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The significance of vegetation for arthropod communities along gradients of climate and land use

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SUMMARY

Plants and arthropods are central components of biodiversity and thus essential for ecosystem functioning. Severe losses in the abundance and diversity of vascular plants and terrestrial arthropods are reported across Europe and worldwide. Effective methods to maintain and promote biodiversity in human-dominated landscapes are needed, since the widespread declines are not restricted to certain habitats, but even occur within protected areas. Climate change and land-use alteration are major threats to biodiversity and ecosystems. Effects of climate and land use are interacting, such that the combination of both factors reinforces or counterbalances their impacts on species communities. However, the relative importance of these stressors in driving declines and community shifts in plants and arthropods is not well understood. Furthermore, plant and arthropod communities may interact in various ways. These include trophic relationships as well as the integrative role of vegetation in reflecting and modulating the local environment perceived by arthropods. However, there is much uncertainty about the extent to which these mechanisms that drive correlations between plants and arthropods at the level of species communities.

The aim of the thesis was to investigate the effects of climate and land use on plant and arthropod communities and to improve the understanding of the relationships between these species groups by exploring correlation patterns between plants and arthropods at the level of species composition, species richness and biomass. Further, the mechanisms behind these correlations were assessed, including direct and integrative aspects of vegetation. In an extensive field study carried out in Bavaria, vascular plants and terrestrial arthropods were sampled across independent gradients of climate and land use. The study sites covered typical habitat types of temperate Europe (forest, grassland, arable land and settlement). Using Malaise traps and DNA-Metabarcoding allowed to include a broad range of trophic and taxonomic arthropod groups in the analyses. Plant species data was collected in vegetation plots at the trap locations and during transect walks covering the further surroundings of the study sites.

Publication 1 investigated the effects of plant species composition, climate and land use on arthropod species composition, and explored which aspects of vegetation contribute to the relationships between plant and arthropod assemblages. Plant species composition explained the major fraction of variance in arthropod composition, while land-cover composition was another important predictor. Furthermore, the local habitat conditions depicted by the indicator values of the plant communities were more relevant for arthropod composition than trophic relationships between certain plant and arthropod species. The results emphasize the value of plants as a proxy for characterizing habitat conditions that are hardly accessible to direct environmental measurements.

Publication 2 investigated the significance of plant species richness as indicator for arthropod species richness and evaluated the importance of habitat amount and landscape configuration for both plant and arthropod richness. Across trophic levels, arthropod richness showed strong positive responses to the richness of plants that indicate protected biotopes. Red-listed plant species numbers promoted the richness of red-listed arthropods and butterflies. Overall, conservation-relevant plants species were more important predictors for arthropod richness than the amount of surrounding semi-natural habitat or landscape configuration. Plant species richness was mainly driven by local land use, with total species richness being highest in settlements and biotope-indicator richness being highest in forests. The results highlight the importance of forests including clearings and fringes for the conservation of plants and arthropods as well as of preserving and restoring high-quality habitats in agricultural and urban areas.

Publication 3 focused on the effects of climate and land use on arthropod biomass and richness. In addition, further analyses within this thesis assessed the relative importance of plant biomass and richness for arthropod biomass. Both biomass and species richness of arthropods increased with local temperature and were highest in forest sites. Arthropod biomass was lowest in urban sites, whereas arthropod species richness was lowest in arable land. Neither plant biomass nor plant richness showed substantial effects on arthropod biomass. The study identifies both intensive agriculture and urbanization as main drivers of arthropod declines. Contrasting responses of arthropod biomass and species richness suggest that these measures should not be considered as equivalent biodiversity indicators.

The overall discussion of the thesis summarizes the results of the three publications. The findings are discussed in the context of ongoing biodiversity losses, climate warming and land-use change, and study limitations are outlined. Based on the results, recommendations for the conservation and monitoring of plant and arthropod diversity in Central European landscapes are derived.

ZUSAMMENFASSUNG

Pflanzen und Arthropoden sind zentrale Bestandteile der biologischen Vielfalt und übernehmen wichtige Ökosystemfunktionen. Starke Verluste in der Anzahl und Diversität von Gefäßpflanzen und terrestrischen Arthropoden werden in Europa und weltweit beobachtet. Diese flächendeckenden Rückgänge sind nicht auf bestimmte Lebensräume beschränkt, sondern finden sogar in Schutzgebieten statt. Wirksamere Methoden für die Erhaltung und Förderung von Biodiversität in Kulturlandschaften sind daher dringend notwendig. Klima- und Landnutzungswandel sind große Bedrohungen für die biologische Vielfalt und Ökosysteme. Diese Faktoren stehen miteinander in Wechselwirkung, sodass sich Effekte von Klima und Landnutzung auf Artengemeinschaften gegenseitig verstärken oder auch abmildern können. Welche Rolle diese Stressoren für die Rückgänge von Pflanzen und Insekten spielen, ist jedoch nicht genau bekannt. Darüber hinaus gibt es vielerlei Interaktionen zwischen Pflanzen- und Arthropodengemeinschaften. Dazu gehören zum einen Nahrungsbeziehungen, aber auch der integrative Aspekt der Vegetation, die die lokale Umwelt abbildet und formt, welche von Arthropoden wahrgenommenen wird. Wie stark diese Faktoren die Zusammenhänge zwischen Pflanzen- und Insektengemeinschaften bestimmen, ist unklar.

Ziel der Dissertation ist es, die Auswirkungen von Klima und Landnutzung auf Pflanzen- und Arthropodengemeinschaften zu untersuchen und das Verständnis der Beziehungen zwischen diesen Artengruppen zu verbessern. Dazu werden Korrelationsmuster zwischen Pflanzen und Arthropoden auf der Ebene von Artenzusammensetzung, Artenvielfalt und Biomasse analysiert. Weiterhin werden die Mechanismen hinter diesen Korrelationen im Hinblick auf direkte und integrative Aspekte der Vegetation untersucht. In einer umfangreichen Feldstudie in Bayern wurden Gefäßpflanzen und terrestrische Arthropoden entlang unabhängiger Klima- und Landnutzungsgradienten erfasst. Die Versuchsflächen repräsentierten typische Lebensräume temperater Regionen in Europa (Wald, Grünland, Ackerland, Siedlungsgebiet). Der Einsatz von Malaise-Fallen und Metabarcoding ermöglichte es ein breites Spektrum trophischer und taxonomischer Gruppen zu analysieren. Zur Erfassung der Pflanzendaten erfolgten Vegetationsaufnahmen an den Fallenstandorten sowie Transektkartierungen in der weiteren Umgebung der Versuchsflächen.

Publikation 1 untersucht die Effekte von Pflanzenzusammensetzung, Klima und Landnutzung auf die Artenzusammensetzung der Arthropoden und analysiert, welche Aspekte der Vegetation die Beziehungen zwischen Pflanzen- und Arthropodengemeinschaften bestimmen. Die Artenzusammensetzung der Pflanzen erklärte den größten Anteil an Varianz in der Zusammensetzung der Arthropodenarten, während die Landnutzung ein weiterer wichtiger Faktor war. Die lokalen Umweltbedingungen, die die Pflanzen widerspiegeln und durch Zeigerwerte quantifizierbar sind, hatten dabei eine höhere Relevanz als direkte

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Nahrungsbeziehungen zwischen Pflanzen- und Arthropodenarten. Diese Ergebnisse heben die Bedeutung der Vegetation als Surrogat für lokale Habitatbedingungen hervor, welche durch direkte Umweltmessungen kaum erfassbar sind.

Publikation 2 betrachtet die Bedeutung der Pflanzenvielfalt als Indikator für Arthropodenvielfalt und bewertet den Einfluss von Habitatmenge und Landschaftskonfiguration auf die Artenvielfalt von Pflanzen und Arthropoden. Über alle trophischen Gruppen hinweg war die Vielfalt der Arthropodenarten stark korreliert mit der Vielfalt an Zeigerpflanzen für geschützte Biotope. Die Anzahl der Pflanzenarten der Roten Liste wirkte sich positiv auf die Anzahl der Arthropodenarten der Roten Liste sowie die Anzahl der Tagfalterarten aus. Insgesamt hatte die Vielfalt naturschutzrelevanter Pflanzenarten einen stärkeren Effekt auf die Arthropodenvielfalt als die Menge an naturnahem Habitat oder die Landschaftskonfiguration. Die Pflanzenartenvielfalt selbst wurde hauptsächlich durch die lokale Landnutzung bestimmt, wobei die Gesamtartenzahl in Siedlungen und die der Biotopzeigerarten in Wäldern am höchsten ausfiel. Die Ergebnisse betonen die hohe Bedeutung von Waldflächen einschließlich ihrer Lichtungen und Waldränder für den Schutz von Pflanzen- und Arthropodenarten sowie die Notwendigkeit für Erhaltung und Wiederherstellung von Flächen mit hoher Habitatqualität in landwirtschaftlichen und besiedelten Räumen.

Publikation 3 untersucht die Effekte von Klima und Landnutzung auf Biomasse und Artenvielfalt von Arthropoden. Ergänzend dazu wurden im Rahmen der Dissertation auch die Effekte von Pflanzenbiomasse und -vielfalt analysiert. Sowohl Biomasse als auch Artenvielfalt der Arthropoden war positiv mit den lokalen Temperaturen assoziiert und erreichten die höchsten Werte in Waldflächen. Während die Biomasse in Siedlungsflächen am geringsten ausfiel, wurden die niedrigsten Artenzahlen im Ackerland gemessen. Weder die Pflanzenbiomasse noch die Pflanzenvielfalt wirkten sich auf die Biomasse der Arthropoden aus. Die Studie stellt sowohl die intensive Landwirtschaft als auch die Urbanisierung als Hauptfaktoren für die Rückgänge in der Arthropodenfauna heraus. Die zum Teil gegensätzlichen Reaktionen von Arthropoden-Biomasse und -Artenvielfalt legen nahe, dass diese Maße nicht als gleichwertige Indikatoren für Biodiversität betrachtet werden sollten.

Die übergreifende Diskussion fasst die Ergebnisse der drei Publikationen zusammen und erörtert die Erkenntnisse vor dem Hintergrund des anhaltenden Artensterbens, der Klimaerwärmung und des Landnutzungswandels. Ferner werden methodische Grenzen der Arbeit aufgezeigt. Basierend auf den Ergebnissen werden Handlungsempfehlungen für Naturschutz und Monitoring von Pflanzen und Arthropodenvielfalt in mitteleuropäischen Landschaften abgeleitet.

GENERAL INTRODUCTION

Significance of plants and arthropods in terrestrial ecosystems

Plants and arthropods are fundamental components of biodiversity, and they provide key functions in all terrestrial ecosystems. As primary producers, plants form the basis of terrestrial food webs and life on land, taking up carbon dioxide from the atmosphere and converting it to sugars and oxygen through photosynthesis. A large number of animal species directly affect plant material, thereof half a million herbivorous insects (Hardy et al., 2020) consuming wood or foliage, sucking plant sap or feeding on pollen and nectar. Further, vegetation structures provide the physical habitat for countless organisms. Living and dead plants serve as oviposition and nesting sites, building material, shelter and hibernation places for animals, while also providing habitat for other plants, lichens and fungi. Moreover, plants reflect and modulate the conditions of their surrounding environment and thus determine the habitat for themselves and other organisms. Vegetation structure controls the microclimate through shading and transpiration, thus influencing ground-level and soil temperatures, light availability and air humidity (Chen et al., 1999), while also affecting air flow and wind speed through plant morphology (Leenders et al., 2007). Forests, for example, develop tall and dense canopies that have a significant impact on the microclimate, e.g. by buffering temperature extremes and thus modulating responses of understory species to macroclimatic warming (De Frenne et al., 2013, 2019). Besides, plants influence soil properties including chemistry, structure and microbial activity through their root systems, and by releasing nutrients through leaf fall (Mitchell et al., 2010; Pastor & Cohen, 1997; Yu et al., 2017).

Arthropods are among the most diverse and abundant groups of organisms on earth, including numerous taxonomic groups across multiple trophic levels. Insects contribute the largest fraction of biomass and species numbers of the global terrestrial arthropod fauna (Rosenberg et al., 2023; Stork, 2018), most of them belonging to five orders, i.e. Coleoptera, Lepidoptera, Diptera, Hymenoptera and Hemiptera (Stork, 2018). Insects and other terrestrial arthropods play critical roles for many ecosystem processes. They are vital for plant reproduction, with about 80% of all flowering plant species depending on pollination by flower-visiting insects (Ollerton et al., 2011). In addition, many plant species rely on seed dispersal by ants (Handel & Beattie, 1990). Detritivores such as saproxylic beetles or carrion-breeding flies are key drivers for the decomposition of dead organic matter. Furthermore, terrestrial arthropods are major components of food webs, including a great diversity of herbivores, predators and parasitoids, while also serving as staple food sources for birds and other animals (Morse, 1971).

Plant and arthropod declines in the past decades

Severe losses in biodiversity are happening across the globe (van Klink et al., 2020; Wagner, 2020). In many regions of Central Europe, local declines in species richness were reported particularly for terrestrial arthropods (Barendregt et al., 2022; Habel et al., 2019a; Seibold et al., 2019), but also for plants (Eichenberg et al., 2020; Jandt et al., 2022; Wesche et al., 2012). One of the most-cited studies in this context is that of Hallmann et al. (2017), describing a reduction of 76% in flying-insect biomass over 27 years based on Malaise-trap data from 63 locations in northwestern Germany. Remarkably, all of these sites were located within protected areas of different habitat types, which suggests that insect declines are a large-scale phenomenon also concerning areas where habitat quality is expected to be high. This is confirmed by recent studies that show reductions in arthropod richness and abundance both in agricultural areas and forests (Seibold et al., 2019; Staab et al., 2023). The declines are especially pronounced for specialists (Abrahamczyk et al., 2020; Scheper et al., 2014) and species with restricted habitat ranges (Neff et al., 2022). A recent analysis of long-term abundance trends of insect species in Bavaria reported declines of species protected by the EU habitat directive since its implementation (Engelhardt et al., 2023), in spite of the goal to maintain and improve the conservation status of these species. Likewise, evidence for declines of common and abundant plant and arthropod species is growing (Jansen et al., 2020; Seibold et al., 2019; Wagner et al., 2021).

