Plants, herbivores, and their interactions in human-modified landscapes

- Kevin Wilhelm Bähner -

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Cover herbivores, from left to right

Forest bug, *Pentatoma rufipes*, *Pentatomidae*; panthophagous, foraging on plant saps and small insects; found on various forest trees.
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Common leaf beetle, *Polydrusus pyri*, *Curculionidae*; polyphagous, feeding on various deciduous trees.
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Lobster moth, *Stauropus fagi*, *Notodontidae*; monophagous on beech.
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Prepare for Glory!

- Leonidas, 300 -

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Contents

Chapter 1

Introduction

Entering the forest for a grand endeavor.
Forest edge near *Hahnweilerhof, Börrstadt.*

PLANT-HERBIVORE BIODIVERSITY AND INTERACTIONS IN THE ANTHROPOCENE

Biodiversity is currently facing its gravest crisis since the last mass extinction event 65 Ma ago (Barnosky et al. 2011, 2012, Dirzo et al. 2014). It is the brevity of human lifespans which may make it hard to notice, yet current extinction rates easily rival those of the Big Five mass extinction events (Pimm et al. 1995, Barnosky et al. 2011).

What makes this sixth mass extinction unique is that it is caused by one single species: *Homo sapiens*. Although ultimate extinction causes are multiple, their genuine origin stems from human influence (Sala et al. 2000). Consequently, this epoch of massive human impact on the ecosphere has frequently been addressed as '*Anthropocene*' (Lewis & Maslin 2015). Among the various anthropogenic agents, the human modification of landscapes is one of the most prominent drivers shaping terrestrial biomes (Sala et al. 2000, Foley et al. 2005). For instance, agriculture covers more than 40% of the land surface, and 68% (27.19 Mkm^2) of the forested area is under human disturbance (Foley et al. 2005, Keenan et al. 2015, Morales-Hidalgo et al. 2015). The inevitable repercussions can ideally be investigated by studying reactions of plants, insect herbivores, and their interactions, as they represent the majority of terrestrial biodiversity, fulfill a multitude of ecosystem functions and are vital for ecosystem stability (Díaz & Cabido 2001, Price 2002, Haddad et al. 2011).

Vascular plants not only encompass high species diversity (298,000 species, Mora et al. 2011), they also perform elementary ecosystem functions (e.g. oxygen generation, habitat provision, micro- and macroclimatic stabilization, or water retention, de Groot et al. 2002, Nadrowski et al. 2010), among which primary production is arguably the most important one (de Groot et al. 2002). Plant biomass provides carbon and energy as primary drivers of practically all biological processes in terrestrial biomes and has stabilizing effects on ecosystems (Chapin III et al. 2011, Haddad et al. 2011).

The significance of insect herbivore diversity is well illustrated by pointing to their importance in the calculation of total global biodiversity. Insects are by far the most speciose group of multicellular organisms (Mora et al. 2011), making up about half of all described species (1.5 million) (May 1992), with about every second insect species considered to be herbivorous (Speight et al. 1999). As insect herbivores are considered to be particularly host specific, global species estimations largely rely on projected plant richness and subsequent calculations of their associated herbivore fauna (Erwin 1982, Ødegaard 2000, Novotny et al. 2002). Present predictions of total insect richness vary between 2.6 and 7.8 million species (Stork et al. 2015). Hence, although we are in the middle of the sixth mass extinction, we still do not know *who* is actually dying out, as the majority of species is still to be discovered (Barnosky et al. 2011, Stork et al. 2015). Concerning their ecological functions, insect herbivores fulfill various roles, most of them associated with their trophic mode, e.g. vectors for plant pathogens (Belliure et al. 2005, Stout et al. 2006), or nutrient delivery to the edaphon (Stadler et al. 2001, Schowalter 2006). But the most important function is without doubt the conversion of plant biomass into zoomass and its distribution to higher trophic levels (note that insects convert phytomass multiple times more efficiently, than vertebrates, Nakagaki & Defoliart 1991, Vogel 2010). This occurs via often unique trophic pathways, which result in complex plant-herbivore food webs. These trophic networks comprise 40% of terrestrial biodiversity (Hunter & Price 1992) and affect various ecosystem properties and processes, e.g. competition amidst plant communities (Novotny et al. 2010), ecosystem stability (Haddad et al. 2001), and not least co-evolutionary processes in the long run (Olesen et al. 2007).

