative effect of distance from plot edge on herbivory in high elevations/steep slopes, as was observed in the lower areas. However, a predation driven effect would be expected to further show between tree species richness levels, but the random plot placement in the hillsides and limited amount of high-tree-species-richness plots did not allow reliable testing of the tree species richness-topography-tree centrality three-way effect.

The expectation of increased herbivory with lower branches (Coley & Barone, 1996; Zhang et al., 2022) was partially supported. In addition to the overall positive trend across years, the results indicated high importance of topographic conditions on the vertical distribution of herbivory. Drier soil types have been observed to reduce differences in the vertical distribution of herbivory (Shao et al., 2021), as drought conditions can, besides reducing leaf water content, further lead to lower leaf defenses (e.g. Walter et al., 2012) and changes in leaf nutritional content (Lambers and Oliveira, 2019), which may diminish the differences in leaf quality between vertical layers. The 2019 herbivory analysis further showed that the increase in herbivory in lower branches was restricted to north-facing hills in the latter half of the growing season/dry season, as high light intensity in south-facing hills may prevent effective shading taking place. The further slightly higher damage in upper branches may be explained by herbivores eating more to compensate for increased metabolism in the sunnier and thus warmer conditions (Clissold et al., 2013; Lemoine et al., 2013; Havko et al., 2020), when differences in leaf quality do not cause preference for lower branches (but see Stoepler and Rehill, 2012).

Further, low branches that were more isolated from the canopy (relative branch height-vertical Gini interaction) did not suffer increased herbivory. The more isolated low branches might attract less attention from herbivores, and experience higher predation pressure (Anttonen et al., 2023). Low branches may also occur under densely packed canopies only when there is a large enough gap to allow ample passage of light, as differences in light conditions can have a strong effect already on individual branches (Henriksson et al., 2003). Although we did not observe any effect on herbivory by the amount of open area surrounding the focal tree, the effect of canopy vertical distribution causing the differences in herbivory through changes in leaf quality was indicated by the tree intraspecific Mg content increasing in lower branches in more equally distributed canopies (Davrinche, data unpublished), similar to herbivory. In addition, Pross et al. (BEF-China experiment; manuscript in preparation) showed that increased light led to systematic increase in leaf phenol content but not in N-, Mg- and C-contents. N- and C-contents increased and Mg-content decreased with higher light availability in high tree species richness, but in monocultures the relationship reversed with N-content in deciduous and with C- and Mg-contents in evergreen trees. No differences in herbivory-branch height relationship were observed between deciduous and evergreen trees in our study, nor in respect to tree species richness (as opposed to e.g. Castagneyrol et al., 2019). However, the dependence of branch height effects on canopy vertical distribution may reflect the varying effect of light conditions in respect to the tree type and tree species richness on leaf quality.

It should be noted that even after accounting for the associational neighborhood, intraspecific leaf trait, and vertical distribution of herbivory, the focal tree identity as random factor still explained relatively high amount of variation in the models, with the overall variation explained by the fixed part remaining fairly low. This is as expected with multiple co-occurring drivers of herbivory and highly variable research site in terms of overall plant and herbivory species richness (e.g. Wang et al., 2020). In a review of associational effects, Barbosa et al. (2009) considered associational susceptibility and resistance to be insufficient to explain the majority of herbivory between trees. Herbivory between branches is further known to be highly variable (Lowman, 1985), and can be expected to be susceptible, for example, to aggregations of herbivores on specific branches, to heavy declines caused by ants (Rosumek et al., 2009). Tree species richness effects in a wider than plot spatial scale may have further affected the amounts of herbivory, as was demonstrated with caterpillar community in wider than plot scales in BEF-China experiment (Li et al., 2023).

Conclusions

Our results demonstrate that the overall herbivory in respect to tree species richness and topographic conditions depend on the relative importance between multiple simultaneously affecting herbivory determinants. Despite the complexity of the overall framework, leaf traits, forest structure, seasonal progression, as well as plot edge effects provided predictable effects on herbivory. These results provide insight into how herbivory in tree species rich forests is determined especially in close neighborhood scale. In order to clarify the role of resource base on herbivory in forests, future studies should focus on the relative balance of the overlapping mechanisms of resource dilution and apparency in contrast to biomass, spillover and resource concentration.

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Competing Interests Statement

The authors declare no conflict of interest.

Author contributions

Perttu Anttonen: Research design, data collection, analyses, and manuscript writing, review and editing. Andreas Schuldt: Research design, supervision, and review and editing. Andréa Davrinche, Goddert von Oheimb, Maria Perles-Garcia and Matthias Kunz and Sylvia Haider: Data contribution, and review and editing. Helge Bruelheide, Chao-Dong Zhu, Yi Li: Important contributions during data collection, and to review and editing of the manuscript. Final approval of the manuscript was received from all authors.

Data Accessibility Statement

The raw data supporting the conclusions is available from the corresponding author upon request.