Taken together, these findings suggest that the current European conservation practices are not sufficient to maintain biodiversity in human-dominated landscapes (Engelhardt et al., 2023). To counteract further losses in species diversity and abundance, more effective conservation strategies are needed that also address normal landscapes, in addition to preserving existing high-quality habitats, which are often small and isolated (Habel et al., 2019a, 2019b). To develop such strategies, it is important to understand the broad-scale drivers of plant and arthropod communities across land-use gradients and to assess the causes of the widespread biodiversity declines.

Effects of climate and land use on plant and arthropod communities

Both climate and land use are main determinants of biodiversity, species distribution and community composition. Distribution patterns of plant species strongly depend on climatic conditions such as temperature, humidity and continentality (Berg et al., 2017; Woodward & Williams, 1987). Thus, plant species composition changes along climate gradients (Otýpková et al., 2011; Zellweger et al., 2017), while regional plant species richness is positively correlated with temperature and water availability (Currie, 1991; Moser et al., 2005; Pausas et al., 2003). Arthropods strongly respond to climatic conditions as well, since they are ectothermic organisms that rely on environmental heat sources (Sears & Angilletta, 2015).

Local temperature determines activity, growth, survival and fecundity of arthropods (Angilletta, 2009), thus being an important driver of species richness and abundances (Hallmann et al., 2017; Pilotto et al., 2020), as well as community composition (Lessard et al., 2011; Uhey et al., 2020).

Although higher temperatures per se promote local plant diversity (Govaert et al., 2021; Steinbauer et al., 2018) and arthropod richness, particularly favoring thermophilic species (Engelhardt et al., 2022), climate warming threatens biodiversity in multiple ways (Harvey et al., 2023). Long-term increases in temperature lead to geographical and phenological range shifts (Boggs, 2016; Chen et al., 2011) and decoupling of biotic interactions (e.g. Schweiger et al., 2008), which results in habitat loss for cold-adapted species (Engelhardt et al., 2022; Neff et al., 2022) and destabilization of entire communities and ecosystems (Harvey et al., 2023). In addition, increases of extreme weather events due to climate change, such as heavy rainfalls, droughts and late frost, have negative effects on population dynamics, leading to higher extinction risks for local and regional populations of numerous species (Harvey et al., 2020; McLaughlin et al., 2002; Thomas et al., 2004).

Human-dominated landscapes that prevail in Central Europe largely consist of agricultural areas including crop fields and grassland, as well as managed forests and settlements, whereas undisturbed natural or semi-natural habitats cover only minor proportions. Within local land-use types, management practices such as timber harvest, mowing or the use of agrochemicals directly affect plant and arthropod communities (Gossner et al., 2016; Penone et al., 2019), but also modify their habitat conditions including vegetation structure, microclimate, soil conditions and nutrient supply (Chen et al., 1999; Duprè et al., 2010). Plant and arthropod communities thus change along gradients of land-use intensity and differ among land-use types (Birkhofer et al., 2017; Blake et al., 2003; Gossner et al., 2016; Weiner et al., 2011). At the landscape scale, the relative proportions of land-use types ('landscape composition') determine the amount of available habitat for plant and arthropod communities, while the spatial arrangement of land-use types ('landscape configuration') controls the connectivity between habitat patches within the landscape matrix, i.e. the chances for organisms to move between suitable habitats (Fahrig, 2013, 2017). Both landscape composition and configuration are thus important factors that influence plant and arthropod diversity and community composition (Concepción et al., 2012; Martin et al., 2019; Steckel et al., 2014). However, these variables are not independent of each other and thus often positively or negatively correlated (Redlich et al., 2021). Landscapes with high edge density, which is commonly used as a measure for landscape configuration, often provide high amounts of semi-natural habitat as well (**Fig. 1**), whereas edge density is typically low in landscapes with high proportions of forest. However, studies that are designed in a way that reduces confounding effects between landscape composition are lacking.

Fig. 1: (a) Example of a structurally rich landscape with a high proportion of semi-natural habitats such as extensively managed grassland, hedges and orchards (south of Bayreuth, Upper Franconia) and **(f) a cleared, intensively used landscape** (north of Würzburg, Lower Franconia), **with (b–e, g–j) species representing typical ecosystems of both landscapes**. (b) *Polyommatus bellargus* and (c) *Dianthus carthusianorum* are typical for dry grasslands; (d) *Vincetoxicum hirundinaria* and (e) *Araschnia levana* occur in forest edges and clearings; (g) *Sisymbrium officinale* and (h) *Thlaspi arvense* represent vegetation of arable land; (i) *Pieris brassicae* and (j) *Trifolium pratense* are widespread species that also occur in intensively used grasslands.

Land-use change has severely impacted the composition and structure of European landscapes during the past decades, with profound consequences for biodiversity and ecosystems (Newbold et al., 2015). Agricultural land-use intensification, that involves increases in the use of pesticides and fertilizer, higher mowing frequency, the conversion of grassland into cropland and the drainage of wetlands, led to widespread losses and fragmentation of habitats (Foley et al., 2005; Warren et al., 2021). Thus, high-quality habitats such as semi-natural grassland, hedges or set-aside areas have been greatly reduced in agricultural landscapes (**Fig. 1**). In addition, many of the remaining fragments of low-nutrient sites suffer from nitrogen deposition causing eutrophication of open (Duprè et al., 2010; Stevens et al., 2004; Wesche et al., 2012) and forest habitats (Roth, 2022; Verheyen et al., 2012). Likewise, forest practices caused habitat fragmentation through the removal of important structural elements such as old trees and dead wood (Müller et al., 2015; Whitehouse, 2006). In addition to land-use intensification, land abandonment has negative effects on biodiversity, particularly for semi-natural grasslands that depend on a certain level of disturbance through regular mowing or grazing (Uchida & Ushimaru, 2014; Uematsu et al., 2010). Beyond stressors related to agriculture and forest management, urbanization significantly contributes to habitat and biodiversity losses, e.g. through increases in sealed surfaces (Scalenghe & Marsan, 2009), chemical pollution of soil, air and water (Wagner et al., 2021), and artificial lighting at night (Owens et al., 2020).

Both land-use and climate change are major threats to biodiversity and ecosystems (Sala, 2000; Wagner et al., 2021). Many studies show that land-use associated drivers contribute to reductions in arthropod biomass and richness (Allan et al., 2014; Habel et al., 2019b; Hallmann et al., 2017; Seibold et al., 2019) and plant species richness (Jansen et al., 2020), while also causing biotic homogenization of plant and arthropod communities (Deguines et al., 2016; Gossner et al., 2016). Likewise, negative biodiversity trends are increasingly associated with climate change, with higher temperatures driving declines of cold-adapted insect species (Fitzgerald et al., 2021; Neff et al., 2022), while higher climatic variability reduces plant species richness and destabilizes plant communities (Zhang et al., 2018). Local extinctions of many plant and insect species across the globe are related to increases in maximum temperatures (Román-Palacios & Wiens, 2020).

Effects of climate and land-use change on biodiversity are interacting (Oliver & Morecroft, 2014), and the combination of both factors can reinforce, but also counterbalance their impacts on species communities (Fox et al., 2014). Thus, high maximum temperatures may exacerbate effects of habitat loss and fragmentation (Mantyka-Pringle et al., 2012), while in other cases, warmer conditions may be beneficial when habitat amount is limited (Müller et al., 2015). In turn, adverse effects of climate change may be reinforced at high levels of land-use intensity or landscape fragmentation (e.g. de Vries et al., 2012; Oliver et al., 2013), but mitigated by

high amounts of (semi-)natural habitat or nature-friendly land-use practices (Oliver et al., 2016; Outhwaite et al., 2022). Investigating independent and combined effects of climate and land use on biodiversity is therefore a major challenge. Although long-term studies are essential for assessing species trends, the explanatory contributions of climate and land-use change including their interactions are hard to assess, as the associated variables are often correlated (Neff et al., 2022; Peters et al., 2019). Thus, much uncertainty exists about the relative importance of these factors in driving plant and arthropod diversity declines and community shifts (Didham et al., 2020; Wagner et al., 2021), but such knowledge is needed to predict future changes and to develop conservation strategies that mitigate further losses (Redlich et al., 2021).

Relationships between plant and arthropod communities

Beyond the responses of plant and arthropod communities to climate and land use, many dependencies and interactions exist between these species groups. Based on data from an extensive observational field study including assessments of plant and arthropod communities along orthogonal gradients of climate and land use (Redlich et al., 2021), the PhD thesis analyses correlation patterns between plant and arthropod communities at the scale of species composition, species richness and biomass. These correlations may be the result of different mechanisms that drive plant-arthropod relationships, and can be separated into direct and indirect links.

Direct links

Vegetation as food resource: Phytophagous arthropods consume living or dead parts of plants, including wood, foliage, sap, seeds, fruits, pollen and nectar. Different degrees of specialization exist: Monophagous species feed on one single plant species or genus, oligophagous species feed on few different plant species or genera, and polyphagous species use many plant species and genera as food resources (Bernays & Graham, 1988). Feeding strategies may vary during a species' life cycle, as for example many butterflies are highly specialized as larvae, but feed on larger spectra of plant species as adults. The majority of phytophagous insects are mono- or oligophagous (Hardy et al., 2020; Ward & Spalding, 1993), mostly due to the chemical properties of the plant biomass (Pastor & Cohen, 1997). Phyllophagous insects that feed on foliage tend to be more specialized than flower-visiting insects consuming pollen and nectar (Castagneyrol & Jactel, 2012; Fontaine et al., 2009; but see Kawakita et al., 2010).

Vegetation as habitat structure: Vegetation provides habitat structures that arthropods require during their life cycle. These can be considered at different scales: At the species level, the fine-scale architecture of individual plants may influence the movement and abundance of arthropods (Crist et al., 1992; Dennis, 2004), while these physical structures are usually less

species-specific than host plants, as the morphology of plants may be typical of a particular species but not unique to it (Beals, 2006). Plant species assemblages build up vegetation structures that shape the three-dimensional space in which arthropods move and live. Vegetation structure is thus closely related to plant species composition (Schaffers et al., 2008), and strongly depends on land-use intensity and management schemes, such as mowing regimes or the type of forestry. It is commonly measured as height, density, or structural heterogeneity of ground vegetation or forest stands (Lengyel et al., 2016; Müller & Brandl, 2009; Schaffers et al., 2008; Zellweger et al., 2016). Plant communities determine vegetation structures, and they are summarized to vegetation formations that constitute general habitats such as forest or grassland, which correspond to land-cover classes as assessed by remote sensing (e.g. CLMS, 2018). Both vegetation type and structure strongly determine the microclimatic conditions including light availability and local temperature (Müller & Brandl, 2009; Prather & Kaspari, 2019; Suggitt et al., 2011).

Indirect links

Vegetation indicating and modulating habitat quality: As sessile organisms, plants are closely adapted to their respective abiotic site conditions. Plant communities change along gradients of climate, light and soil resources. For the European flora, Ellenberg indicator values are 'pseudo-quantitative' measures to describe these habitat conditions (Ellenberg et al., 1991). In addition, vegetation itself modulates habitat quality, e.g. by creating microclimatic gradients (Prather & Kaspari, 2019; Suggitt et al., 2011) and altering soil properties (Mitchell et al., 2010; Pastor & Cohen, 1997; Yu et al., 2017). Thus, arthropods are indirectly linked to vegetation in the sense that they respond to their local environment, which is both reflected and shaped by the plant communities.

Trophic cascades: Another indirect dependency between arthropods and plants exists via trophic effects propagating through food webs. Predatory or parasitoid arthropods feed on phytophagous insects, thus linking plant communities with arthropods of higher trophic levels via their prey (Scherber et al., 2010). Although this aspect modulates the responses of arthropod communities to vegetation, it is not studied further within the thesis.

Current scientific knowledge

Overall, the relationships between plant and arthropod communities have been addressed by many studies, but most of them show some deficits. The study design often does not sufficiently account for the underlying environmental variables including abiotic gradients, habitat amount or landscape configuration, which may drive correlations between plants and arthropods due to shared responses of communities to these variables (Bucher et al., 2019; van Schalkwyk et al., 2019). Thus, the independent effects of vegetation on arthropod communities after controlling for environmental factors and variables related to land use have

rarely been quantified. Studies that considered this point suffer from other restrictions, as they included only a small range of arthropod taxa and trophic levels (Müller et al., 2011; Sanderson et al., 1995; Zellweger et al., 2017), or were limited to single habitat types and small study areas (Schaffers et al., 2008; Uhl et al., 2020; van Schalkwyk et al., 2019). Furthermore, most publications focus on the relationships between plant species richness and the richness or abundance of various arthropod groups (Castagneyrol & Jactel, 2012; Moreira et al., 2016), although species richness represents only one aspect of biodiversity, and ignores differences in species composition of plants and arthropods, which is a less investigated topic (Schaffers et al., 2008).

Species composition: Previous studies that assessed correlations between plant and arthropod assemblages reported strong effects of vegetation composition on arthropod species composition (e.g. Müller et al., 2011; Sanderson et al., 1995; Schaffers et al., 2008; Zellweger et al., 2016). Müller et al. (2011) tested the role of trophic interactions in driving these effects. Although plant species composition explained a high amount of variance in the composition of specialist herbivores, this could not be attributed to the presence of their associated host plants (Müller et al., 2011). Similarly, Schaffers et al. (2008) found that a simplified plant dataset, i.e. summarized to characteristic species groups, performed equally well in explaining patterns in the species composition of herbivore and carnivore arthropods as a detailed plant dataset containing the full information at the species level. These findings suggest that direct links between plant and arthropod species may play a subordinate role in explaining correlations between plant and arthropod assemblage composition. In turn, the integrative character of plant communities reflecting the local habitat conditions of arthropods could be a more significant factor that determines such patterns. However, to what extent these mechanisms drive the relationships between plant and arthropod communities of different trophic levels remains largely unknown (Müller et al., 2011; Schaffers et al., 2008).