It is hence crucial to analyze the disruptive effects of human forest modification on these intricate interactive systems. The sheer proportion of plant-herbivore interactions among ecosystem processes, and their described importance clearly imply potentially dramatic reactions, not only for biodiversity, but also for elementary ecosystem functioning and stability. As plant-herbivore interactions build the base of the trophic pyramid, it is further reasonable to expect cascading effects across the entire ecosystem (Fowler 2013).

Among types of human forest modification, two interdependent drivers emerge as particularly important for Central Europe: Forest fragmentation and silviculture (Frey & Lösch 2010). Although research in other biomes is increasing and intensive (Laurance & Lovejoy 2002, Girão et al. 2007), temperate European forest ecosystems are far from being understood in their relation to fragmentation and management. The bulk of international research in other bioregions generally shows homogenizing and disruptive effects on plant-herbivore diversity and interactions (Laurance et al. 2006, Wirth et al. 2008), but the scarce evidence for European forests suggests more nuanced and partly deviating reactions (Honnay et al. 1999, 2002b).

Hence, if we want to understand how these ecosystems are restructured by human landscape modification, how they might interact with other anthropogenic disturbances (such as climate change), and how they can be proactively managed towards biodiversity, functionality and stability, research on this matter is an elementary necessity. This thesis contributes to this endeavor in analyzing effects of fragmentation and silviculture of Central European temperate forests on the diversity of plants, their insect herbivores, and the complexity, and stability of their interactions. But before I formulate specific questions to answer with this thesis, and before outlining the core chapters (whose purpose is to answer them), I will have to briefly review how forest fragmentation and silvicultural management have shaped Europe’s forest ecosystems.

PLANTS, HERBIVORES, AND THEIR INTERACTIONS IN FRAGMENTED FORESTS

Deforestation Results In Fragmented Landscapes – Human modification of landscapes, which is the single largest threat to the ecosphere (Pimm & Raven 2000, Laliberté et al. 2010, Barnosky et al. 2012), manifests in manifold different forms, and many of them are interdependent (Thomas et al. 2004, Pielke Sr 2005, Brown & Zarin 2013). Among them, deforestation and the resulting forest fragmentation are the most notorious forms of land use affecting terrestrial ecosystems (Laurance & Lovejoy 2002, Fahrig 2003, Hansen et al. 2013). Pre-agricultural global tree cover is given by Matthews (1983) with 61.51 Mkm^2 (41% of land cover), yet estimates and measurements of deforestation report a remaining forest area of 54.4 Mkm^2 by 1700 AD (12% reduction, Goldewijk 2001), and 32.69 Mkm^2 by 2000 AD (47% reduction, Hansen et al. 2010). Alone between the years 2000 and 2012, net forest loss was 1.5 Mkm^2, which is over four times the size of Germany (Hansen et al. 2013). Deforestation serves the need for wood (e.g. for fuel or construction), accessibility of other resources (e.g. mineral resources), and availability of usable (e.g. agriculture, pastures) or habitable (e.g. settlements) land (Saunders et al. 1991, Harper et al. 2005). Although the spatial pattern of deforestation may vary, more often than not the result is a patchy landscape, in which remaining forest islands of various sizes and distributions are surrounded by an anthropogenic used area, termed '*matrix*' (Fahrig 2003, Laurance 2008). Globally, 70% of remaining forests are within 1 km of the forest's edge (Haddad et al. 2015). While it is self-evident that such a large-scale modification of natural landscapes has fundamental effects on species biodiversity and interactions, it is wisest to review this topic by separating the three most prominent (and in reality naturally highly correlated) aspects of forest fragmentation – isolation, area reduction, and forest edge proliferation (**Figure 1**, Fahrig 2003, Laurance 2008, Didham et al. 2012) – and discuss their individual direct and indirect effects on plants, herbivores, and their interactions.