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CHAPTER 5

Synthesis

Decades of biodiversity-ecosystem functioning research has produced extensive amounts of knowledge on producer-consumer relationships (Eisenhauer et al., 2019). Based on the accumulated wealth of knowledge, new and more precise experiments have been able to be built in order to address the relationships between biodiversity-ecosystem functioning and multiple interacting drivers of trophic interactions. An important aspect that requires further study regards the mechanisms driving biodiversity relationships at close-neighborhood scales (Trogisch et al., 2021) and across spatial-scales (Eisenhauer et al., 2019), which can provide understanding of the mechanistic foundations of ecosystem functioning. In this thesis, I estimated how caterpillar functional traits, predation pressure, and herbivory are related to tree species richness. I further extended the scope of the study by including the relationship to leaf quality (Chapters 2 and 4), forest structure (Chapters 3 and 4), and spatial determinants through plot size (Chapters 3 and 4). As areas can rarely be considered to be completely homogenous even at small scale, I additionally estimated how the topography of the experimental site, as representative of abiotic and soil conditions, affects predation and herbivory (Chapters 3 and 4). Finally, as seasonal progression causes abiotic conditions to change, leaf quality to decline (Mattson, 1980; Scriber and Slansky, 1981), and species occurrences and abundances to vary (Murakami et al., 2005; Seifert et al., 2021), I investigated these dynamics in respect of the other determinants of bottom-up and top-down drivers of herbivory. In this chapter, I summarize the findings and discuss their importance in a broader context. Through this, I aim to contribute to an improved understanding of the BEF relationships, and to determining the specific needs for future research.

Summary of the results

In **chapter 2**, I investigated how leaf quality (N, Mg, and C) of tree species together with tree species richness and seasonal progression shapes caterpillar functional traits, focusing on the interspecific differences, and overall functional diversity per tree species. In addition, I investigated the caterpillar trait variation between tree species, and the caterpillar species sharing between tree species. Most caterpillar species were caught only rarely. However, the increase in caterpillar species richness found on each tree species per richness level was related to the occurrence of the generalist species, i.e. caterpillar species that were found most frequently across tree species.

The study revealed that with higher nutritional content (Mg) the overall caterpillar species richness declined but the caterpillar abundance and community generalism increased. The abundance increase was further indicated to occur mainly as an increase of small, and likely early instar, individuals, and the proportion of small individuals was yet higher in spring. Additionally, the generalist species occurred on low-Mg-content trees only in high tree species richness where the caterpillar fauna was more mixed between tree species. Caterpillars were, similar to Mg content, smaller on high-N-content tree species in monocultures, but on low-N-content in high tree species richness. This demonstrates a possible contrasting effect of an increased number of early instars in monocultures but decreased growth in tree species mixtures where caterpillars are more likely to end up on less suitable host plants. In addition, poorer nutritional quality of leaves led to an increase in caterpillar defensive traits, supporting the expectation that decreased growth leads to an increased need for defenses in herbivores.

The presumed decline in leaf quality further drove caterpillar communities to be more dissimilar between tree species in terms of generalism and aposematic coloration; also, it caused the caterpillar community to consist of smaller individuals and be overall less generalized. This supported the expectation of leaf quality driving herbivore diet breadth and growth, as well as of warning coloration being most important against predation by birds outside fledgling season. However, as the caterpillar hair coverage was instead higher in early season, this indicates that defensive traits can differ in their seasonal relationships even if they demonstrate an overall defensive syndrome.

In **chapter 3**, using artificial caterpillars, I tested how predation pressure by predatory arthropods, birds and rodents is shaped by tree species richness and forest structural variables across spatial-scales. The predation pressure estimation was further addressed in accordance with seasonal context in terms of differences in herbivore prey abundances between seasons, as observed in Chapter 2, and through differences in abiotic conditions between rainy and dry seasons in relation to forest structure and topographical conditions.

The results demonstrated that predation pressure was highly dynamic between forest structural features, as well as forest structure and tree species richness. Additionally, the forest structural complexity was shown to be a poorer estimator of predation pressure than a more specified approach using multiple structural measures and their interactions between spatial-scales. Different predator groups further responded differently to tree species richness and forest structure in respect of spatial-scale, likely representing their movement capabilities and habitat size restrictions. In general, predation by arthropods increased with higher tree species richness going from densely branched close neighborhoods to more variable surroundings around the focal plot. In turn, predation by birds and rodents was not affected by tree species richness, but rodents favored larger, more densely vegetated areas.

The effects of small-scale variables that affect the visibility of the caterpillars and can work as cues of herbivore presence for predators - placement on trunk, open area, and presence of leaves - were largely dependent on a wider-scale forest structure, demonstrating in general that the cues and small-scale visibility determinants are more important the scarcer they are. The interaction between small-scale branch density and wider-scale vegetation density on predation by arthropods further demonstrated that predators may concentrate on the most promising sources of prey in small-scale when in low vegetation density areas, and in turn, higher visibility may increase predation pressure in an overall denser vegetation.

Predation by arthropods and rodents was highest from early to mid-summer, when herbivores are expected to be most abundant, indicating that predation pressure follows seasonal differences in prey abundance. In turn, predation by birds increased toward autumn, probably due to higher likelihood of inexperienced fledglings attacking artificial caterpillars and winter migration increasing bird abundance during a period of low prey abundance. Otherwise, seasonal shifts in predation pressure showed similar overall trends across all predator groups, with the most sun-prone and presumably warmest areas in respect to topography generally experiencing higher predation during the rainy season but lower during the dry season. Bud burst can be expected to be earlier in more sun-prone topographic locations, and warmer conditions may themselves be beneficial for predators during the cooler season. In turn, predators may avoid unfavorably high temperatures and shift to more shaded habitats in the dry season. A similar effect was seen with predation by arthropods and canopy vertical stratification, with predation shifting during the dry season to closed canopy plots which can be expected to be more shaded.