Species richness: Positive correlations between plant and arthropod species richness are frequently reported across different habitat types and trophic levels. Particularly herbivores show strong responses to plant species richness (Castagneyrol & Jactel, 2012; Scherber et al., 2010), but positive effects are also found for higher trophic arthropod groups (Haddad et al., 2009; Schuldt et al., 2019). Depending on the studied taxa, several pathways may explain these effects:

- Higher plant species richness provides a greater diversity of food resources, which promotes the species richness of primary consumers that are specialized on different host plants (*Resource Specialization Hypothesis*; Keddy, 1984; Moreira et al., 2016);

- Higher plant species richness promotes plant productivity, increasing the abundance of herbivores, which in turn results in a higher species richness of herbivores (*More Individuals Hypothesis*; Moreira et al., 2016; Srivastava & Lawton, 1998)

- Higher plant species richness increases the range and heterogeneity of available habitat niches, favoring a higher number of arthropod species requiring specific habitat structures (Joern & Laws, 2013; Schuldt et al., 2019);

- Increases in the richness of secondary consumers with the number of plant species are mediated by cascading bottom-up effects of plant species richness through herbivore richness and abundance (Castagneyrol & Jactel, 2012; Haddad et al., 2009; Scherber et al., 2010);

- Both plant and arthropod richness show similar responses to environmental gradients, such as climate, soil conditions or land-use variables (Bucher et al., 2019; van Schalkwyk et al., 2019).

Although these hypotheses are frequently discussed when explaining correlations between plant and arthropod diversity, their actual contribution in driving these relationships is unclear (Moreira et al., 2016). This is partly due to the fact that plant species richness is often correlated with other variables such as the amount of available habitat or landscape heterogeneity (Billeter et al., 2008; Uhl et al., 2020). Furthermore, most studies only consider the responses of arthropods to overall plant species richness, although not all plant species are equally important for promoting arthropod richness, particularly in modified landscapes with high proportions of non-native vegetation, such as or arable land or urban areas (Perre et al., 2011; Salisbury et al., 2015). Subsets of indicator species that are characteristics for high-quality habitats might thus be more suitable surrogates to estimate arthropod richness. Yet, the relevance of these subsets for predicting arthropod richness compared to total plant species richness is unclear, and may also vary depending on the investigated taxa and trophic groups. While the richness of primary consumers may be more strongly correlated with overall plant species numbers representing a greater diversity of food resources, higher trophic groups such as predators, which are often habitat specialists (Woodcock & Pywell, 2010), may rather respond to overall habitat quality reflected by indicator plants.

Biomass: Arthropod biomass is influenced by the amount of captured individuals, the number of species as well as their body sizes. It is therefore only a rough measure of biodiversity, but still allows to derive information on the general state of the local entomofauna (Hallmann et al., 2017). Results from field experiments showed positive responses of arthropod biomass and abundance to plant biomass (Borer et al., 2012) and plant species richness (Scherber et al., 2010). However, the positive effects of plant species richness seemed to be more driven by plant productivity that increases with plant species numbers (Borer et al., 2012; Haddad et al., 2011) than by the diversity of food resources or habitat niches increasing arthropod abundance

through higher species richness (but see Scherber et al., 2010). However, these experimental approaches ignored further environmental effects such as local climate, land use or habitat quality, which may vary considerably under real conditions. High plant productivity often coincides with high land-use intensity, which reduces arthropod biomass, e.g. through the use of pesticides, thus counteracting positive effects of plant productivity. Furthermore, a field study in riparian forests of North America found that resource quality (i.e. the proportion of deciduous vegetation) was a more important predictor for nocturnal insect biomass than the amount or diversity of plant resources (Ober & Hayes, 2008). Similarly, Hallmann et al. (2017) found positive responses of arthropod biomass to tree species richness, but not to herb species richness. Thus, the amount of semi-natural vegetation determining habitat quality seems an important driver of arthropod biomass. However, representative field studies that explore the influence of plant productivity and habitat quality on arthropod biomass are lacking.

OBJECTIVES AND OUTLINE

The PhD thesis is based on data from an extensive correlative field study carried out in Bavaria, Southern Germany. Vascular plants and terrestrial arthropods were sampled along orthogonal gradients of climate and land use (Fig. 2). The study sites covered typical habitat types of temperate Europe (forest, grassland, arable land and settlement), and were embedded in three contrasting landscape types (forest-dominated, agricultural, urban). The obtained arthropod data covered a broad range of taxonomic groups and trophic levels.

The aim of the thesis is to improve the understanding of the relationships between plant and arthropod communities as well as the relative importance of climate and land-use variables for both species groups. These aspects are analyzed based on correlation patterns between plants and arthropods at the level of species composition, species richness and biomass. In addition, the mechanisms behind these relationships are explored, including direct and integrative aspects of vegetation. Specifically, the following objectives and hypotheses are addressed:

1. Determine the importance of vegetation, climate and land use to arthropod species composition, species richness and biomass
   ⇨ The importance of vegetation for arthropod species composition and richness is expected to differ among trophic groups of arthropods, with stronger effects on primary consumers than on secondary consumers.

2. Disentangle direct and integrative effects of vegetation on arthropod assemblage composition
   ⇨ Direct trophic links between herbivores and host plants should be more relevant in determining the species composition of primary consumers, while local habitat conditions reflected and shaped by plant species composition should be more important for higher trophic groups.

3. Test the suitability of plant species richness as a proxy for arthropod species richness and biomass
   ⇨ Plants indicating high habitat quality should be a better predictor for arthropod species richness and biomass than total plant species richness

These points are examined within three publications included in this thesis (Fig. 2).

The overall discussion of the thesis summarizes the results of the three publications. The findings are discussed in the context of ongoing biodiversity losses, climate warming and land-use change, and study limitations and further research perspectives are outlined. Based on the results, recommendations for the conservation and monitoring of plant and arthropod diversity are derived.
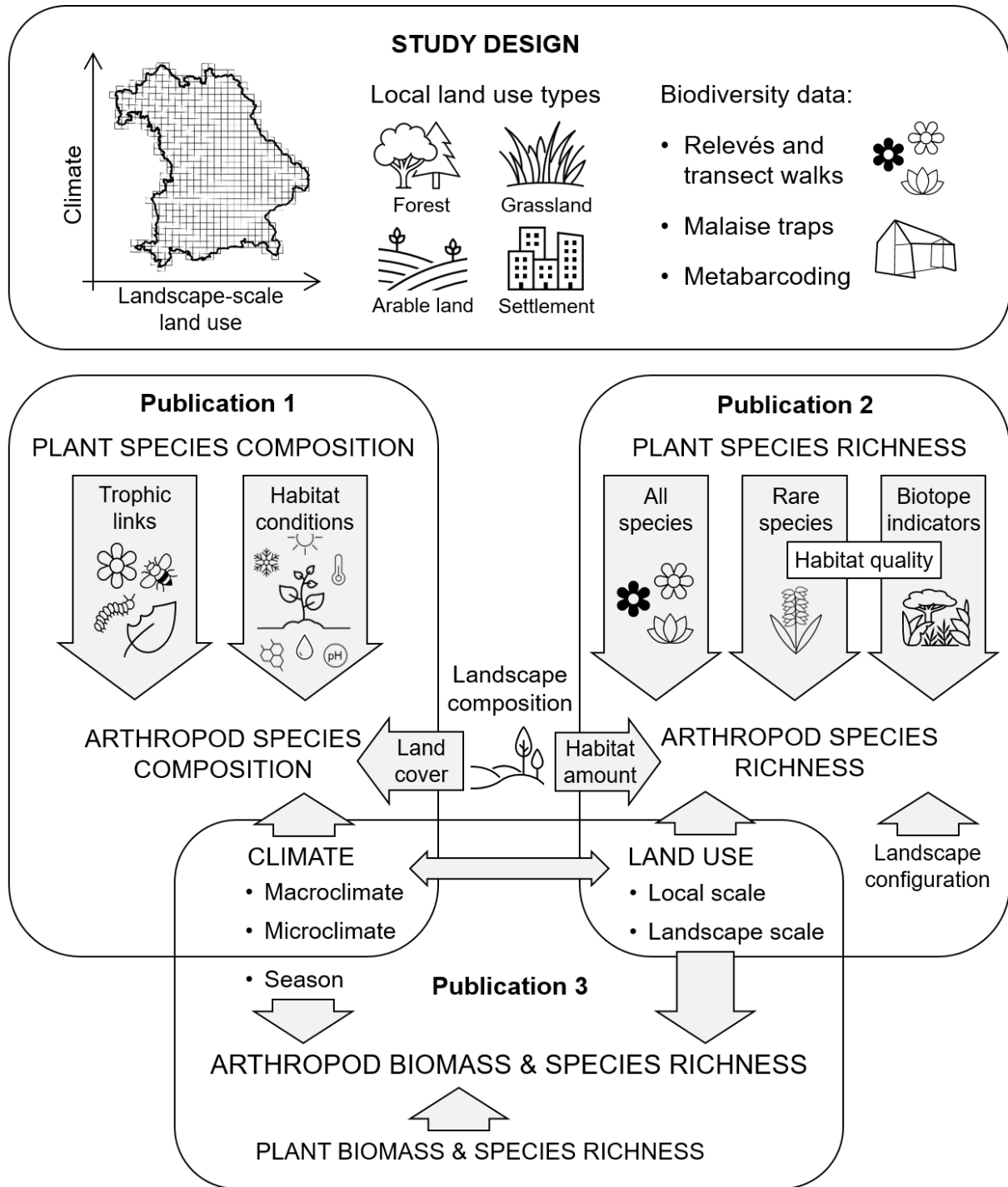
Fig. 2: Graphical overview of the thesis showing the key aspects of the study design and the main contents of Publications 1-3. The multi-scale design covers orthogonal gradients of climate and landscape-scale land use as well as four local land-use types in which the study sites were established. The datasets on vascular plants and terrestrial arthropods collected on these sites are the basis of the three publications. **Publication 1** focuses on the relationships between plant and arthropod species composition and disentangles which aspects of vegetation are relevant in shaping arthropod communities. **Publication 2** addresses effects of plant species richness on arthropod richness and investigates the importance of habitat quality, habitat amount and landscape configuration. **Publication 3** focuses on the responses of arthropod biomass and richness to climate and land use considering both small- and large-scale effects. The effects of plant biomass and richness on arthropod biomass were included in an additional analysis within this thesis, complementary to the findings of Publication 3.

METHODS

All data used for the publications within this thesis were acquired within the framework of the joint LandKlif project (https://www.landklif.biozentrum.uni-wuerzburg.de), aimed at understanding and disentangling the effects of climate and land use on biodiversity and ecosystem services at multiple spatial scales. The project included an extensive field campaign carried out in 2019 and 2020 throughout the State of Bavaria in Southern Germany.

Study design

The LandKlif project is built on an innovative sampling design that allowed assessing biodiversity data along orthogonal gradients of climate and land use at both local and landscape scale (Redlich et al. 2021). Based on topographical map quadrants of ca. 5.8 km x 5.8 km grid cell size, the state of Bavaria was stratified into five climate zones and three landscape-scale land-use types (urban, agricultural and forest-dominated), hereafter named 'landscape types'. One quadrant represents a quarter of a map sheet of the German ordnance map at the scale of 1:25.000 (TK25). These quadrants are commonly used for floristic and faunistic grid mapping (Ehrendorfer & Hamann, 1965). The climate zones were defined based on mean annual temperature values for the period 1981–2010 (<7.5, 7.5–8.0, 8.1–8.5, 8.5–9.0, >9 °C). The land-use types were classified based on CORINE land cover data (urban >14% settled area or traffic infrastructure; agriculture >40% arable land or managed grassland; near-natural i.e. forest-dominated >85% near-natural vegetation and >50% forest; Redlich et al., 2022; CLMS, 2018). Four replicates of each combination of climate zone and landscape type resulted in a selection of 60 quadrants distributed across Bavaria (Fig. 3).

Within each quadrant, three study sites were established in the prevalent local land-use types (forest, arable field, grassland and settlement). Wherever possible, the sites were selected such that the correlation between landscape composition (i.e. area percentages of land-use types) and landscape configuration (i.e. edge density) was minimized (Redlich et al., 2021).
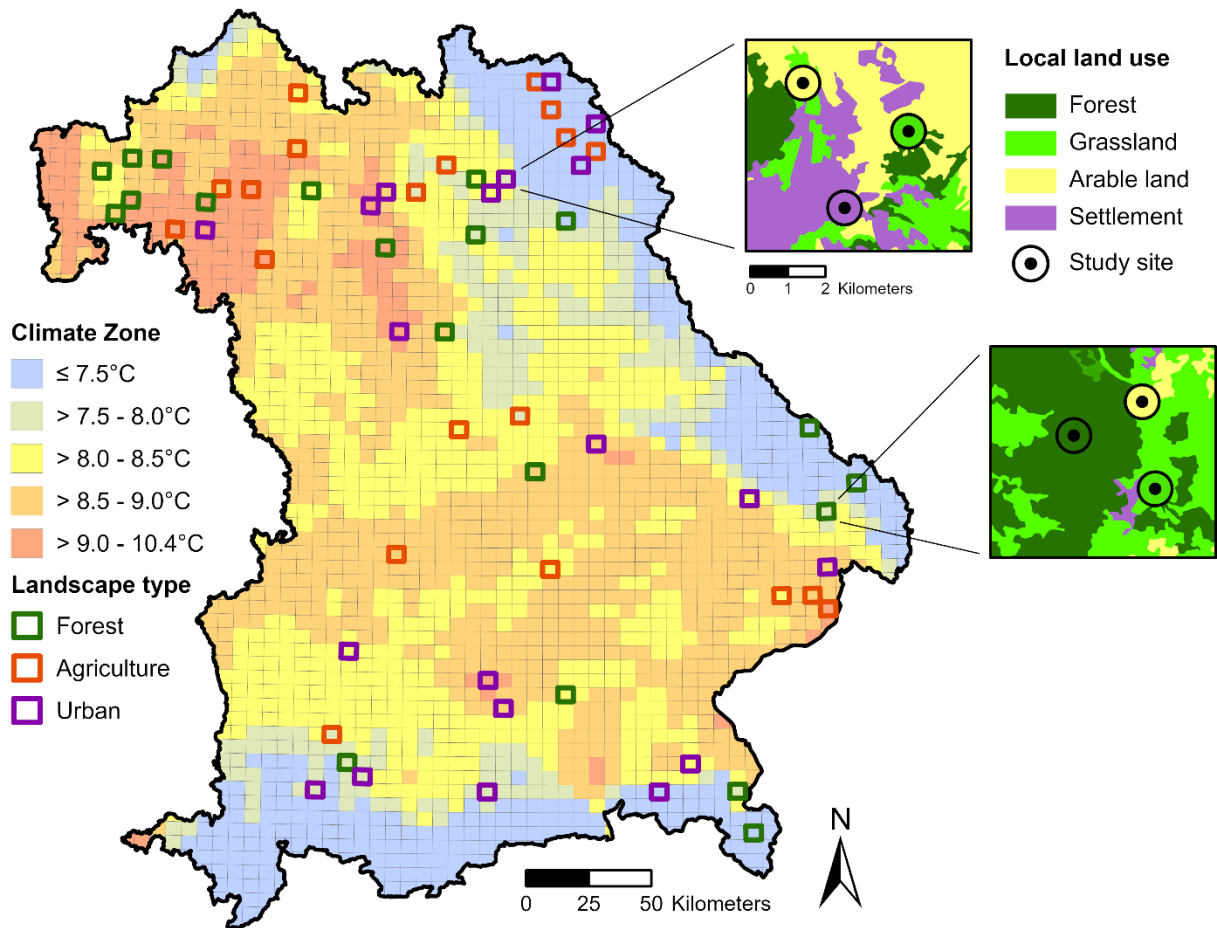
Fig. 3: Sampling design of the PhD thesis on regional and local drivers of plant and arthropod communities. Distribution of 60 quadrants (5.8 km x 5.8 km) across Bavaria, representing five climate zones and three landscape types (forest-dominated, agricultural, urban), each containing three study sites representing the prevailing local land-use types (forest, grassland, arable land, settlement).