Isolation – The isolation of forest islands is forest fragmentation in a strict sense. Hence, scientific understanding benefited distinctively from island biogeography theory (MacArthur & Wilson 1967, Fahrig 2003, Prevedello & Vieira 2010). Common ground is that both types of habitat islands are surrounded by an area, which is deemed inhospitable for their inhabitants (Prevedello & Vieira 2010). Both, spatial arrangement of remaining islands, as well as matrix inhospitality determine the island connectivity (**Figure 1**, Saunders et al. 1991, Tscharntke et al. 2002a). For landscapes under forest fragmentation, such matrix adversity might arise from detrimental (more extreme) microclimates, missing resource and shelter availability, or increased predation risks due to higher exposure (Rodríguez et al. 2001, Kupfer et al. 2006, Haynes & Crist 2009). Hence, isolation affects forest biota

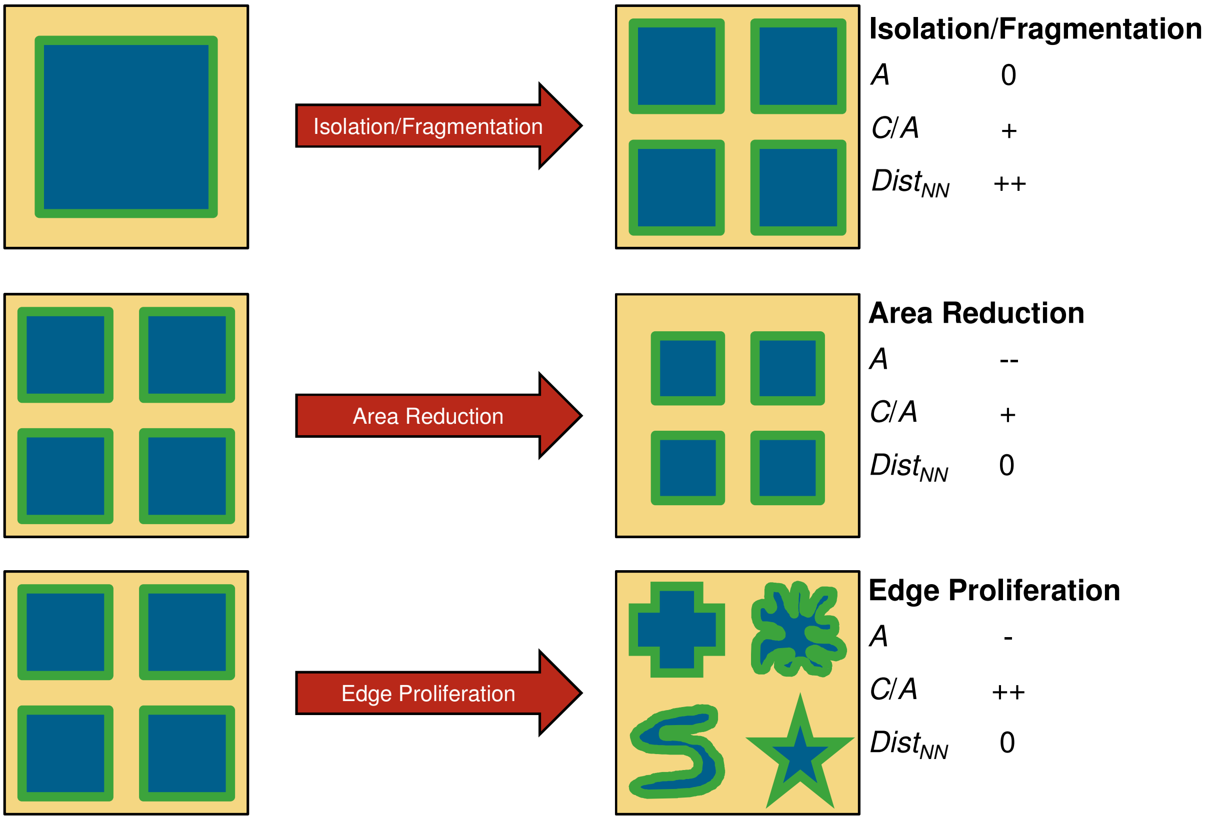

Figure 1: Conceptual modes of action for the three most relevant operators in forest fragmentation. Top isolation and fragmentation *per se*, **Middle** area reduction, and **Bottom** edge proliferation. Symbols (++, +, 0, -, --) indicate direction and magnitude of change in fragmentation related parameters (*A*: summed patch area; *C/A*: circumference/area ratio; $Dist_{NN}$: distance to nearest neighbor patch). Blue shapes: core area of forest fragments unaffected by edge effects. Green banners: edge zones within the forest margin. Bright yellow/brown shape: matrix surrounding forest fragments.