In **chapter 4,** I estimated how herbivory, measured as damaged leaf area, is shaped in response to tree species richness, leaf quality, forest structure, topography, and season. Seasonal effects in this chapter were addressed by analyzing herbivory separately for mid-summer (one year) at the end of rainy season and for the end of the growing season (two years). The results demonstrated the importance of seasonal timing for understanding the dynamics of herbivory, and are largely interpreted in light of the decrease in leaf quality amid growing season as leaves mature. Early-season herbivory was highest on trees in the Fagaceae family, deciduous and evergreens alike, but was otherwise more evenly distributed between trees compared to after the latter half of the growing season. By autumn, herbivory increased most with high-N-content deciduous trees.

A second notable pattern in herbivory occurred with tree species richness. Herbivory increased in deciduous trees and further in those of the Fagaceae family with increasing tree species richness, demonstrating a resource dilution effect as their abundance per plot decreased. The increase in herbivory with the high-N-content trees also led to subsequent spillover of herbivory on lower-N-content trees when surrounded by higher ones. Spillover effects further occurred as a biomass effect, with herbivory increasing on focal trees when surrounded by large neighbors. In contrast to spillover, higher herbivory due to increased apparency was observed with trees larger than their neighboring ones growing close to plot edges, and when large neighboring trees had higher C content than the focal tree. The results, thus, demonstrate that the positive effects of biomass and tree apparency depend on both leaf quality as well as tree spatial location. Spatial location further drove differences in herbivory between monocultures and tree species mixtures, since trees growing in highest tree species mixtures suffered higher herbivory closer to plot edges, whereas herbivory was higher closer to central positions in monocultures. The difference in herbivory in relation to edge effects between tree species mixtures further explains why lower herbivory in monocultures compared to mixtures in smaller plots turned to higher herbivory in larger plots, as the amount of trees farther away from the edge increases with plot size.

Increase of herbivory further followed leaf quality by increasing intraspecifically in trees with the highest leaf quality (Mg and N content). However, in high tree species richness, herbivory was higher in low-N-content trees, possibly due to an increased difficulty in finding a high quality host, or by generalist herbivores being more susceptible to nitrogen-based defensive compounds. In addition, herbivory was higher on lower branches, as expected based on shade conditions improving leaf quality for herbivores. However, these differences disappeared when the canopy was vertically more unequally distributed, demonstrating the importance of canopy structure on within-tree herbivory distribution.

Finally, topography was shown to shape herbivory response to other variables, ranging from tree type as deciduous/evergreen and branch height to tree spatial location. The drier soils in high elevations/steep slopes can increase the difference between deciduous and evergreen trees, presumably through the lower drought tolerance in deciduous trees. In contrast, the high elevations/steep slope conditions, as well as sun-prone south-facing hills, may decrease the difference in leaf quality between branches of different heights. The additional effect of topography negating the trend of higher herbivory in central positions demonstrates the importance of taking into account the environmental conditions in BEF-experiments that can cause obfuscation on the role of treatment effects, such as tree species richness.

Tree species richness and local tree neighborhood effects

In this thesis, I have shown multiple ways in which tree species richness partakes in modifying herbivory through bottom-up and top-down mechanisms. These effects extend from the local neighborhoods around focal trees to plot level, and yet further to interactions between plots. Support for several basic assumptions of trophic level interactions with regard to tree species richness was found, and the novel findings in this thesis shows these effects were in most cases further modified by other environmental quality determinants and spatial relationships. With increasing tree species richness, the caterpillar fauna became more species rich, i.e. diversity of producers increased diversity of consumers (e.g. Siemann et al., 1998; Ebeling et al., 2018) (Chapter 2), predation pressure increased, i.e. supported the "Enemies Hypothesis" (Root, 1973), however only in regards to more densely branched neighborhoods and early season (Chapter 3), and herbivory was more concentrated on the host trees as their abundance declined, i.e. demonstrated resource dilution (e.g. Otway et al., 2005; Plath et al., 2012), and additionally increased in central positions of monocultures, i.e. supported the "Resource Concentration Hypothesis" (Root, 1973) (Chapter 4). The results regarding the effects of tree species richness in the different chapters can be seen in part to form a unified framework, but some contradictions also arose which demonstrate more case-specific responses between herbivores and predators. Overall, the results emphasize the importance of local neighborhood interactions between tree species, which modifies the caterpillar community, predation pressure, as well as the amount of herbivory each tree experiences.

The increase in caterpillar species richness per tree species, and increase in herbivory along the tree species richness gradient fit together in general, demonstrating a bottom-up effect from diverse vegetation on herbivores (Scherber et al., 2010). Further, herbivory was overall higher on deciduous trees than on evergreens, also after accounting for differences in herbivory between the dominant family Fagaceae and other trees, which corresponds to higher caterpillar abundance on high-Mg-content tree species (non-Fagaceae deciduous trees). However, differences in herbivory between deciduous and evergreen trees increased with increasing tree species richness, whereas caterpillar communities became more similar between tree species. The differences in caterpillar community generalism between tree species alongside increasing Mg content also faded along increasing tree species richness. However, the caterpillar species sharing patterns were investigated in Chapter 2 simply as a response to tree species richness and not specifically between neighboring trees. In general, a spillover effect would be expected to occur especially from trees holding the highest abundance compared to their surroundings, as has been observed with caterpillars (White and Whitham, 2000). To this extent, the increased species sharing between tree species along increasing tree species richness does fit the spillover pattern of herbivory from high leaf quality (N content) neighborhood trees to their neighboring trees.