Each site consisted of an open patch of herbaceous vegetation of 3 m x 30 m size within or next to the respective local land-use type. Specifically, forest sites were set up within clearings or forest glades and sites representing arable land on field margins. Sites within settlements were mostly located in green areas such as cemeteries or public green spaces, sometimes also in undeveloped real estate or private gardens. One site could not be established due to denial of landowner permission, resulting in a total set of 179 sites (instead of 180 as intended by the study design).

Fig. 4: Examples of study sites representing the four local land-use types investigated for the PhD thesis. Sites were standardized to open areas with herbaceous vegetation within a) forest, b) grassland, c) arable land and d) settlement.

Vegetation survey

Vegetation sampling took place in two field campaigns. In 2019, vegetation was assessed within seven subplots (10m^2 in total) within each 3 m x 30 m plot. All vascular plant species were listed and cover values of each species was estimated using the Braun-Blanquet scale (Dierschke, 1994). In addition, cover of different strata (trees, shrubs, herbs and grasses, moss, litter, bare rock) was estimated for each subplot. Each study site was visited once between mid-May and end of July 2019. In the same year, aboveground plant biomass was sampled within each 3 m x 30 m patch. Vegetation was cut at ground level within three randomly selected quadrats of 20 cm x 20 cm size. Each study site was sampled once between May and July 2019. The samples were oven-dried and their dry weight was measured with a precision scale.

In 2020, plant species pools were assessed during transect walks in 200-m buffer areas around the study sites, leading along existing roads and tracks (smaller ones were preferred), similar to the methodology of the Swiss Biodiversity Monitoring (Koordinationsstelle BDM, 2014). Each buffer was visited once between mid-May and early-August 2020. All plant species within sight were mapped while slowly walking along predefined routes that were chosen such that they covered the dominant land-cover types within the buffers (forest, agriculture including grassland and arable land, as well as settlement area; water bodies and traffic areas were ignored). Walking time was standardized to 60 min and proportional to the named land-cover

percentages within the circle. Area percentages below 10% were not considered. Land-cover data were obtained from a combined map containing information from CORINE Land Cover (CLMS, 2018), ATKIS 2019 (German Official Topographic-Cartographic Information System) and IACS 2019 (Integrated Administration and Control System).

For all analyses performed for Publication 1 and 2, plant species data of both surveys (2019 and 2020) were aggregated into a single presence-absence dataset. This was done in order to represent the plant species pools surrounding the Malaise traps as completely as possible, as the captured arthropod species reached the trap from various distances.

Arthropod survey

Arthropods were sampled using Malaise traps, with ethanol (80%) as capture fluid. The traps matched the Townes Malaise trap model, however, with a black roof and slightly smaller dimensions (for details, see Uhler et al. 2021). Malaise traps are known to capture a high diversity of arthropod species mainly consisting of flying insects, while also non-flying arthropods may crawl into the trap from the ground (Karlsson et al., 2020; Uhler et al., 2022). Where applicable, the traps were placed orthogonally to vegetation structures that determined insect flight corridors. On each study site, one Malaise trap was set up from mid-April 2019 to mid-August 2019. Traps were emptied every two weeks, resulting in eight sampling rounds per site. Individual sampling intervals varied slightly due to logistic reasons. Vegetation close to the trap entrance was cut regularly during the sampling period.

Each Malaise trap sample was sieved and its weight determined at the moment when the time between two drops of ethanol reached ten seconds (Uhler et al., 2021). Out of 1432 possible samples, 93 were not collected due to delayed sampling start or breakdown of the traps, and three samples were lost after weighing. Thus, 1339 samples were considered in the biomass analyses (Publication 3), and 1336 in the analyses addressing arthropod species richness and composition (Publication 1 and 2).

Arthropod species were identified via DNA-metabarcoding, based on CO1-5P (mitochondrial cytochrome oxidase 1). BINs (Barcode Index Numbers) were used as taxonomic units, based on the Barcode of Life Data System (BOLD; Ratnasingham & Hebert, 2007). BINs are clusters of DNA sequences that show close concordance with species (Ratnasingham & Hebert, 2013). For more details on the bioinformatics methods, see Uhler et al. (2021) and Hausmann et al. (2020). For the analyses of Publication 2, arthropod data from all eight sampling rounds were pooled, containing presence-absence data of all BINs (hereafter referred to as 'species') identified in the traps throughout the season. In Publication 1 and 3, only three sampling rounds (second half of May, June and July, respectively) were included to calculate arthropod species

richness, because the remaining samples were sequenced after these manuscripts were written.

Local temperature and humidity

During Malaise trap sampling, temperature and humidity on the study sites were measured hourly using ibutton thermologgers. The loggers were fixed on a wooden pole at 1.1 m height above ground, facing north. For the analyses in Publication 3, mean temperature and humidity values were calculated for each study site, based on the trap-specific sampling intervals (Uhler et al., 2021).

Data analyses

All statistical analyses were conducted with R Versions 4.0.3 and 4.2.0 (R Core Team, 2022). Spatial data processing including the calculation of land-cover percentages and edge density was done in ArcGIS Pro. Statistical methods mainly involved variance partitioning, mixed effect models, and general additive models, depending on the research questions. Table 1 provides an overview of the methods used in each publication including the independent and explanatory variables. In all analyses of Publication 2 and 3, model coefficients were extracted using *cftest* (package *multcomp*; Hothorn et al., 2008), and significant differences from multiple post-hoc comparisons between land-use categories were obtained with function *glht* (package *multcomp*; Hothorn et al. 2008).

In **Publication 1**, variance partitioning (function *varpart*, package *vegan*; Oksanen et al. 2020) was used to assess the responses of arthropod species composition to plant species composition, Ellenberg indicator values, land cover and climate, additionally including latitude and longitude of the study sites to account for spatial autocorrelation. This method partitions the variation in community data using adjusted R^2 in distance-based redundancy analysis (RDA; Borcard et al., 1992). Presence-absence data of plants and arthropod groups were therefore transformed into distance matrices using the Sorensen coefficient (Legendre & Legendre, 2012; Sørensen, 1948). Distance matrices of all other explanatory variables were created using Euclidean distances. All Ellenberg indicator values considered in the analysis (light, temperature, continentality, moisture, soil pH and nutrient values) were included in one predictive distance matrix calculated based on the relative frequencies of the respective values in each category. In addition, the multivariate correlation of arthropod composition to single categories of Ellenberg values were quantified using Mantel tests (function mantel, package vegan; Oksanen et al., 2020; Legendre & Legendre, 2012). Finally, the responses of arthropod composition to a subset of plant species known to be hosts of monophagous insects were tested against randomly selected plant subsets using t-tests.

In **Publication 2**, mixed effect models (functions *lmer* and *glmer.nb*, package *lme4*; Bates et al. 2015) were used to investigate the effects of plant species richness, temperature and land-use related variables on arthropod species richness. To account for the nestedness of the study sites, quadrant (containing three study sites) was set as a random term. Significant differences between local land-use categories and landscape types were tested with the *glht* function in the *multcomp* package (Hothorn et al., 2008). Explained variance (adjusted R^2 values) of the predictors as well as marginal and conditional R^2 values of the models were calculated using the *glmm.hp* package (Lai et al., 2022). Normality and homoscedasticity of the model residuals were validated using the *DHARMa* package (Hartig, 2022).

In **Publication 3**, generalized additive models (package mgcv; Wood, 2004) were calculated to assess effects of land use and climate variables on arthropod richness and biomass. In contrast to Publication 1 and 2, arthropod data were not pooled for the entire sampling season, but were analyzed at the level of single samples taken at approximately two-week intervals. The models accounted for seasonality, variation in sampling intervals, spatial autocorrelation, and repeat measurements on each study site (Uhler et al., 2021). Further, correlations between arthropod richness and biomass were assessed using linear mixed effect models with study site as a random factor, considering four taxonomic orders (Diptera, Hymenoptera, Coleoptera, Orthoptera) as well as a group containing all other taxa. Both arthropod richness and biomass were log-transformed in these models.

Within this thesis, further analyses were conducted in addition to Publication 3, considering the responses of arthropod biomass to plant biomass and plant species richness (Appendix A1). For each study site, the mean daily biomass collected throughout the complete sampling season was calculated as target variable. The mean dry weight of plant biomass was based on the three samples of each study site. The effects of plant biomass and plant species richness on arthropod biomass and richness were tested using linear mixed effect models using the same methods as described for Publication 2, further including local temperature and humidity, as well as local and landscape-scale land use as fixed factors, and quadrant as a random term. Likewise, the effects of land use and local climate on plant biomass were tested (Appendix A1).

Table 1: Variables and methods used in the data analyses for the three publications included in the thesis. All long-term climate data were obtained for the period 1991–2020.

	Publication 1	Publication 2	Publication 3
Target variables	Arthropod species composition[1]	Arthropod species richness Plant species richness	Arthropod biomass Arthropod species richness[1]
Explanatory variables	Plant species composition Ellenberg indicator values Land-cover percentages Climate variables[2] Space (coordinates of the study sites)	Plant species richness Semi-natural area Mean annual summer temperature (May-September) Edge density Local land use[4] Landscape-scale land use[5]	Mean annual temperature and precipitation Local temperature and humidity[3] Local land use[4] Landscape-scale land use[5]
Statistical methods	Variance partitioning (distance-based redundancy analysis) Mantel tests T-tests	Mixed effect models Post-hoc tests	Generalized additive models Mixed-effect models Post-hoc tests
Arthropod groups considered	*Functional groups:* Herbivores, Pollinators, Predators, Parasitoids, Detritivores. *Taxonomic orders:* Lepidoptera, Coleoptera, Hymenoptera, Diptera.	All arthropods Red-listed arthropods *Functional groups:* Herbivores, Predators, Parasitoids, Detritivores. *Taxonomic groups:* Butterflies, Cicadas, True bugs, Beetles, Hoverflies, Wild bees.	All arthropods[1] Red-listed arthropods[1]

[1]Subset of three out of eight sampling rounds (second half of May, June and July, respectively)

[2]Including elevation a.s.l. of the study sites, mean annual summer temperature and precipitation (May–September), and mean annual temperature range (difference between January and July temperatures)

[3]Measured with data loggers placed on the study sites during arthropod sampling 2019

[4]Factor with four levels: forest, grassland, arable land, settlement

[5]Factor with three levels: forest, agriculture, urban

SUMMARY OF PUBLICATIONS

Publication 1: Plant species composition and local habitat conditions as primary determinants of terrestrial arthropod assemblages

Tobisch, C., Rojas-Botero, S., Uhler, J., Müller, J., Kollmann, J., Moning, C., Brändle, M., Gossner, M.M., Redlich, S., Zhang, J., Steffan-Dewenter, I., Benjamin, C., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Uphus, L., Ewald, J., 2023. Plant species composition and local habitat conditions as primary determinants of terrestrial arthropod assemblages. *Oecologia*.

Author contributions

Jörg Müller (JM), Jörg Ewald (JE) and Cynthia Tobisch (**CT**) conceived the idea of this manuscript. Ingolf Steffan-Dewenter (ISD), JM, Jie Zhang (JZ) and Sarah Redlich (SR) developed the overall study design. **CT**, Sandra Rojas-Botero (SRB), Johannes Uhler (JU), JE, Johannes Kollmann (JK), Christoph Moning and JM designed the methods of plant and arthropod surveys. **CT**, SRB, JU, Caryl Benjamin, Jana Englmeier, Ute Fricke, Cristina Ganuza, Maria Haensel, Martin Brändle, Martin M. Gossner, Rebekka Riebl, SR and Lars Uphus collected or provided data. **CT** analyzed the data and wrote the manuscript; all authors critically commented on the manuscript.
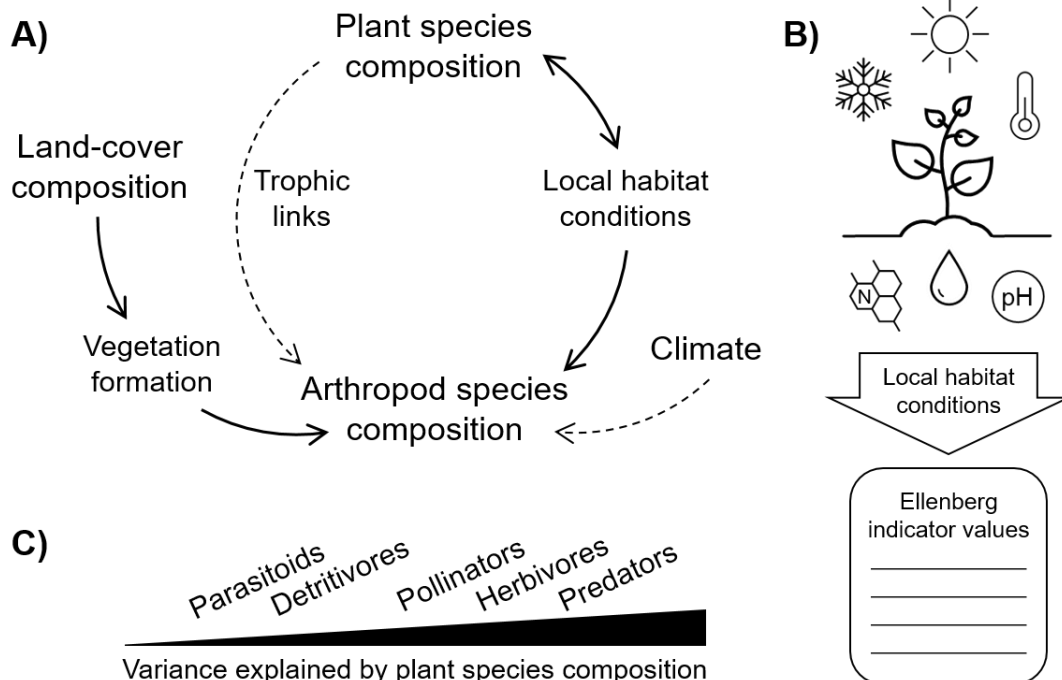
Graphical abstract

Fig. 5: Graphical abstract of Publication 1 presenting the resulted pathways that mainly determine the relationships between plant and arthropod species composition (A). This includes the integrative aspect of vegetation indicating local habitat conditions that are quantified by Ellenberg indicator values (B). Variance in arthropod species composition was partitioned among plant species composition and the other environmental drivers to compare the explanatory power of the predictors for the studied groups covering different trophic levels (C).