directly by impairing their dispersal abilities, thereby threatening the maintenance of a meta-population (den Boer 1990, Hagen et al. 2012). Yet, the effect size of matrix adversity is modified by a herbivore's individual dispersal traits, as well as by matrix composition (den Boer 1990, Ricketts 2001, Prevedello & Vieira 2010). For instance, higher/more complex vegetation structures may result in more lenient microclimates and increased hiding opportunities in the matrix, but also physical hindrance upon migration (Ricketts 2001, Schooley & Wiens 2005, Kupfer et al. 2006). Furthermore, the availability of palatable sustenance for herbivores can increase, if there is similarity in plant communities between patch and matrix, or if the matrix offers complementary resources (Haynes & Cronin 2004, Haynes et al. 2007, Abbas et al. 2011). Hedgerows seaming agricultural fields can accomplish these purposes and hence serve as habitat corridors (Forman & Baudry 1984, Saunders et al. 1991). Traits increasing a species' dispersal abilities include body size (as large species dehydrate slower), travel mode (walking vs. flying), movement speed, energy efficiency and trophic generality (den Boer 1990, Conradt et al. 2003, Haynes et al. 2007, Abbas et al. 2011, Bonte et al. 2012). Indirect isolation effects come into play when species interactions are altered. This can happen when taxa, trophic levels, or functional groups are differently affected by isolation, and in turn change e.g. competition dynamics. For instance Cramer et al. (2007) found dispersal advantages for small seeded, avian dispersed trees over large seeded, mammalian dispersed ones, as in the latter case hunting pressure in the open habitat was considered to be higher for mammals than birds. Hence, in summary, the effective isolation organisms experience are rooted in species' inherent traits, as well as in matrix attributes (Ricketts 2001).

Area Reduction – Area reduction of formerly large, continuous habitats is one of the most devastating processes during habitat fragmentation (Laurance & Lovejoy 2002, Fahrig 2003), as the fundamental regularities of island biogeography come into effect. The carrying capacity for species populations on an individual habitat island is dependent on its area and exponentially declines with the area approaching zero (MacArthur & Wilson 1967). Hence, species populations in small habitat fragments are more likely to approach their extinction threshold, which increases extinction rates (Shaffer 1981, Tscharntke et al. 2002b). This process is further accelerated by decreasing population viability through inbreeding depression (Young et al. 1996). In turn, extinctions open available niches for immigrating species, hence increasing species turnover and therefore beta diversity (Shaffer 1981, Tscharntke et al. 2002a, Benedick et al. 2006, Laurance 2008). Beta diversity is further enhanced by the sample effect (Laurance & Lovejoy 2002). This means, in a continuous habitat, species populations are not distributed evenly and homogeneously, but often rather patchy (Laurance & Lovejoy 2002). Hence, when this continuous habitat is destroyed into small fragments, only those populations remain, which originally occurred there in the first place. Therefore, the originally clustered assemblage of species is even more pronounced across the fragmented landscape (Laurance 2008).

For forest plants, the most important interactions affected by fragmentation are pollination (if zoophilous, Murcia 1996), dispersal (if zoochorous, Cramer et al. 2007), and herbivory (Valladares et al. 2006). Herbivory by insects is dependent on their abundance and species composition (Ebeling et al. 2014). It can generally be assumed that herbivores decline in abundance during area reduction, as their host plants decline in parallel (Cagnolo et al. 2009). Yet, certain traits, particularly body size, might help to mitigate this effect. Populations of small herbivores are less likely to fall under the extinction threshold (Cagnolo et al. 2009). If certain herbivore species are more prone to local extinction, local herbivore assemblages might become not only more species poor but also biased in their composition. As herbivores are generally rather host specific (Haddad et al. 2001, Lewinsohn & Roslin 2008), this might translate into shifts in feeding pressure on particular plant taxa, hence diminishing or increasing their competitiveness, and in turn shifting plant community composition as well.

Conversely, as herbivores depend on host availability (Jeffries et al. 2006), shifts in plant community composition during area reduction might in turn alter herbivore communities. Plant traits facilitating plant persistence and hence herbivore persistence might include e.g. low population variability, and high tolerance for more extreme microclimates found in small fragments (Henle et al. 2004, Laurance et al. 2006).

Plant-herbivore food webs are important ecosystem elements, as they are influenced by alpha diversity of both participating trophic levels, host specifity of herbivores, and the resulting trophic pathways (Novotny et al. 2010). Although there is evidence for detrimental effects of area reduction on species richness of both trophic levels and the connectivity between them, their reactions to forest fragmentation remain practically unexplored (Valladares et al. 2012), and are nonexistent for temperate forests.