The importance of the herbivore movement was indicated also by the tree species richness relationship with tree centrality. This result is an important addition to the knowledge of BEF relationships between tree species richness and herbivory, as it was further shown to have the potential to affect the relationship with regard to plot size. As discussed in Chapter 4, the observed pattern in herbivory may be affected by the contrasting pattern in predation in terms of spatial location within the plot (see e.g. Harmon et al., 2003). However, all in all, as herbivory was modified by the distance to plot edges between tree species richness levels, as well as in respect to tree apparency, the results indicate the importance of migration of herbivores between plots (see e.g. Bach, 1988; reviewed in Finch & Collier, 2000). Yet, this does not mean that the patterns observed with predation would be of no importance, as they may further amplify the migration induced differences in herbivory in relation to tree species richness and tree location within a plot. The results of Chapter 4 demonstrated additionally that edge effects modify herbivory on trees also in continuous vegetation, as compared to edge effects facing openings in forests (De Carvalho Guimarães et al., 2014; Régolini et al., 2014).

The results from Chapters 2 and 4 highlight the importance of N content on herbivores (see review in Mattson, 1980), but show that the effect is important to consider in relation to the variation in the tree species composition. However, it needs to be noted that comparisons of the results between the two chapters are not very straightforward, as one shows the differences between trees interspecifically on caterpillar body weight (Chapter 2) and other intraspecifically on herbivory (Chapter 4). Nevertheless, the contrasting effect of N content between monocultures and tree species mixtures on caterpillar size and herbivory does indicate an interference effect of mixtures on herbivore performance due to increased difficulty in finding a high quality host plant. This interpretation of tree species richness interfering with optimal host plant finding is further supported by the effect of Mg content on caterpillar generalism disappearing in high tree species richness.

Seasonal and topography effects

This thesis demonstrates that when aiming to evaluate the importance of top-down control on herbivory, the seasonal differences in the response of herbivores, herbivory, and predation are of high relevance. The seasonal effects were found to affect caterpillar functional traits, predation, as well as herbivory, but the effects on herbivores and predators notably differed from each other. The seasonal effect on caterpillar community and herbivory can be in large part attributed to a seasonal decline in leaf quality with leaf maturation, which can further lead to increased differences in tree susceptibility to herbivores (Mattson, 1980; Scriber and Slansky, 1981; Coley, 1983). In contrast, effects on predation can be explained in part by the seasonal differences in herbivore prey abundance, and in part by abiotic differences between seasons (Wolda, 1978; Richards and Windsor, 2007; Remmel et al., 2009; Molleman et al., 2016).

Most of the herbivory had accumulated by mid-summer when the caterpillar species richness and abundance were highest, as was also the predation pressure by arthropods, indicating a bottom-up trophic cascade from high early season leaf quality through higher herbivore prey abundance on predator abundance and activity (see e.g. Scherber et al., 2010). The bottom-up control of herbivory through seasonally changing leaf quality was strongly indicated with N and C content. However, the role of N, Mg and C content, and the tree family identity on herbivore community composition and herbivory is somewhat complex. The highest caterpillar abundance in mid-summer in high-C-content trees and the high early-season herbivory on Fagaceae family correspond with the higher C content in deciduous and evergreen Fagaceae compared to deciduous trees in other families. However, this effect is unlikely to be driven by high C content, but rather by young early season leaves being more palatable before the C content has reached the levels measured in autumn (Feeny, 1970). The young leaves are further expected to have higher N contents than mature ones in late season (Mattson, 1980). Similarly, the observed higher herbivory during mid-summer in low-Mg-content trees surrounded by higher-Mg-content neighboring ones is more likely an effect of Fagaceae family trees being more apparent in their surroundings in early season than spillover from the neighbors. The high-Mg-content non-Fagaceae deciduous trees did suffer high herbivory especially in 2018, and the increase from-mid-summer to autumn in 2019 was higher in them than in evergreens, but by mid-summer 2019 the herbivory was lower than in Fagaceae. Highest caterpillar abundances on the Fagaceae family trees in spring and early summer are common (Feeny, 1970; Murakami et al., 2005), but to which extent this connection is due to phylogenetic conservatism in host plant use and to which in nutritional leaf quality is less clear. However, these explanations are not mutually exclusive and leaf nutritional quality may be one of the drivers of the phylogeny-phenology relationship of herbivore host plant use. In addition, high-C-content trees hosted more generalist caterpillar communities in spring and mid-summer, which further indicates the importance of a high quality of young leaves on herbivores (see e.g. Coley, 1983). Moreover, during the second half of the growing season when herbivory accumulated primarily on deciduous trees, the caterpillar community became more dissimilar in terms of species composition and generalism between tree species. Altogether, the effects of C content on caterpillar community composition and herbivory indicate the expected negative effect based on structural carbon and tannins (Feeny, 1970; Scriber and Slansky, 1981; Behmer, 2009), rather than any positive effect due to higher sugar content.