Summary

Arthropod communities may be linked to vegetation in different ways, with plants serving as food resources, building physical habitat structures and reflecting habitat conditions. Yet, to what extent these mechanisms drive correlations between plant and arthropod assemblages is unclear. In addition, the relative importance of vegetation compared to other environmental drivers such as climate and land use for arthropod species composition of different trophic levels are not well studied. **Publication 1** investigates the independent and combined effects of plant species composition, climate and land use on arthropod species composition and explores how different aspects of vegetation affect arthropod assemblages.

According to the LandKlif design, vascular plants and terrestrial arthropods were sampled along orthogonal gradients of climate and land use on 179 study sites across Bavaria in Southern Germany. Arthropod species were captured using Malaise traps and determined by DNA-Metabarcoding. Plant species pools were assessed within 200-m buffers around the trap locations. Using variance partitioning based on dissimilarity matrices, the responses of arthropod composition to plant species composition, climate and land cover as well as to the combined effects of the predictors were assessed. Further, Ellenberg indicator values and a subset of host plants of specialized insects were included to evaluate the contribution of direct trophic relationships and local habitat conditions in explaining arthropod composition. Four taxonomic orders (Lepidoptera, Coleoptera, Hymenoptera and Diptera) and five functional groups (herbivores, pollinators, predators, parasitoids and detritivores) were considered as target groups.

Plant species composition was an important predictor for arthropod species composition in all investigated groups, and shared a significant fraction of explained variance with land-cover composition. Including Ellenberg indicator values in the analysis revealed that the local habitat conditions indicated by vegetation – particularly temperature and light availability – were more relevant in determining arthropod composition than direct relationships at the species level, i.e. between single arthropod species and their associated host plants. Explained variance of vegetation in arthropod composition showed no consistent decrease towards higher trophic levels. Plant species composition had indeed stronger effects on herbivores and pollinators than on parasitoids and detritivores, but responses of predators were most pronounced.

The results point out the strong integrative character of plant communities reflecting the habitat conditions of arthropods across various taxa and trophic levels. Plants may thus serve as valuable surrogates to assess such habitat conditions that are otherwise hard to detect by physico-chemical measurements. The findings suggest that climate and land-use change altering small-scale environmental conditions may likely lead to shifts in arthropod community composition.

Publication 2: Conservation-relevant plant species indicate arthropod richness across trophic levels: Habitat quality is more important than habitat amount
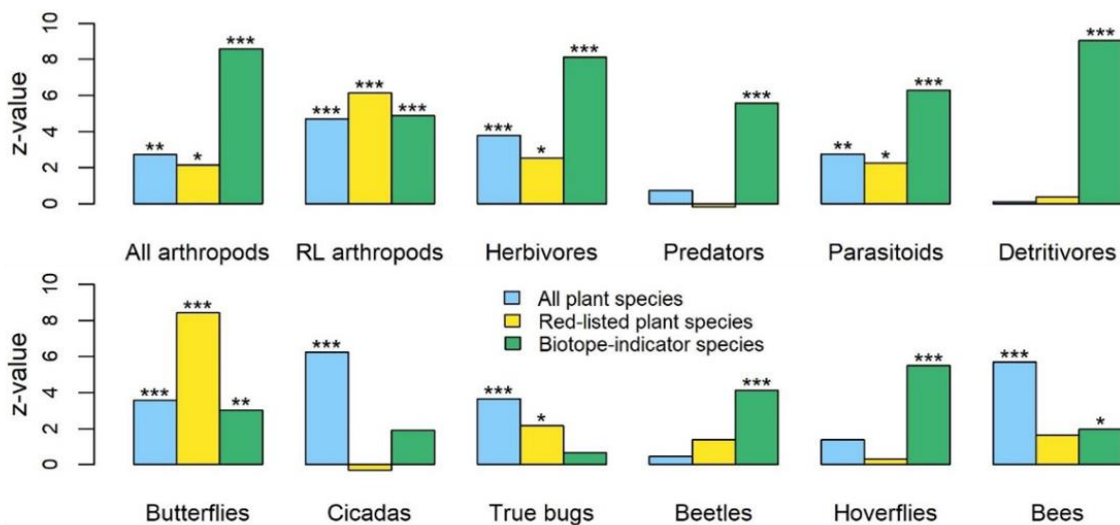
Tobisch, C., Rojas-Botero, S., Uhler, J., Kollmann, J., Müller, J., Moning, C., Redlich, S., Steffan-Dewenter, I., Benjamin, C., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Uphus, L., Ewald, J., 2023. Conservation-relevant plant species indicate arthropod richness across trophic levels: Habitat quality is more important than habitat amount. *Ecological Indicators* 148, 110039.

Author contributions

Cynthia Tobisch (**CT**) and Jörg Ewald (JE) conceived the idea of the manuscript. Ingolf Steffan-Dewenter, Jörg Müller (JM) and Sarah Redlich (SR) developed the overall study design. **CT**, Sandra Rojas-Botero (SRB), Johannes Uhler (JU), JE, Johannes Kollmann (JK), Christoph Moning (CM) and JM designed the methods of plant and arthropod surveys. **CT**, SRB, JU, Caryl Benjamin, Jana Englmeier, Ute Fricke, Cristina Ganuza, Maria Haensel, Rebekka Riebl, Sarah Redlich and Lars Uphus collected data. **CT** analyzed the data and wrote the manuscript. All authors commented on the manuscript.
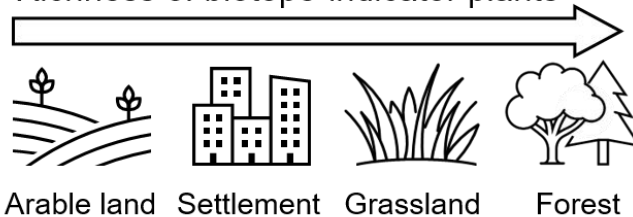
Graphical abstract

Fig. 6: Graphical abstract of Publication 2 showing the significance of different plant species groups as indicators for arthropod richness (A) and the distribution of biotope-indicator plant richness among local land-use types (B).

Summary

As reports on arthropod losses in European landscapes are increasing, there is strong need to understand the causes of species declines and to develop efficient monitoring and conservation strategies. Plant species richness has often been suggested as indicator for the species richness of other taxa, but evidence on correlations between plant and arthropod diversity is mixed. Furthermore, studies assessing the partial effects of plant species richness, climate, land-use intensity and landscape characteristics on arthropod richness are lacking. **Publication 2** investigates the significance of plant species richness as indicator for arthropod species richness while comparing the effects of overall plant species pools and subsets of conservation-relevant plant species. Besides, it addresses the relevance of climate and land-use variables including habitat amount and landscape configuration for plant and arthropod richness.

Vascular plants and terrestrial arthropods were surveyed on the 179 study sites in Bavaria, representing different land-use types and climate zones defined within the LandKlif design. Malaise traps were used for arthropod sampling and plants were surveyed within 200-m buffer areas around the trap locations. Correlations between local species richness of plants and arthropods were assessed, while distinguishing between three plant groups (all species, red-listed species and biotope-indicator species) and twelve arthropod groups representing various taxa and trophic levels. Linear mixed effect models were used to assess partial effects of plant species richness, climate and land-use related drivers including habitat amount and landscape configuration (i.e. edge density) at different scales. Likewise, the responses of plant species richness to the named environmental variables were evaluated.

Species richness of most arthropod groups was strongly correlated with species numbers of plants indicating protected biotopes, and species numbers of red-listed arthropods and butterflies were best predicted by red-listed plant species richness. Comparing the effects of the studied predictors, plant species richness was more important for arthropod richness than the amount of semi-natural habitat (except for cicadas, true bugs and beetles). Edge density of the surrounding land-use types had no significant effects on arthropod richness. Local land use mainly determined overall plant species richness, with highest total species numbers found in settlements. In contrast, the richness of biotope-indicator plants was greatest in forest gaps and areas where edge density and the amount of semi-natural habitat was high. Red-listed plant species richness was equally low across all local habitat types, but positively responded to edge density at the landscape scale.

The findings show that conservation-relevant plant species such as red-listed plants, but particularly plants indicating protected biotopes, have great potential for monitoring habitat quality and diversity of arthropod across multiple taxa and trophic levels. Forests and clearings

play an important role for plant and arthropod diversity, while the conservation of semi-natural habitats is needed to maintain and improve habitat quality in agricultural and urban landscapes.

Publication 3: Relationships of insect biomass and richness with land use along a climate gradient

Uhler, J., Redlich, S., Zhang, J., Hothorn, T., **Tobisch, C.**, Ewald, J., Thorn, S., Seibold, S., Mitesser, O., Morinière, J., Bozicevic, V., Benjamin, C.S., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Rojas-Botero, S., Rummler, T., Uphus, L., Schmidt, S., Steffan-Dewenter, I., Müller, J., 2021. Relationship of insect biomass and richness with land use along a climate gradient. *Nature Communications* 12, 5946.

Author contributions

Jörg Müller (JM), Johannes Uhler (JU), Sarah Redlich (SR) and Sebastian Seibold (SS) perceived the idea of this manuscript. JM, Ingolf Steffan-Dewenter ISD and Jie Zhang (JZ) designed the experiment. JU, SR, **Cynthia Tobisch**, Caryl Benjamin, Jana Englmeier, Ute Fricke, Cristina Ganuza, Maria Haensel, Rebekka Riebl, Sandra Rojas-Botero and Lars Uphus collected data. Torsten Hothorn, Oliver Mitesser, JM and JU analyzed the data. Simon Thorn and JZ designed the graphs. JU, JM, SS, SR and ISD wrote the first manuscript draft and finalized the manuscript. All authors commented on the manuscript.
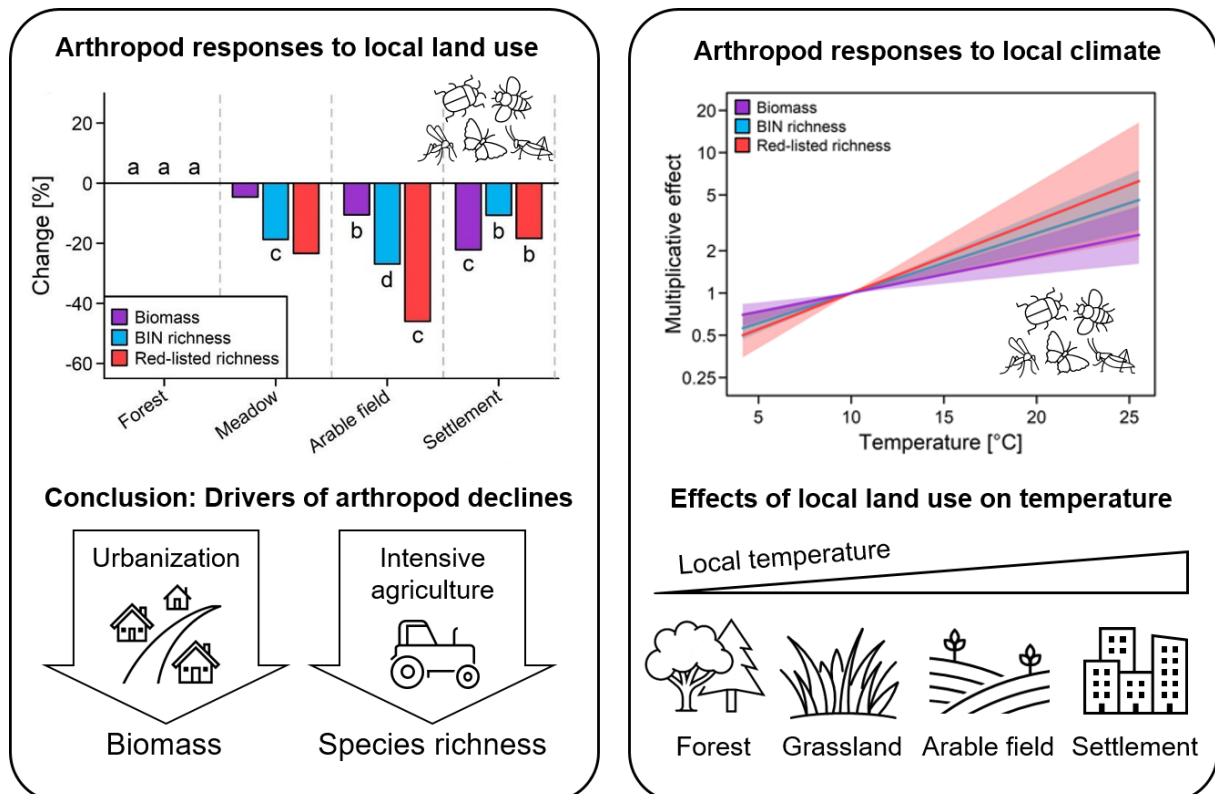
Graphical abstract

Fig. 7: Graphical abstract of Publication 3 showing effects of local land use (left) and climate (right) on arthropod biomass and richness as well as relationships between these predictors (bottom right).