Apart from bottom-up effects, top-down forces also shape herbivore assemblages, although the empirical evidence is mixed. For one, area reduction is indeed likely to disproportionally affect predators of insect herbivores (Cagnolo et al. 2009). With increasing trophic level, critical habitat size increases, meaning that predators suffer from higher extinction probabilities than herbivores (Kruess & Tscharntke 1994, Cagnolo et al. 2009). This is likely to lessen predation pressure on herbivores. On the other hand, predation rates in small fragments might benefit from better visual prey location, habitat accessibility (e.g. for birds), and spillover effects from both adjacent habitats, in turn suppressing herbivory rates (Strelke & Dickson 1980, Valladares et al. 2006, Rand et al. 2006).

Edge proliferation – The proliferation of forest edges is an inevitable geometric process accompanying deforestation, as the ratio of circumference and area increases with forest area reduction, as long as fragment shapes do not change significantly (**Figure 1**, '*area reduction*'). Total edge length can further increase with emergence of new forest islands during fragmentation and with alterations in forest shape, e.g. into more irregular, longitudinal, or dendritic shapes (**Figure 1**, '*edge proliferation*', Ranta et al. 1998).

Why is this geometric peculiarity of biotic relevance? Naturally, with increasing proximity to the forest margin, forest biota are increasingly influenced by permeating matrix and edge effects (Harper et al. 2005). Most prominent direct effects concern alterations in microclimate. The forest edge is the interface to the open landscape, and as such coined by generally harsher microclimatic conditions (particularly more light, wind, extreme temperatures, and hence evapotranspiration and lower moisture, Harper et al. 2005, Tuff et al. 2016). Other abiotic edge effects include nutrient inputs from the matrix, such as fertilized fields or air pollutants from nearby urban structures (Kleijn & Snoeijing 1997, Weathers et al. 2001). While reach into the forest varies among variables and also depends on forest and matrix type (Matlack 1993, Laurance & Lovejoy 2002, Harper et al. 2005), Honnay et al. (2005) reported the transient zone for temperate forests to be within 20 – 50 m. Furthermore, most abiotic parameters lose their influence within the first 100 m into the forest (Laurance & Lovejoy 2002, Honnay et al. 2002b, Urbas et al. 2007). Hence, forest biota, which are unable to cope with these altered conditions (forest specialists), are refined to a forest zone much smaller than the actual fragment, i.e. the core area (Harper et al. 2005). A special peculiarity arises, when forest margins are notably sinuated: core areas within a fragment can be divided by edge zones, which me might call *inner fragmentation* within a fragment (compare **Figure 1**, '*edge proliferation'*, the highly dendritic fragment on the upper right and **Figure 4**). Now, how are forest biota affected by edge conditions? While we still know little about temperate forests, we can learn a lot from the tropical realm, as the bulk of studies has been done there (Laurance & Lovejoy 2002, Haddad et al. 2015).

For plants, research shows that communities erode from formerly hyperdiverse, trait rich, and shade adapted interior floras (with many so called '*loser species*', Tabarelli et al., 2012) to early-successional communities of heat/desiccation tolerant pioneers (so called '*winner species*') with low/homogenized alpha, beta, and functional diversity (Girão et al. 2007, Tabarelli et al. 2008, 2012). Insect herbivores, as ectotherms, are likely to benefit from these higher energy inputs via increased metabolic rates, and decreased mortality, in turn increasing herbivory rates (Emmerson et al. 2005, Wirth et al. 2008, Lindner et al. 2010, Traill et al. 2010). Furthermore, simplification of plant communities generally has pivotal importance for associated herbivores (Haddad et al. 2001, de Sassi et al. 2012). For one, pioneer plants which are promoted in tropical forest edges offer leaf material of higher palatability, which increases herbivory, particularly by generalist herbivores (Urbas et al. 2007, Wirth et al. 2007). Furthermore, alterations in plant diversity and community composition alter host availability, which affects specialized herbivores the most (Steffan-Dewenter & Tscharntke 2000, Cagnolo et al. 2009). Hence, during taxonomic homogenization of edge floras, generalist herbivores might emerge as '*winner*' species (Steffan-Dewenter & Tscharntke 2000, Wirth et al. 2008), as they can react to loss of a host plant by simply switching to another host species. Proliferation of leaf cutting ants in the fragmented Atlantic rain forest in Brazil is a suitable example of a generalist herbivore benefitting from fragmentation (Urbas et al. 2007, Wirth et al. 2007). Although higher presence of polyphagous herbivores in forest edges might imply higher connectivity of plant-herbivore food webs, the scarce evidence instead suggests a contraction of network connectance via depletion in species richness (Valladares et al. 2012), hence constricting and limiting energetic pathways across trophic levels.