Aposematic coloration in the caterpillar community also increased toward autumn, as did predation by birds, supporting the expectation of the importance of warning coloration after fledgling season (Mappes et al., 2014). Putting together decreasing aposematism with increasing tree nutritional content and increased variation in aposematism between tree species toward autumn, the results support the expectation of poorer nutritional leaf quality tree species leading to increased need for defenses due to slower growth rates (Mattson, 1980; Loader and Damman, 1991). The increased variation in generalism toward autumn, similar to aposematism, further indicates that the growth rate differences may be emphasized between specialist and generalist herbivore species. Altogether, these results provide detailed information about seasonal and leaf trait related patterns on both herbivore functional traits and herbivory, rarely addressed in such tree species rich environments.

Overall, the Chapters 3 and 4 demonstrated that forest structure shapes herbivory and predation in a fairly complex way, and these effects were further seasonally modified. Herbivory in general responded mostly to tree sizes, whereas the response of predation to forest structure was much more dynamic between variables indicating higher predator and prey population sizes, increased visibility, and attractants for predators. In case of herbivory, forest structure mainly affected herbivory through biomass and tree apparency. However, the tree apparency effects caused by the high C content of large neighborhood trees appeared only in the latter half of the growing season, which fits together with the negative effect of high C content on caterpillar community generalism in autumn, and demonstrates the importance of seasonal decline in leaf quality specifically in terms of increasing carbon based compounds on herbivores (Feeny, 1970; Coley, 1983).

In case of predation, forest structure had systematic effects across seasons, but several effects were additionally seasonal, namely the effects of vegetation and small scale branch density, as well as canopy vertical stratification. The increase of both, herbivory and predation, on more densely branched height layers toward autumn indicates a localized small-scale bottom-up effect on predators through herbivore abundance. However, possible top-down effects on herbivory arose from the canopy vertical stratification. Abiotic conditions can cause predation pressure to lose connection to prey abundance (Richards and Windsor, 2007). Thus, the shift of predation pressure by arthropods away from the highly vertically stratified high-tree-species-richness plots in the dry season may have affected the (fairly weak) effect of increased herbivory in these plots. Similarly, the decline in high elevations and steep slopes during the dry season in conjunction with the loss of plot edge effects in high elevation/steep slope conditions, indicates that the seasonally changing top-down control may lead to changes in herbivory between habitats. However, as the tree species richness as well as topography effects on herbivory were low in the year observed for seasonal comparison, the effect of seasonal changes in predation pressure on controlling herbivory must remain rather speculative for now. In addition, the tree species richness effect on herbivory being in part dependent of plot size and tree centrality complicates the issue further. Edge effects can modify herbivore populations through predation pressure (Harmon et al., 2003), and the edge effect may then also respond to relaxation of predation pressure due to abiotic conditions, but this topic requires further study. Additional potential across-season top-down control effects arose with canopy structure. The effect of isolated leaves in the more unequally distributed canopies attracting more predation, and isolated branches simultaneously attracting less herbivory, indicates a localized top-down control. However, due to alternate explanations based on light availability induced leaf quality effects (see e.g. Coley & Barone, 1996), which can be also very localized between branches (Henriksson et al., 2003), the precise strength of the top-down effects on herbivory require further investigation.

Another potential effect of predation pressure on herbivores arises in comparison to caterpillar species richness. Predation pressure was highest in high-tree-species-richness plots during the spring to mid-summer period. As caterpillar abundance and species richness were highest in mid-summer, and caterpillar species richness also in high tree species richness levels in general, this may indicate a diversifying effect of top-down mechanisms on herbivore species composition (e.g. Siemann et al., 1998). However, it cannot be ascertained here to which effect the increase in caterpillar species richness in high tree species richness is the response to predation pressure and to which extent it is a bottom-up effect, as this would require a more precise approach on herbivore and predator community dynamics than what was possible within the scope of this study. Overall, despite the difficulty in linking the observed patterns of predation pressure to herbivory and caterpillar communities, the results bring forth novel insights. Predation pressure was shown to be highly dynamic between habitats and seasons, and the results in this thesis bring important new findings especially on the connection between tree species richness, but also plant species richness in general, and top-down control. The expectation of higher top-down control in plant species mixtures has received mixed support (Root, 1973; Staab and Schuldt, 2020; Stemmelen et al., 2022). The findings in this thesis suggest that this may be in part due to the seasonal nature of predation pressure between habitats. Further, the results show that the interplay between spatial-scales in respect of forest structure and tree species richness is highly important to take into account for predation estimates, since the indicated mechanisms underline that otherwise it can remain unclear which effect is measured; visibility, predator attraction, or prey and predator abundance.

Future directions

Several new findings of how bottom-up and top-down mechanisms affect herbivore and predator response are presented in this thesis. In addition, the results bring forth further aspects of BEF relationships that require attention. As discussed throughout the thesis, herbivore diet breadth is a key functional trait for understanding both bottom-up- and top-down-driven relationships between herbivorous insects and plants. Whereas the results provide further information on herbivore generalism patterns in respect to leaf nutritional quality and tree species richness, the results also raise new questions about how generalist and specialist herbivorous insects respond to plant communities. Controlled tree species richness experiments in a herbivore species rich subtropical area seem ideal for herbivore community diet breadth studies, but in practice suffer from limited knowledge regarding the herbivore species' identities in the climatic region. To overcome this lack of knowledge, studies conducted in the BEF-China experiment have used DNA based molecular operational taxonomic units (MOTU), as in Chapter 2, and morphospecies to distinguish arthropod species. Because of this, the species usually cannot be connected to ecological literature on their host plant use, if such exists, and thus the herbivore species diet breadth has been estimated using plant-community-based metrics (Chapter 2; Zhang et al., 2017; Wang et al., 2020). The community-based diet breadth estimates are accurate in the sense that they inform the diet breadth in regard to the actual host availability in the community (Fox and Morrow, 1981). However, their accuracy in between tree species richness level comparisons suffers from being based on herbivore occurrences and abundance, and because of local plant communities affecting them at two levels, at the whole field site and at individual plots. As increasing tree species richness per plot increases herbivore species sharing in the local neighborhoods (Chapter 2), as indicated also by the spillover effects on herbivory (Chapter 4), it renders the herbivore generalism dynamic in respect to host plant richness. Thus, the same herbivore species can be more generalist in higher tree species richness than in monocultures. It is, therefore, not surprising that tree species richness has not been observed to affect generalism of the caterpillar fauna in the BEF-China experiment when the caterpillar diet breadth is estimated across the tree species richness levels (Chapter 2; Wang et al., 2020). Estimating generalism across tree species richness levels makes the studies in the BEF-China experiment robust in their estimates, but the neighborhood aspect in diet breadth determination of herbivores requires further investigation.