Summary

Agricultural land-use intensification involving pesticide loads and reductions of habitat amount and quality is often reported as main cause of arthropod biodiversity losses occurring across Europe. However, declines in arthropod biomass and richness are not restricted to agricultural areas, but occur independent of local land-use intensity. Thus, the role of intensified agriculture in driving these declines compared to other factors such as climate change is still unclear. Moreover, separating the effects of climate and land use on species trends is difficult, as these drivers are often correlated in space and time. In addition, climate and land use may affect arthropods at different scales. However, studies with a suitable design to address these issues are lacking. **Publication 3** investigates the responses of arthropod biomass and richness to climate and land use including local and large-scale effects. Further analyses carried out within this thesis assess the relative importance of plant biomass and richness for arthropod biomass, adding to the findings of Publication 3.

Following the multi-scale study design developed within the LandKlif project, vascular plants and terrestrial arthropods were sampled on 179 study sites along orthogonal gradients of climate and land use throughout the Federal State Bavaria. Arthropod biomass was determined and species were identified via Metabarcoding. Plant biomass was sampled at the trap locations and species pools were surveyed within 200-m radii around the study sites. Generalized additive models were used to obtain partial effects of macro- and microclimate as well as local and landscape-scale land-use categories including their combinations. The models accounted for effects of season, sampling duration, repeated measurements and spatial arrangement of the study sites.

Arthropod biomass, overall species richness and red-listed species numbers positively responded to local temperatures measured on the study sites during the sampling season. Arthropod biomass and richness followed different seasonal patterns and varied in their responses to land-use categories. While overall species richness and particularly threatened species numbers were lowest in arable land, biomass was lowest in urban habitats. Forest sites contained highest species numbers and biomass values. Similar patterns were observed at the landscape scale, albeit differences between landscape types were less pronounced than those between local habitats. Additional analyses showed that arthropod biomass was independent of plant biomass and plant species richness (Appendix A1). Local land use strongly influenced local climate, as temperatures were higher towards increasing land-use intensity, although these variables independently affected arthropod richness and biomass.

The findings point out the role of urbanization as a major driver of arthropod declines in addition to agricultural intensification, and emphasize the significance of forests for the conservation of arthropod populations. Positive effects of local temperatures on all target variables suggest

that warmer conditions still largely promote arthropod diversity and biomass within the studied region, albeit negative impacts of climate change, e.g. through extreme weather events, are likely to increase particularly in agricultural and urban environments.

DISCUSSION

Given the severe declines in arthropod biomass and diversity (Hallmann et al., 2017; Seibold et al., 2019) as well as plant diversity (Eichenberg et al., 2020; Jandt et al., 2022), there is a strong need to understand the causes of these losses and to implement effective measures that maintain and promote biodiversity in cultural landscapes. The objective of the publication-based dissertation was to determine the relative importance of climate and land-use effects for plant and arthropod communities, and to improve the understanding of plant-arthropod relationships at a macro-ecological scale.

Publication 1 (Tobisch et al., 2023b) investigated the independent and combined effects of plant species composition, climate and land use on arthropod species composition, and explored which aspects of vegetation contribute to the relationships between plant and arthropod assemblages. These included direct trophic links and responses of arthropods to habitat conditions mediated by vegetation. **Publication 2** (Tobisch et al., 2023a) addressed the significance of plant species richness as indicator for arthropod species richness and evaluated the relative importance of climate, land use and landscape characteristics for plant and arthropod richness. **Publication 3** (Uhler et al., 2021) focused on the responses of arthropod biomass and richness to climate and land use at the local and landscape scale. Complementary to this publication, an additional analysis within this thesis assessed the relative importance of plant biomass and richness for arthropod biomass (Appendix A1).

The main findings of the three publications are summarized in **Fig. 8**. The results are reviewed in the context of available literature and discussed with respect to current global trends including biodiversity losses, climate and land-use change. Further, methodological restrictions relating to study design and data sampling are outlined and recommendations for conservation management are derived.
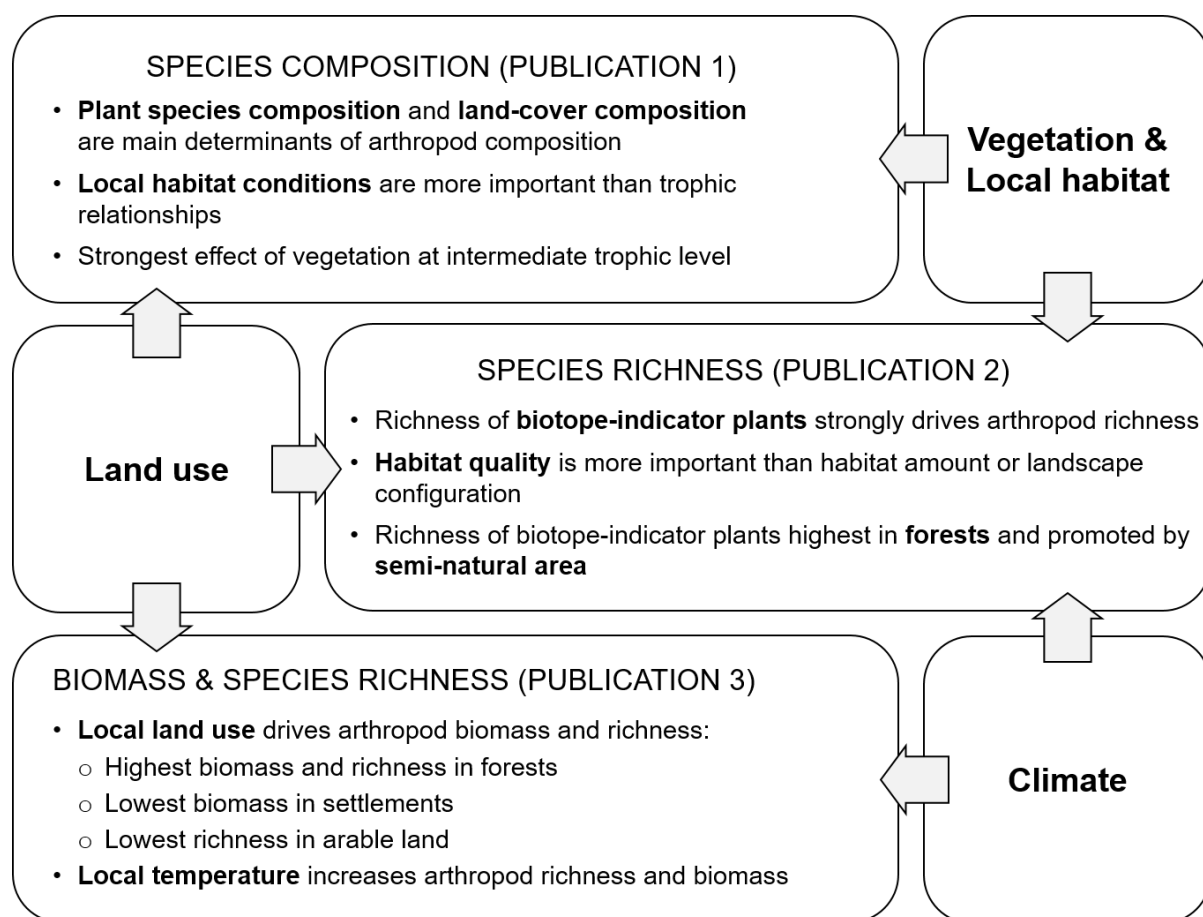
Fig. 8: Main findings of the PhD thesis displaying the primary determinants of arthropod species composition, richness and biomass as assessed in Publications 1–3.

Effects of climate and land use on plant and arthropod communities

The diversity and composition of plant and arthropod communities strongly depend on climatic conditions. In line with earlier literature (Hallmann et al., 2017; Pilotto et al., 2020), temperature significantly increased local arthropod richness and biomass (Publications 2–3) and showed positive effects on total plant species richness (Publication 2). However, Publication 1 did not detect correlations between macroclimatic variables and the composition of plant or arthropod communities, in contrast to other studies that observed significant shifts in local plant and arthropod composition along climatic gradients (Bässler et al., 2010; Govaert et al., 2021; Zellweger et al., 2017). Local land-use effects might have masked responses of species composition to climate. Temperatures measured on the study sites differed significantly between local land-use types, increasing from forests to agricultural to urban areas (Supplementary Table 2 in Publication 3). In addition, local temperature was a more important determinant of total arthropod richness and biomass than long-term mean annual temperatures (Publication 3). This shows that microclimatic conditions are an important driver of arthropod communities, which is consistent with earlier studies (Müller et al., 2020; Prather & Kaspari, 2019; Rebaudo et al., 2016). Effects of microclimate on arthropod species

composition can also be observed through plant communities, as shown in Publication 1; among the local habitat conditions displayed by vegetation through Ellenberg indicator values, temperature and light values showed the highest correlations with arthropod species composition.

These findings are relevant with respect to current climate change and land-use alterations. Climate change modifies microclimatic conditions through increasing temperatures, thus leading to shifts in vegetation composition. This was shown by De Frenne et al. (2013) who observed significant increases in the dominance of warm-adapted species ('thermophilization') in temperate forests of Europe and North America during the past decades. Such processes may be reinforced locally through forest management, with higher wood harvest activities leading to increased canopy openings that raise ground-level temperatures (Blumröder et al., 2021). However, the overall tree growth and forest densities in temperate forests are increasing due to climate warming, eutrophication and changes in management regimes (Gold et al., 2006; McMahon et al., 2010; Rautiainen et al., 2011). Thus, macroclimate warming can be buffered through increased canopy closure that moderates thermophilization effects (De Frenne et al., 2013). Likewise, this results in a decrease in light-demanding species, as shown by Verheyen et al. (2012). Buffering effects are not only driven by local stand density, but can also be observed at the landscape scale through increased forest cover, as recently shown by Borderieux et al. (2023) for temperate forests in France. They found that the average thermal optimum of understory plant communities was significantly lower within forested landscapes compared to landscapes with low forest cover, albeit forest cover was also correlated with soil conditions.

Publications 2–3 did not detect negative effects of high temperatures on arthropod species richness or biomass. Another analysis of Malaise trap data collected throughout Germany also showed overall increases of arthropod biomass with temperature, but this effect turned negative when temperatures exceeded long-term averages during hot summer months (Welti et al., 2022). Moreover, long-term studies observed declines in cold-adapted insect species associated with increasing temperatures (Fitzgerald et al., 2021; Neff et al., 2022). As insects are generally thermophilic, it is plausible that there are currently more species that benefit from warmer temperatures than those threatened by climate warming, resulting in overall positive responses of arthropod populations to temperature in Publications 2–3. However, a related Publication based on the same Malaise trap dataset found that higher temperature led to more homogeneous communities of pollinating insects at the landscape scale (Ganuza et al., 2022). These findings clearly indicate that plant and arthropod communities will shift under future climate change, and highlight the role of forests as important refuges particularly for cold-adapted plant and arthropod species.

Local land use was a main determinant of plant and arthropod communities, affecting species composition, species richness and biomass (Publications 1–3, Appendix A1 Fig. A2). Importantly, arthropod biomass differed in its responses to land use. While both arthropod richness and biomass were highest in forest clearings, the lowest species numbers were observed in arable land, whereas the lowest biomass amounts were measured in settlements. This underscores the role of urbanization as a major driver of arthropod declines, along with intensive agriculture. Recent studies confirmed negative impacts of urbanization on arthropod populations. Svennigsen et al. (2022) found negative correlations between flying-insect biomass and urban cover based on car net samples across broad land-use gradients in Denmark and northern Germany. Likewise, consistent decreases in arthropod diversity and abundance along urbanization gradients have been observed for multiple taxonomic and functional groups (Fenoglio et al., 2020; Piano et al., 2020), probably due to high levels of disturbance and expansion of sealed area leading to losses of habitat and connectivity (Fenoglio et al., 2020).

In turn, certain arthropod groups may benefit from urban environments. For instance, species richness of Hymenoptera was higher in cities compared to rural sites studied in Eastern Germany (Theodorou et al., 2020) and Great Britain (Baldock et al., 2015). This is probably due to higher habitat heterogeneity and availability of floral and nesting resources provided in urban areas, even though much of the flora in cities is exotic (Perre et al., 2011). Comparing arthropod species richness between local land-use types in Publication 2 showed that species numbers in settlements are often similar to, or even exceed those in forests, as was the case for bees and cicadas (Supplementary Fig. S5 in Publication 2). However, it should be noted that the study sites within settlements were not selected based on the amount of ambient urban cover. In fact, they were surrounded by high proportions of either forest, agriculture or urban area, due to the nested study design covering different types of landscape-scale land-use intensity (Redlich et al., 2021). Therefore, urban study sites were rather heterogeneous, being located in meadows within small agricultural villages as well as in cemeteries within larger cities, where they were surrounded by high proportions of green area. Despite negative impacts of urbanization, these findings show that urban areas can harbor high arthropod diversity in some taxonomic groups, even if total biomass is low.

In most arthropod groups, the lowest species numbers were found in arable land (Supplementary Fig. S5 in Publication 2). This is in line with recent studies reporting that temporal declines in arthropod richness and abundances were most severe in agricultural landscapes with high land-use intensity in Germany (Seibold et al., 2019) and worldwide (van Klink et al., 2020). From a global perspective, these findings support that land-use change is the major driver of biodiversity losses, and negative impacts of land use currently still outweigh those of climate (Díaz et al., 2019). Importantly, land use threatens biodiversity not only

through changing intensity, such as land abandonment, conversion of grassland to cropland, or increases in the frequency of agronomic measures. Likewise, the continuity and repetition of unfavorable management practices further reduce biodiversity from year to year through additive effects (Blüthgen et al., 2022). Therefore, it is essential to preserve high-quality habitats as important sources of biodiversity in anthropogenic landscapes (Habel et al., 2019a; Outhwaite et al., 2022; Steckel et al., 2014). This is supported by Publications 2–3, showing the highest biomass and species richness of arthropods on sites surrounded by forest, which represents the lowest land-use intensity in the studied region. High amounts of natural or semi-natural habitat may to a certain extent mitigate negative effects of intensive land use as well as climate change (Outhwaite et al., 2022). In turn, small patches of natural or semi-natural habitat surrounded by intensive agriculture are not sufficient to prevent arthropod declines, as shown by Hallmann et al. (2017).