Bridging from the tropics to the temperate zone is difficult, as we can transfer only some general patterns, due to the inherent differences between biomes (one example outlined below). Moreover, the empirical data base for forest fragmentation effects on plants, herbivores, and interactions in the temperate zone is still rudimentary. For instance, these topics are hardly mentioned in standard forest ecology textbooks (Wirth et al. 2009, Bartsch & Röhrig 2016). Also, in a comprehensive review on forest fragmentation by Harper et al. (Harper et al. 2005) only 2 of the 44 studies addressed temperate Europe. Nevertheless, we can sketch a picture of probable mechanisms and remaining gaps. Tropical and temperate floras are remarkably different in their proportional species richness of shade adapted vs. light demanding species. In tropical biomes temperature is not a limiting factor, but may cause harsh microclimatic conditions in open habitats (such as forest edges, Laurance & Lovejoy 2002). Hence, the pool of light demanding pioneers is much poorer than the pool of shade adapted species of the hyperdiverse forest interior (Laurance et al. 2006, Tabarelli et al. 2012). Opposed to this, temperate interior forests are limited by energy regimes (light and temperature), and edges exhibit much more lenient climatic conditions, leading to relatively higher richness in light/temperature demanding woody plant species (Honnay et al. 1999, 2002a, Whittaker et al. 2006). It is hence reasonable to assume that this higher host availability translates into equally diverse herbivore communities in forest edges, although the evidence is scarce (van Halder et al. 2010). Potentially, more lenient edge conditions might further benefit herbivore abundances and hence herbivory rates (Wirth et al. 2008), but again, studies on these processes are practically unavailable (but see e.g. Dohm 2009). Based on the assumption of both high plant and herbivore diversity in forest edges, one might expect the emerging food webs to be comparatively more complex. Both, herbivore diversity and food web complexity, further are plausibly modulated by herbivore specialization (Novotny et al. 2010). Niche partitioning in forest edges is difficult to predict, but high plant diversity might facilitate specialist herbivores (Haddad et al. 2001, Novotny et al. 2010).

Temperate forest fragmentation and edge proliferation cannot be studied without addressing silvicultural management in parallel, as these two factors have been determining factors of Central European forests for centuries (if not millennia) and are mutually dependent (Ellenberg & Leuschner 1996, Williams 2000). Hence, the following section will specifically address European deforestation and human forest use, from the dawn of the Holocene to the present, while keeping focus on the implications for forest ecosystems.

A BRIEF HISTORY OF CENTRAL EUROPEAN FORESTS AND IMPLICATIONS FOR BIODIVERSITY

As already hinted, human modifications of Central European forests fundamentally differ from their counterparts in other biomes. Two major and interdependent factors determine these differences: first, the extremely early onset of anthropogenic deforestation and second, the persistent and extensive silviculture (forest management), which conjointly led to a unique cultural landscape. As these factors are fundamental to understanding and contextualizing effects of human land-use on plant-herbivore interactions in European forests, I deem it inevitable to briefly review the history of European forest use while focusing on the consequential effects on biodiversity and ecosystem function.