Moreover, as the estimates are based either strictly on herbivore occurrences (Chapter 2), abundance-weighed occurrences (Zhang et al., 2017), or tree- and herbivore-community-weighed occurrences (Wang et al., 2020), they are all dependent on the abundance of herbivore species, since the more abundant the herbivore species is, the more likely it is to be found also from secondary hosts. Although using abundance thresholds, such as including as a host plant species only those of which held at least 5% of the herbivore species abundance (Zhang et al., 2017), can exclude rare hosts, the thresholds work best for common species, as rarely found species will always appear as specialists, and excluding rare species from analysis disproportionately weighs the effect of the common ones. It should be noted that rarity does not necessarily indicate specialism, as specialists are often more abundant than generalists on their shared host plants (e.g. Braga and Diniz, 2015). In addition, poorer-dispersing species in high plant species richness surroundings may need to be generalists due to low abundance of any specific tree species (Barone, 1998). Further, if a generalist herbivore species specifically favored high-tree-species-richness plots for example due to dietary mixing possibility, it would have lower chances of being caught than a more specialized counterpart in monocultures because of a lower amount of tree replicates per species in tree species mixtures, and a lower amount of high-tree-species-richness plots themselves in the BEF-China experimental design. There is, however, a clear indication of robustness in the used measures of the herbivore community generalism in the studies conducted in the BEF-China experiment. The generalist species abundance was found to increase in high tree species richness (Zhang et al., 2017), which would not be expected if the species were largely specialist species drifts from monocultures in high tree species richness. Generalism was also seen to be higher in high-Mg-content tree species (essentially deciduous non-Fagaceae) in Chapter 2 instead of the low Mg content ones, which corresponds to the most species rich family - the Fagaceae - and demonstrates that the generalism estimates are not driven simply by host tree richness and abundance within the most common family. Future studies in the BEF-China experiment should aim to form a still more detailed picture of how the generalism-specialism relationship in terms of tree species richness is affected by the herbivores' diet breadth in its entire geographical range, neighborhood interactions between tree species, and abundance differences between herbivore species. This can be addressed by estimating how the generalism within common herbivore species changes per tree species richness level and, with a much more effort demanding approach, by building a herbivore host plant use database based on field observations across studies within the BEF-China experiment and further supplementing it with feeding trials.

The results in this thesis showed that neighborhood interactions between trees simultaneously respond to the abundance of the host trees, i.e. resource dilution, as well as the functional leaf traits between neighboring trees, i.e. spillover and apparency. Future studies should further investigate how declining host tree abundance along increasing tree species richness gradient in combination with functional trait differences between neighboring trees affects the balance of herbivore spillover and concentration on preferred host trees due to resource dilution. Moreover, though caterpillars are a highly important herbivore group (e.g. Novotny et al., 2006), they represent only part of the total herbivore fauna, and other herbivores may respond differently to the resource dilution and associational neighborhood effects (Plath et al., 2012). Therefore, future tree neighborhood interaction studies should also include more mobile herbivores, such as grasshoppers and adult beetles, that can easily change their host tree and balance their diet even during the course of the day, as grasshoppers are well known to do as a model species group in nutritional ecological studies (e.g. Barnes, 1955; Behmer et al., 2001).

Since herbivory was shown in this thesis to respond to plot edge effects in respect of tree species richness, an interesting follow-up study would be to test how the edge effects shape the herbivore composition between tree species richness levels in heterogeneous continuous vegetation, as in the BEF-China experiment. If the herbivory community analysis was further conducted between different herbivory groups that have different movement capabilities, this would offer a highly detailed picture of the vegetation-edge relationships. This was not possible in the current caterpillar functional trait analysis structure in Chapter 2, which focused on how the interspecific differences in caterpillar functional traits shape the community between tree species and tree species richness levels. Analysis at the individual tree level would have essentially made the results dependent on the differences in abundance between caterpillar species, and, thus, answered fairly different questions. Nonetheless, the suggested study direction is well achievable in future studies within the BEF-China experiment.