Plant–arthropod relationships

Publications 1–2 showed that vegetation is a prime determinant for the species composition and species richness of terrestrial arthropods in cultural landscapes of Central Europe. Arthropod species composition strongly responded to plant species composition, but also to the combined effect of plant species composition and land cover (Publication 1). Arthropod richness was mainly driven by plant species richness – specifically the number of plant species associated with high-quality habitats – and temperature (Publication 2). Earlier studies identified vegetation as a strong driver of arthropod assemblages (Schaffers et al., 2008; Zellweger et al., 2017) and richness (Schuldt et al., 2019; Uhl et al., 2020), but these effects also varied depending on taxonomic groups and trophic levels (Bucher et al., 2019; Haddad et al., 2009). Contrary to expectations, correlations between plant and arthropod communities did not clearly decrease towards higher trophic levels. Plant species composition had less strong effects on the composition of parasitoids and detritivores than that of herbivores and pollinators, but showed the strongest effects on predator assemblages (Publication 1). Plant species richness had strong effects on the richness of herbivores, parasitoids and detritivores, while the effect on predator richness was less pronounced (Publication 2). Previous studies found that correlations between plant and arthropod communities were strongest for primary consumers directly depending on plants as food resources, while effects were less pronounced for detritivores and secondary consumers, i.e. predators and parasitoids (Castagneyrol & Jactel, 2012). However, Publication 1 revealed that direct trophic relationships only played a minor role in driving correlations between plant and arthropod species composition. Instead, these correlations were more driven by the local habitat conditions depicted by vegetation composition. Analyzing correlation patterns in species richness, Publication 2 found similar results, as subsets of plants indicating high-quality habitats led to stronger correlations

between plant and arthropod species numbers than the complete set of plant species. This was consistent across all trophic levels. Earlier studies already proposed that correlations between plant and arthropod communities are not the result of direct relationships at the species level (Müller et al., 2011; Schaffers et al., 2008). Certainly, specialized species rely on the occurrence of their host plant. However, as discussed in Publication 1, specialists do not necessarily occupy the entire range of their host plants (Bogusch et al., 2020; Quinn et al., 1998). Further, habitat requirements of specialized insects are often complex, going beyond the availability of food resources (Stewart & New, 2007). Thus, entire plant communities likely summarize habitat conditions of these species more effectively than the pure information on host plant occurrence (Müller et al., 2011; but see Krämer et al., 2012).

The integrative nature of vegetation and its significance for arthropod communitites is meaningful in several ways. As described in Publication 1, plant communities reflect multivariate ecological gradients that describe local habitat conditions of arthropods, and that can be interpreted via Ellenberg indicator values. This is particularly relevant to assess how environmental gradients determine patterns in arthropod assemblage composition. Moreover, Publication 2 showed that vegetation can serve as a valuable surrogate to estimate arthropod species richness, but this depends on the selection of plant species. Most studies that investigated correlations between plant and arthropod species richness included the entire set of sampled plant species, with mixed support for the adequacy of plant species richness as surrogate for arthropod richness (Billeter et al., 2008; Bucher et al., 2019; Haddad et al., 2009; Scherber et al., 2010; Uhl et al., 2020). As demonstrated in Publication 2, a subset of plant species that characterizes high-quality habitats significantly improves the indicator value of plant species richness for arthropod richness across trophic levels. Importantly, this variable was more important for most arthropod groups than the amount of high-quality habitat or edge density. This is in line with earlier studies finding that local habitat quality was a more important determinant for the diversity of butterflies (Krämer et al., 2012), moths (Uhl et al., 2020) and wild bees (Rollin et al., 2019) than the composition or configuration of the surrounding landscape. However, these findings should not underestimate the importance of habitat amount and connectivity at the landscape scale. Evidence exists that these factors influence biodiversity patterns of multiple taxa (Concepción et al., 2012; Martin et al., 2019; Rösch et al., 2013; Steckel et al., 2014), and recent declines in arthropod richness and abundances have been linked to landscape-level drivers (Seibold et al., 2019). Indeed, Publication 2 showed that the number of plant species indicating protected biotopes was positively associated with the amount of semi-natural area and edge density in 1-km radius. This suggests that both habitat amount and connectivity at the landscape scale promote local habitat quality, which in turn benefits arthropod diversity.

In contrast to strong effects of vegetation on arthropod species richness and composition shown in Publications 1–2, arthropod biomass was not correlated with plant biomass or plant species richness (Appendix A1 Table A1). Experimental studies found strong effects of vegetation on terrestrial arthropod biomass, which were mainly due to increased productivity with higher plant species richness (Borer et al., 2012; Haddad et al., 2011). Such effects could not be detected in the observational dataset underlying the thesis. Other observational studies did not detect correlations between arthropod and plant biomass either (Hallmann et al., 2017; Ober & Hayes, 2008). Among local land-use types, plant biomass was highest in sites in arable land (i.e. within grass strips next to arable fields), although the difference was only significant compared to forests (Appendix A1, Fig. A2). Effects of intensive agriculture such as habitat loss, high disturbance rates and pesticide application in the surroundings of these sites probably cancelled out positive effects of plant productivity. Further, plant biomass was sampled directly on the study sites which were standardized to open patches of herbaceous vegetation. This was representative for the Malaise trap locations, but provided little information on the surrounding vegetation. For instance, samples taken within forest clearings underestimated the amount of plant biomass available to arthropods, as only ground-level vegetation was included.

Contrary to expectations, arthropod biomass was not associated to the number of biotope-indicator plants reflecting the presence of high-quality habitat (Appendix A1 Table A1). According to earlier studies, variables related to the canopy layer seem to be more important habitat components determining arthropod biomass, specifically tree species richness (Hallmann et al., 2017) and the proportion of deciduous canopy cover (Ober & Hayes, 2008). This matches the results of Publication 3, showing that arthropod biomass was highest in forest sites. Deciduous foliage is an essential source of nutrition for phytophagous and detritivorous insects, due to high nitrogen content and other chemical properties that contribute to palatability (Pastor & Cohen, 1997; Ober & Hayes, 2008 and references cited therein). Besides, canopy foliage provides a higher amount of food resources per area unit compared to ground-level vegetation. Thus, high forest cover, especially deciduous forest, promotes biomass of primary consumers, which in turn benefits higher trophic groups and contributes to higher overall arthropod biomass (Ober & Hayes, 2008; Scherber et al., 2010; Schuldt et al., 2019). This suggests that the quality of resources is a key determinant of arthropod biomass, rather than overall resource diversity or habitat quality reflected by biotope-indicator plants, which was, however, an important determinant of arthropod richness (Publication 2). As already discussed in Publication 3, the findings of the additional analyses confirm that arthropod biomass and species richness follow different patterns and should not be treated as equivalent biodiversity measures.

Methodological restrictions and further research perspectives

Due to the high number of study sites resulting in time and logistic constraints, species abundances could not – or only to a limited extent – be assessed during the sampling campaign. Arthropods were identified via DNA-Metabarcoding, which allows to process large amounts of samples within short time periods. Further, it provides the same level of identification for all groups of taxa, independent of how well the respective group is studied (Ratnasingham & Hebert, 2013). However, information on species abundance can only be derived from the number of reads, i.e. the number of times distinct DNA sequences were detected. This measure is strongly influenced by the size of the sampled arthropods, as larger individuals contain more DNA than small ones. Even though large and small individuals were treated as separate groups before extracting the DNA (Publication 3), the number of reads still can only be a rough estimate of relative abundances, which is why using occurrence data was preferred as a more reliable option (Deagle et al., 2019). Plant species abundances could only be assessed within ten square meters close to the Malaise traps. However, as the study sites were standardized to open patches of herbaceous vegetation, the plant communities therein did not always reflect the surrounding habitats. This was particularly the case for forests, but also for settlements that often contained highly heterogeneous vegetation. Therefore, and to account for the fact that arthropods may have reached the traps from various distances (Publication 1), plant data from the study sites was pooled with the presence-absence data collected during the transect walks within 200-m buffer areas around the sites. Thus, all analyses conducted within this thesis were based on presence-absence data. Information on species abundances would certainly have added further insights into plant and arthropod community structures. However, Wilson (2012) found that using abundance data in ordination of vegetation data is only useful when studying homogeneous communities across small scales, and that presence-absence data match even better with environmental conditions than abundance data. As the thesis is based on a large set of study sites covering broad environmental gradients, the sampled occurrence data well reflect principle patterns in the assemblage composition of plants and arthropods and their relationships to climate and land use, even without information on species abundances.

The findings of this thesis are based on an observational field study following a space-for-time approach, with study sites chosen such that they covered independent gradients of climate and land use (Redlich et al., 2021). Based on a large set of sampling locations representing typical landscapes of temperate regions, this approach allowed to assess independent and combined effects of both factors on biodiversity. Space-for-time studies certainly cannot replace long-term field observations. For instance, spatial analyses are not able to account for potential time lags in the responses of biodiversity to changes in climate or land use (Outhwaite et al., 2022). Further, local arthropod populations are subject to strong fluctuations that

encompass up to three orders of magnitude within few years (den Boer, 1985), due to demographic and environmental stochasticity (Melbourne & Hastings, 2008). As the arthropod data underlying the thesis were sampled within one season, it was not possible to consider inter-annual variation of the sampled populations or time-lag effects in the analyses. Such patterns can only be captured by long-term field observations or experiments. These provide important information on trends in species abundance and diversity, although existing evidence on arthropod trends across several decades is scarce and not well replicated (Blüthgen et al., 2022; Montgomery et al., 2020). Indeed, many long-term monitoring campaigns have recently been implemented, due to increased political interest and debate on biodiversity declines. However, to halt further biodiversity declines, it is less important to prove the statistical significance of temporal declines, but rather to understand the drivers of the present losses (Blüthgen et al., 2022). This can also be achieved by comparing locations within different land-use categories or along environmental gradients, as the potential causes of temporal declines can also be identified through the analysis of spatial patterns (Blüthgen et al., 2022). Finally, space-for-time approaches have the advantage that results are available after short time periods and can be implemented into conservation practice within few years.

The study design underlying this thesis allowed to compare the state of biodiversity between contrasting and well-replicated land-use categories. However, it was not possible to include more detailed variables on land-use intensity, such as the frequency of agricultural measures or the extent of light pollution in urban areas. Therefore, the exact mechanisms that determined the differences in arthropod biomass and richness between land-use categories found in Publications 2–3 remain to be tested. For instance, field experiments with a before-after-control-impact (BACI) design controlling for differences in management within land-use types are a possible approach to build on the results, exploring which agricultural practices are most detrimental to arthropod richness in arable land and which aspect of urbanization causes low levels of arthropod biomass within settlement areas. Such frameworks may also be used to validate the findings of Publication 2 by implementing conservation measures aiming to improve habitat quality in agricultural landscapes, using biotope-indicator plants as a benchmark. Likewise, the research design did not cover the role of transitional habitats between the studied land-use types, which is particularly relevant for forest edges. As the forest sites were located within clearings that varied in size and structure, the question raises to which extent the presence of these ecotones contributed to the high average biomass and species numbers of arthropods found in forest sites (Publications 2–3). Further studies addressing this aspect will help to better understand the mechanisms through which forests promote biodiversity, and to derive appropriate management strategies.

Implications for conservation management

The findings of this thesis are relevant for biodiversity monitoring and conservation practice in Central Europe. As discussed in Publication 2, monitoring of arthropods is usually time-consuming and causes high costs. It requires expert knowledge, which, depending on the taxonomic group, is often limited to few specialists. Novel methods of DNA sequencing, such as Metabarcoding, provide efficient and promising alternatives, but are still cost-intensive. Further, arthropods are killed during the sampling process, which is controversial especially in studies that explore insect declines and options to preserve and restore biodiversity. Indeed, there are promising technologies providing non-lethal methods to monitor arthropods, but this still requires further research and development (Rydhmer et al., 2022; van Klink et al., 2022). An alternative approach is the use of surrogate taxa. Publication 2 demonstrated that vegetation assessments provide a useful alternative to estimate arthropod species richness of a given area. Importantly, this does not require surveys of entire plant species pools. Instead, a subset of plants indicating protected biotopes emerged as a strong indicator for total arthropod species richness as well as the species richness of all trophic groups (Publication 2). Thus, plant lists that are used to characterize and determine protected biotopes can also be used as an approach to monitor arthropod biodiversity even in areas with high land-use intensity (Publication 2). In Europe, habitat mapping based on floristic information is a widely used method in conservation practice, particularly in the context of Natura 2000 based on the Habitats Directive (European Environment Agency, 2014). Thus, lists of plant species that characterize high-quality habitats are available for many European countries (European Environment Agency, 2014). The determination key for protected biotopes in Bavaria which was used in Publication 2 (Bayerisches Landesamt für Umwelt, 2020) is a positive example for such lists since it covers a wide range of habitat types present in Central Europe. These habitats can either be identified by few or single rare species or a combination of several more widespread species. Therefore, it is also applicable in areas of higher land-use intensity where rare species are hard to find (Publication 2).

Habitat quality depicted by conservation-relevant plant species was more important than the amount of semi-natural area surrounding the study sites (Publication 2). This emphasizes the need to preserve and restore high-quality habitats particularly in agricultural landscapes where habitat amount is limited (Habel et al., 2019a). Yet, small and isolated fragments of semi-natural area within a matrix of intensive agriculture are not sufficient to maintain arthropod populations in anthropogenic landscapes (Habel et al., 2016; Hallmann et al., 2017). To prevent further biodiversity losses, it is important to promote and re-establish biotope networks that connect forests, where biomass and species richness of arthropods is still highest (Publications 2–3), with habitat patches in the open landscape, such as hedgerows, orchards, semi-natural grassland or set-aside areas.

Agri-environmental schemes play an important role for maintaining biotope networks in agricultural regions. However, most agri-environmental measures are action-oriented, i.e. subsidies are based on their area size, while only few measures are result-oriented, i.e. payments depend on a specific outcome (Mack et al., 2020). Examples for result-oriented measures include the maintenance of species-rich grassland in agri-environmental programs of Bavaria (Bayerisches Staatsministerium für Ernährung, Landwirtschaft und Forsten, 2020) and Switzerland (Mack et al., 2020), where the occurrence of certain indicator plant species is used as a benchmark. Based on the findings of Publication 2, result-oriented subsidies should be increased in order to reward landowners for the establishment of high-quality habitats. This is supported by an extensive survey that questioned Bavarian farmers about their ideas for the improvement of agri-environmental schemes (Zindler, 2022). According to the answers, farmers wish for a stronger focus on result-oriented subsidies, likely due to higher flexibility and cost-effectiveness (Matzdorf & Lorenz, 2010). Thus, promoting success-based subsidies would both improve habitat quality in agricultural landscapes and raise the motivation of landowners to implement biodiversity-friendly measures.