Neolitic And Antique: Baseline As Pristine Forests? – It is next to impossible to determine a proper baseline for pristine European forests, as human influence was already noticeable in the Neolithic, while various tree species were still reconquering the continent after the last glaciation (ca. 10,000 BC, Williams 2000). Nevertheless, we can draw a quick picture as to how forests and forest use changed until the present. The periods following the glacial retreat (Preboreal, 9,600 – 8,700 BC, dominated by *Pinus* spp. and *Betula* spp.; Boreal, 8,700 – 7,300 BC, dominated by *Corylus avellana* and *Quercus* spp.) were coined by rather light and open forests, with little, yet noticeable, human influence (Vera 2000, Williams 2000, Frey & Lösch 2010). Mesolithic and Neolithic settlements during and after these periods already cleared forests for agriculture and used the remaining wooded areas for browsing, requiring ca. 6 km² of forest per settlement of 30 people (Williams 2000). Acorns are ideal fodder for domesticated animals, and hence the temporal coincidence of Neolithic cultures and the development of widespread mixed oak forests (particularly with *Tilia* spp. and *Ulmus* spp.) during the Atlanticum (7,300 – 3,700 BC) implies a facilitative effect of humans (Frey & Lösch 2010). It was not until the Bronce Age that *Fagus sylvatica* returned from its glacial refugia (Frey & Lösch 2010). It reached its present distribution and succeeded *Quercus* spp. as the dominant forest tree as late as the Subatlanticum (450 BC – present, Frey & Lösch 2010, Bartsch & Röhrig 2016). Although in Central Europe fuel wood became increasingly important in the Bronze and subsequent Iron Age for smelting, forest degradation was most severe in the Mediterranean (where forests had already yielded to garrigue vegetation in classical antiquity) (Williams 2000).

Intensive Forest Use Since The Middle Ages And The Slow Transition To Modern Practices – Socioeconomic consolidation and population growth lead to decreasing forest cover in Central Europe, reaching about 30% in the 13th century and remaining fairly constant ever since, only (positively) modulated by large epidemics and wars (Williams 2000, Büntgen et al. 2011). It is noteworthy that particularly poor soils were kept forested, as more fertile grounds were used agriculturally (Hahn & Fanta 2001). Please, bear in mind, that these medieval and post-medieval forests where far from being closed, homogeneous, or beech dominated. Forests were subjected to a multitude of ecosystem services. Hence, a forest's appearance corresponded to its individual main use (e.g. coppice forests, pollarding, wood pastures, etc.,