The results in Chapters 2 and 4 in general indicated a positive effect of N content and a negative effect of C content on herbivores. However, the negative effects on caterpillar body size and herbivory of N content in high tree species richness, the negative effect of C content on caterpillar hair coverage, and the systematically negative effect of N, Mg and C on caterpillar head size call for further investigation on these topics. Future studies should aim to disentangle to which extent these effects on herbivores are driven by positive effects of N content (Mattson, 1980) and negative ones through nitrogen based defensive compounds (War et al., 2012; Campbell and Vallano, 2018), as well as the role of negative effects of structural carbon and tannins, and the positive effects of sugars (Elser et al., 2000; Chapman, 2013). The studies should further extend to the potentially different response of generalist and specialist herbivores to the nutritional and defensive leaf quality (Cornell and Hawkins, 2003; Coley et al., 2006; Lee et al., 2006; Ali and Agrawal, 2012). Further inclusion of connections of N and C content to water stress (Mattson and Haack, 1987; Huberty and Denno, 2004) and light availability (Henriksson et al., 2003; Barber and Marquis, 2011; Pons, 2016), would elucidate the role of the abiotic environment on shaping the BEF relationships between herbivores and leaf traits.

Bottom-up control from plants to higher trophic levels tends to be more dominant in terrestrial ecosystems than top-down control (Polis, 1999), but rather than a dichotomy of one or the other, both effects can be expected to play out simultaneously on herbivores (Walker and Jones, 2001). Predation pressure was shown in this thesis to be highly seasonal with respect to tree species richness and topography, and further to depend simultaneously on several forest structural features. Therefore, the connection to herbivory and herbivore community composition remains elusive. The role of top-down control should be addressed in future studies by predation exclusion treatments spanning across seasons and different topographical conditions, and further include targeted herbivore and predator collections with regard to different small scale forest structural habitats within the canopies. The latter can be achieved by passive trapping and also by using the active telescopic beating tray collection method used in Chapter 2, which allows targeting specific branches in the canopy. In addition, the same trees can be re-evaluated for herbivory and predation as in Chapters 3 and 4, as it is not just the plots and the tree positions that can be traced in the field site, but the sampling points can be often traced with very high precision in space in terms of vertical position and the environment surrounding them at a given time. Combining the evaluation of the change in the surrounding environment of the previous sampling points with new approaches and estimations of other environmental variables, such as direct light availability in small scale, would open new venues for research that would provide a highly detailed and dynamic picture of the ecosystem functioning in the BEF-China experiment.

Further focus in BEF relationships would be highly beneficial to explore how the seasonal and topography related trait variation affect the tri-trophic interactions between trees, herbivores and predators from a producer- and consumer-trait perspective. For example, generalist herbivores can be more strongly affected by predation than specialists (Singer et al., 2014), as they can be higher quality food for generalist predators (Dyer, 1995). Generalist caterpillars were further demonstrated in Chapter 2 to be more common in spring and favor higher-nutritional-leaf-quality trees, and lower-leaf-quality trees to increase caterpillar defensive traits. Thus, leaf traits may indirectly affect predators by moderating the quality of prey. As mentioned earlier, the effect of topography could not be taken into account with the current approach of caterpillar functional trait analysis. The leaf nutritional content was also not included in Chapter 3’s study because of the focus on how the small and large-scale factors interact in driving predation pressure. In order to accurately estimate the effect of leaf quality on predation with high spatial accuracy, the measurements should represent the overall leaf quality surrounding the artificial caterpillars. This includes the focal and surrounding tree species composition, the specific branch locations within the canopy, as well as tree intra-individual leaf trait variation. Determining the surrounding leaf quality of the artificial caterpillars in such detail was not within the scope of this thesis. Thus, future investigations into how the leaf quality effects cascade on herbivory and predation through herbivore defensive traits, diet breadth and body size would offer further insights into BEF interactions between trophic levels. They would further aid disentangling to which effect the early season predation pressure is follows the prey abundance or thermal conditions per se.

Finally, a further important broad-scale approach for investigating the effects of herbivory on ecosystem functioning would be to address how the changes in herbivore damage within the observed ranges affect tree condition either negatively as the loss of biomass or positively through nutrient circulation. The overall leaf area loss to herbivory was fairly low and similar to earlier studies from several different forest ecosystems (reviewed in Mattson & Addy, 1975; Kozlov & Zvereva, 2017). Similarly, the changes in herbivory caused by tree species richness and other variables were mainly fairly small. However, even low amounts of herbivory can reduce tree growth, seed production and overall biomass production (reviewed in Kozlov & Zvereva, 2017), and especially with saplings if the damage occurs constantly across years (Zvereva et al., 2012). However, some studies have noted no systematic effects of low level herbivory on tree condition (Vanderklein & Reich, 1999; see also review in Mattson & Addy, 1975), or low levels of herbivore damage having only minor effects on tree growth, with larger trees being further more tolerant to damage (Alfaro et al., 1982). Tree growth in mixtures has also been shown to be higher regardless of higher herbivore damage (Haase et al., 2015), and higher herbivore abundance and species richness (in BEF-China experiment; Li et al., 2023). As herbivory can affect tree species differently depending on their growth strategy and soil nutritional conditions (Coley et al., 1985), and in turn, an increase in herbivory can accelerate nutrient turnover (Belovsky and Slade, 2000), the overall effect of herbivory on tree growth, fecundity, and mortality can be expected to depend on tree identity, tree species richness and soil conditions. In future, BEF-studies using controlled setups should track tree growth, herbivore and predator dynamics, as well as soil conditions in order to address the strength of negative and positive impacts of herbivory on ecosystem functioning. To this extent, this thesis demonstrates the need to focus especially on the leaf-quality and biomass-related associational neighborhood effects, but also on the relationships between plot size and tree position within plots.