CONCLUSION

Climate change and intensive land-use practices are major threats to biodiversity. There is strong need to understand how these factors drive the current declines in plant and arthropod populations, and to derive effective strategies that prevent further losses. The focus of this thesis was to investigate the effects of climate and land use on plant and arthropod communities and to explore plant–arthropod relationships at the macro-ecological scale. Based on an observational field study designed to separate effects of climate and land use, correlation patterns in species composition, species richness and biomass of plants and arthropods were analyzed.

Temperature positively affected total plant species richness and significantly increased arthropod species richness and biomass, indicating that critical temperature thresholds were not yet reached during the field study. In contrast, species composition of plants and arthropods was not driven by climate variables. However, arthropod assemblage composition was associated with local microclimate reflected by vegetation. Thus, species communities of plants and arthropods will likely shift under future climate change that alters microclimatic conditions. In this context, forests including clearings and fringes will play an important role in buffering effects of climate change particularly for cold-adapted species. Further, local land use was a strong driver of plant and arthropod communities, with significant effects on species composition, species richness and biomass of both groups. However, arthropod biomass and richness followed different patterns. Both variables were highest in forests, but biomass was lowest in urban areas and species richness was lowest in arable land. This supports the view that land-use intensity is currently the major threat to biodiversity in temperate landscapes, involving both urbanization and intensive agriculture as drivers of recent arthropod declines.

Vegetation was a main determinant of arthropod species richness and composition. However, the predictive power of plant communities showed no consistent trends along trophic groups. Instead, the integrative nature of vegetation reflecting local habitat conditions was an important factor driving the correlations between plant and arthropod communities across trophic levels, while direct relationships between arthropod and plant species appeared to be less relevant. Hence, the number of plant species indicating high-quality habitats emerged as a strong predictor for arthropod species richness. These findings emphasize the significance of habitat quality for maintaining arthropod biodiversity in anthropogenic landscapes and point out the need to preserve and restore biotope networks that connect forests as important biodiversity sources with semi-natural habitat patches in the open landscape. This may be promoted by shifting the focus of conservation policies from action-orientated towards success-orientated measures.

Given the severe biodiversity declines happening across Europe during the last decades, measures to halt further losses are urgently needed to maintain ecosystem functioning. Therefore, the findings of this thesis should be validated within further studies that implement conservation measures aiming to improve habitat quality in cultural landscapes. Importantly, such studies provide best practice examples for landowners and gain further evidence on how to effectively protect biodiversity in the face of climate change and land-use intensification.

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ACKNOWLEDGEMENTS

APPENDIX

A1 Additional analysis relating to Publication 3

A2 Publication list

A1 Additional analysis relating to Publication 3

Publication 3 investigated the responses of arthropod biomass to climate and land-use, but did not include variables related to vegetation. Therefore, additional analyses were carried out that test the effects of plant biomass and plant species richness on arthropod biomass, complementary to the effects of climate and land use. As both plant species richness and plant biomass were sampled only once per site, arthropod biomass amounts were also averaged across the sampling period by calculating mean biomass values per day for each study site, which was used as target variable. Concordant to **Publication 2**, three groups of plant species richness (all species, red-listed species and biotope-indicator species) were considered as predictors for arthropod biomass in separate model versions. Further, the effects of land use and local climate on plant biomass were tested.

Results of linear mixed effect models showed no significant effects of plant biomass on arthropod biomass (Table A1, Fig. A1). Likewise, none of the three sets of plant species richness significantly affected arthropod biomass (Table A1, Fig. A1). Plant biomass was not correlated with plant species richness of any of the three groups (Pearson coefficients were all below |0.2|).

Table A1: Results (z-values) of linear mixed effect models with arthropod biomass as target variable. Three model versions were calculated with varying sets of plant species richness (ALL: all plant species; RL: red-listed species; BIO: biotope-indicator species). Asterisks indicate significance levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). Marginal R^2-values indicate variance proportions explained by fixed effects and conditional R^2-values indicate variance proportions explained by fixed effects and the random effect (60 quadrants, each containing three study sites).

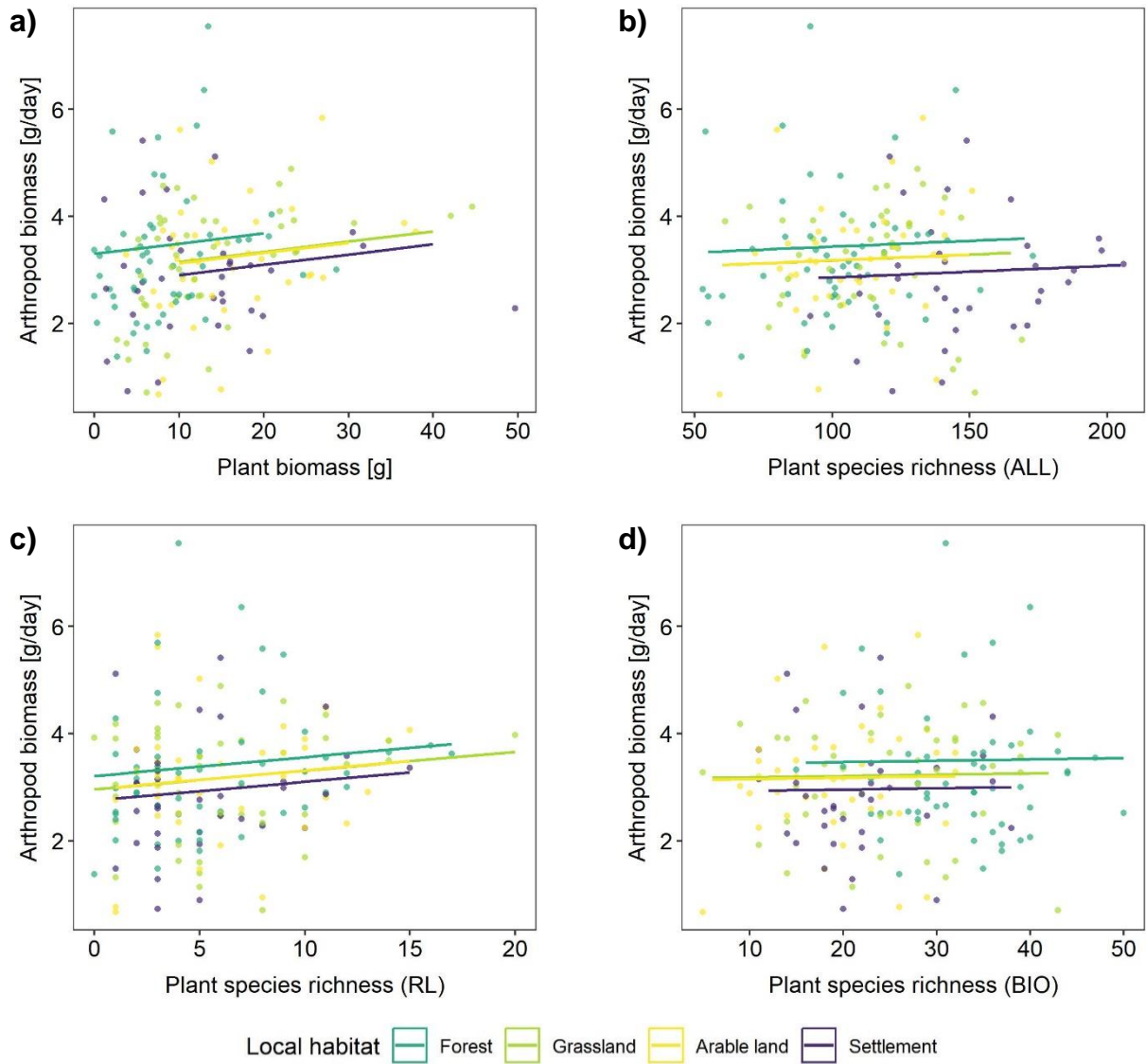|	Effects on arthropod biomass (z-values)		
Plant species richness	*ALL plants*	*RL plants*	*BIO plants*
	0.603	1.534	0.067
Plant biomass	0.424	0.475	0.359
Local temperature	**2.775****	**2.786****	**2.906****
Local humidity	1.466	1.692	1.404
Local land use: Forest			
Grassland	-1.149	-1.125	-0.951
Arable land	-1.073	-1.037	-0.863
Settlement	-1.856	-1.733	-1.670
Landscape type: Forest			
Agriculture	0.387	0.467	0.246
Urban	-1.865	-1.544	**-1.962***
Expained variance:			
Marginal R^2	0.11	0.14	0.10
Conditional R^2	0.12	0.14	0.15

Fig. A1: Partial effects of plant biomass (a) and plant species richness (b-d; ALL: all plant species; RL: red-listed plant species; BIO: biotope-indicator species) on mean daily arthropod biomass.

Plant biomass was positively associated with local temperature and local humidity, while the effect of temperature was more pronounced (Table A2). Biomass values in forests were significantly lower than in the other local land-use types, whereas biomass values in forested landscapes were higher than in urban ones (Fig. A2).

Table A2: Results (z-values) of generalized linear mixed effect model with plant biomass as target variable. Asterisks indicate significance levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). Marginal R^2-values indicate variance proportions explained by fixed effects and conditional R^2-values indicate variance proportions explained by fixed effects and the random effect (60 quadrants, each containing three study sites).

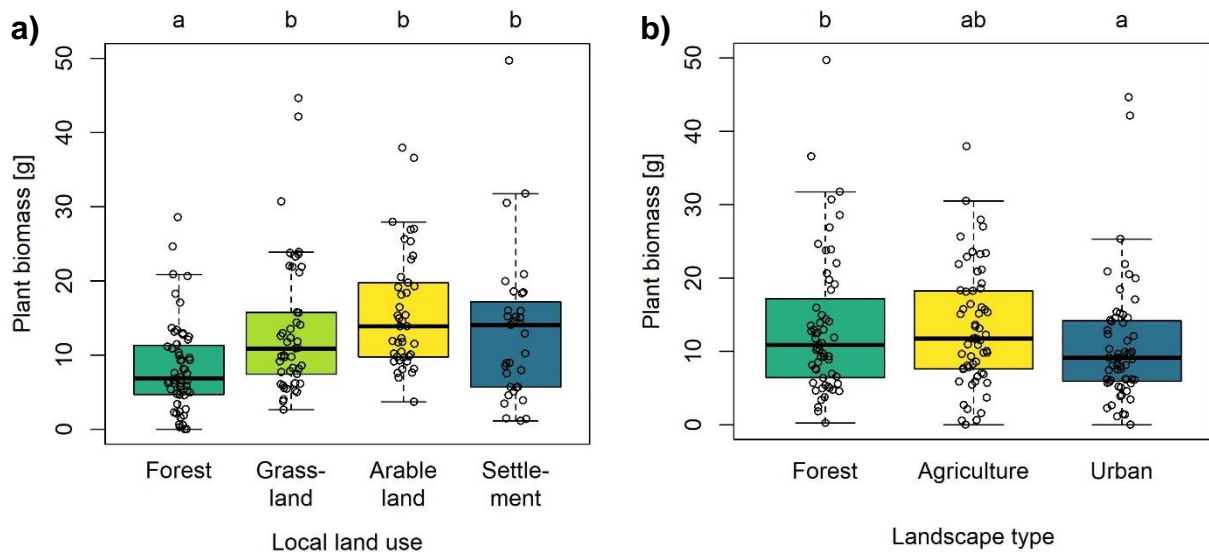|	Effects on plant biomass (z-values)
Local temperature	**4.242*****
Local humidity	**2.573***
Local land use: Forest	
Grassland	**2.989****
Arable land	**4.781*****
Settlement	**3.374*****
Landscape type: Forest	
Agriculture	-0.415
Urban	**-2.534***
Expained variance:	
Marginal R^2	0.27
Conditional R^2	0.37

Fig. A2: Differences in plant biomass between a) local land-use types and b) landscape-scale land-use types. Different letters above the boxes indicate significant differences ($p < 0.05$) between local land-use types, as obtained from multiple posthoc comparisons.

A2 Publication list

Peer reviewed journal publications

2023

Englmeier, J., Mitesser, O., Benbow, M. E., Hothorn, T., von Hoermann, C., Benjamin, C., Fricke, U., Ganuza, C., Haensel, M., Redlich, S., Riebl, R., Rojas Botero, S., Rummler, T., Steffan-Dewenter, I., Stengel, E., **Tobisch, C.**, Uhler, J., Uphus, L., Zhang, J., & Müller, J. (2023). Diverse effects of climate, land use, and insects on dung and carrion decomposition. Ecosystems, 26(2), 397–411. https://doi.org/10.1007/s10021-022-00764-7

Englmeier, J., Rieker, D., Mitesser, O., Benjamin, C., Fricke, U., Ganuza, C., Haensel, M., Kellner, H., Lorz, J., Redlich, S., Riebl, R., Rojas-Botero, S., Rummler, T., Steffan-Dewenter, I., Stengel, E., **Tobisch, C.**, Uhler, J., Uphus, L., Zhang, J., Müller, J., & Bässler, C. (2023). Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria. Ecography, 2023(11), e06807. https://doi.org/10.1111/ecog.06807

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Tobisch, C., Rojas-Botero, S., Uhler, J., Kollmann, J., Müller, J., Moning, C., Redlich, S., Steffan-Dewenter, I., Benjamin, C., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Uphus, L., & Ewald, J. (2023). Conservation-relevant plant species indicate arthropod richness across trophic levels: Habitat quality is more important than habitat amount. Ecological Indicators, 148, 110039. https://doi.org/10.1016/j.ecolind.2023.110039

Uphus, L., Uhler, J., **Tobisch, C.**, Rojas-Botero, S., Lüpke, M., Benjamin, C., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Redlich, S., Zhang, J., Müller, J., & Menzel, A. (2023). Earlier and more uniform spring green-up linked to lower insect richness and biomass in temperate forests. Communications Biology, 6(1), 1052. https://doi.org/10.1038/s42003-023-05422-9

2022

Benjamin, C. S., Uphus, L., Lüpke, M., Rojas-Botero, S., Dhillon, M. S., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Redlich, S., Riebl, R., **Tobisch, C.**, Uhler, J., Zhang, J., Menzel, A., & Peters, W. (2022). Modelling the relative abundance of roe deer (Capreolus capreolus L.) along a climate and land-use gradient. Animals, 12(3), Article 3. https://doi.org/10.3390/ani12030222

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