Conclusion

This thesis demonstrates that tree species richness and neighborhood interactions between trees of different species shape the bottom-up and top-down effects on herbivory through multiple mechanisms. The novel results in this thesis emphasize the dynamic nature of the determinants of herbivore community functional trait composition, predation, and herbivory ranging from immediate neighborhoods of trees to gradients in topography and seasonal progression. Yet, even though the relationships between tree species richness, leaf traits, forest structure, seasonal progression and topography were shown to be complex, systematic patterns are demonstrated to be found based on ecological theory. Finally, this thesis provides important information on herbivory relationships in subtropical forests, which are underrepresented in studies on in studies on the relationships between tree species richness and herbivory in comparison to such in temperate and tropical forests.

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APPENDICES

Author's contributions

Chapter 2

PA and YL conceptualized the ideas and methodology with the support of DC, AS and C-DZ. PA conducted the field collection with the help of YL. YL conducted the laboratory analyzes with assistance of J-TC and support of PA. AD and SH contributed data. PA conducted the statistical analysis with the support of AS, YL and DC. The results were visualized by PA and YL. PA led the writing of the manuscript, supported by YL and AS, and with important input from AD, C-DC, DC, HB, J-TC, K-PM, M-QW and SH. All authors contributed critically to the drafts. My overall contribution was 45%, my intellectual contribution was 60%.

Chapter 3

PA and AS conceptualized the ideas and methodology. PA conducted the field work. MP-G, MK and GvO contributed data. PA conducted the statistical analyzes with the support of AS. PA led the writing of the manuscript with important contributions from AS, C-DZ, GvO, MK, MP-G, HB, K-PM and YL. All authors contributed critically to the drafts. My overall contribution was 75%.

Chapter 4

PA and AS conceptualized the ideas and methodology. PA conducted the field work. AD, SH, MP-G, MK and GvO contributed data. PA conducted the statistical analyzes with the support of AS. PA led the writing of the manuscript with important contributions from AD, AS, C-DZ, GvO, MK, MP-G, HB, K-PM, SH and YL. All authors contributed critically to the drafts. My overall contribution was 75%.

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Curriculum vitae

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Education

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2014 – 2017	**M.Sc. Ecology** University of Oulu Thesis title: Ekolokeroiden laajuuden vaikutus kasvinsyöjähyönteisten geneettiseen monimuotoisuuteen. (English title translation: The Effect of Niche Width on Genetic Diversity in Herbivorous Insects) Supervisors: Dr. Tommi Nyman and Dr. Marko Mutanen
2009 – 2014	**B.Sc. Biology** University of Oulu Thesis title: Kasvinsyöjähyönteisten ravinnonkäyttö. (English title translation: Diet Breadth of Herbivorous Insects) Supervisor: Dr. Heikki Pöykkö

Professional experience

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9.2017	**Research assistant** - University of Oulu Electrofishing, water and aquatic invertebrate sampling, processing samples of invertebrate, litter and algae.
10.2016 – 4.2017	**Intern** – City of Oulu/University of Oulu Botanical Garden, Botanical Museum and Zoological Museum Wide variety of museum sample and botanical garden related tasks.
5.2014 – 8.2014	**Intern/Seasonal aid** – Finnish Game and Fisheries Research Institute Sonar monitoring of migrating salmon of River Tornio.
6.2012 – 7.2012	**Research assistant** – Sole proprietor Olli van der Meer (for Finnish Game and Fisheries Research Institute) Electrofishing and surveillance of trout and freshwater pearl mussel.
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Publication list and conference contributions

Published

Anttonen, P., Perles-Garcia, M., Kuntz, M., von Oheimb, G., Li, Y., Bruelheide, H., Ma, K-P., Zhu, C-D. & Schuldt, A. (2023). Predation pressure by arthropods, birds and rodents is interactively shaped by tree species richness, vegetation structure and season. Front. Ecol. Evol. 11:1199670. https://doi.org/10.3389/fevo.2023.1199670

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In preparation

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Conference contributions

Annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ) 2023 (Germany)
Oral contribution: Seasonal effects on herbivory and predation in a subtropical tree species richness experiment

iDiv conference 2022 (online)
Oral contribution: Effects of tree richness, structural variation and leaf traits on herbivory and predation in different local scales in a subtropical BEF-experiment

International Congress of Entomology 2022 (Finland)
Oral contribution: Effects of tree richness, structural variation and leaf traits on herbivory and predation in different local scales in a subtropical BEF-experiment

TreeDì-BEF China Seminar Series 2022 (online)
Oral contribution: Herbivory and predation in relation to neighbourhood interactions

TreeDì-BEF China Seminar Series 2021 (online)
Oral contribution: Bottom-Up and Top-Down Drivers of Herbivory

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Poster: Tree neighborhood interactions and the drivers of herbivory and arthropod diversity across forest tree diversity levels

TreeDì Doctoral Conference 2019, Beijing (China)
Oral contribution: Bottom-Up and Top-Down Drivers of Herbivory

TreeDì Kick-off Meeting 2018, Beijing (China)
Oral contribution: Bottom-Up and Top-Down Drivers of Herbivory

iDiv conference 2018 (Germany)
Poster: TreeDì - 林地 - Tree Diversity Interactions

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Bottom-Up and Top-Down Drivers of Herbivory“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Perttu Anttonen, Göttingen, 11.12.2023