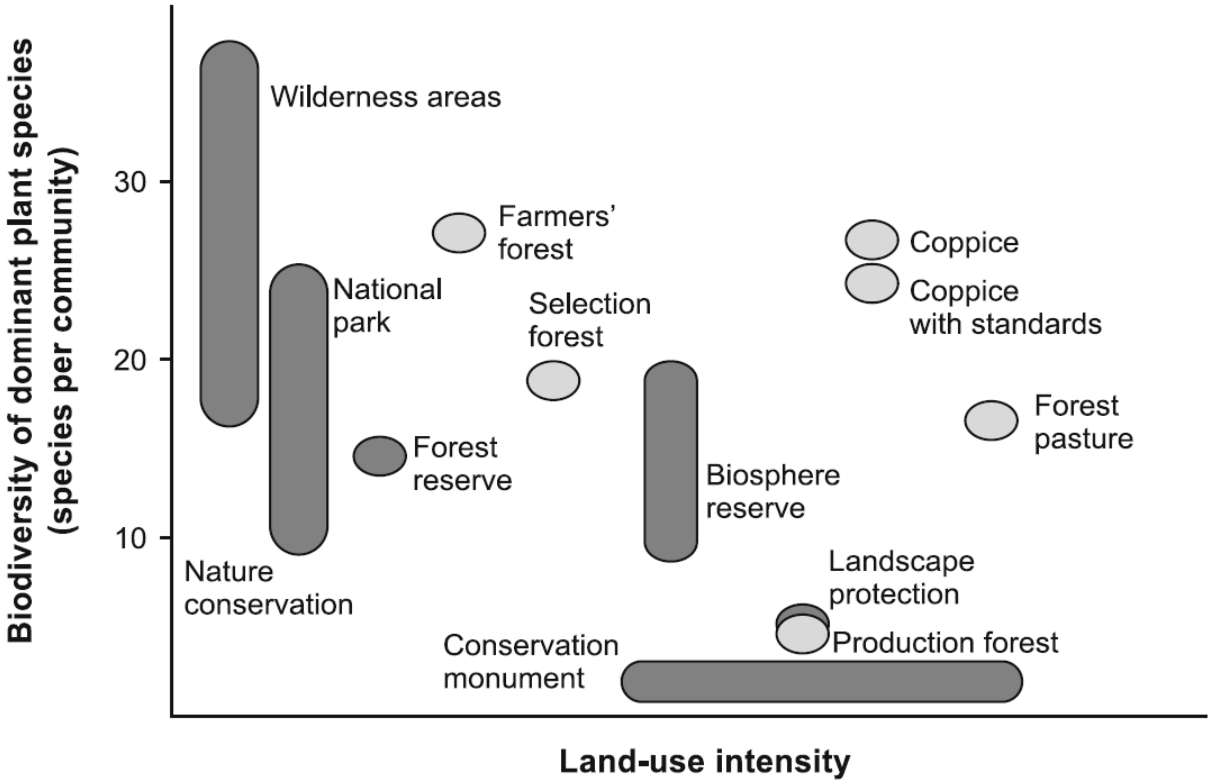

Figure 2: Conceptual relationship between plant species biodiversity in forests and management type and intensity, including modern and still practiced historic management regimes (from Schulze et al. 2009). Dark grey: protected forests, including the following. Wilderness areas: no historic human impact. National parks: historic management, but now without silviculture. Forest reserves: Similar to National parks, but single stands of small scale. Biosphere reserves: large forest tracts, but retain some silviculture. Landscape protection: landscape with regular agriculture and forest management but restricted industrial development. Conservation monuments: single tree individuals within completely variable land-use intensity (e.g. 1,000-year-old lime tree in a village). Light grey: Different forest management systems, including the following. Farmers' forests: small plots with the high tree diversity needed to operate a farm in historic times. Selection forest: single tree extraction. Coppice forests: fuel wood generation by clear-cutting shoots of tree stools (e.g. hazel, birch, or oak) in a 30-year rotation. Coppice with standards: coppice forests with an upper canopy of tall trees for construction wood. Forest pastures: Thinly spread large fodder trees (e.g. oaks, beech, or maple) over a cover of grasses for grazing. Production forest: an age-class forest.

Ellenberg & Leuschner 1996, Frank et al. 2009). This, of course, had decisive implications for woody plant diversity and composition, various abiotic conditions (e.g. light climates, nutrient contents, soil conditions), and hence subsequently for the entire ecosystem (Vandenberghe 2006, Gimmi et al. 2008, Schulze et al. 2015, **Figure 2**). Rising political importance of consolidated national states, as well as local forest overexploitation (due to imbalances between ecosystem service demands and limited forest performance capabilities) led to an increasing administrative regulation of forestry, and emphasis on sustainability of wood production (von Carlowitz 1713, Ellenberg & Leuschner 1996, Hölzl 2010). What followed, were reforestation measures (particularly on soils of low stability), as well as a focus shift on productivity and profit maximization, often via clear-cutting, age class forestry, and proliferation of fast-growing conifers (compare 'Production forest' in **Figure 2**, Hahn & Fanta 2001). Productivity-motivated spruce monocultures established since the late 19th century (Klimo et al. 2000, Angelstam et al. 2005) are tightly associated with detrimental ecological consequences, such as homogenization in biodiversity and age structure, lessened physical and ecological stability, and increased soil acidification (Spiecker 2000, Tesař 2000, Hasenauer & Sterba 2000, Emmer et al. 1998, Hahn & Fanta 2001). In response, since the 1980s close-to-nature management practices were developed and implemented as countermeasures. These included e.g. selection cut forestry, in order to mimic natural disturbances found in old-growth forests and to promote biodiversity and ecosystem functioning and services (compare '*Selection forest*' in **Figure 2**, Landeswaldgesetz Rheinland-Pfalz 2000, Hahn & Fanta 2001, Bauhus et al. 2009, Brunet et al. 2010). Hence, selective cutting and age class forests can be considered as the most widespread forms of silviculture in Central Europe (Schulze et al. 2015). Nevertheless, the classification of management regimes in the context of ecosystem research is usually difficult, as foresters hold a lot of freedom in the interpretation of forest regularities, and silvicultural interventions are usually very site-, and personality-specific.

Forest Management And It's Relations To Biodiverity – If one intends to study the effects of human forest exploitation on species diversity and interactions in Germany, it is elementary to first develop quantitative indices, which integrate various aspects of management (Schall & Ammer 2013). Another obstacle arises from the blatant lack of adequate controls, as at present only 0.2% of Central Europe's forests are under no active silviculture ('*unmanaged*') (Frank et al. 2009). Furthermore, less than 6% (42) of Germany's natural forest reserves are unmanaged for more than 50 years and less than 10% (71) of them are larger than 1 km² (Bundesanstalt für Landwirtschaft und Ernährung 2016). Consequently, interest in the effects of silviculture on biodiversity has been gaining in the last decades. However, empirical results are still rare, and we are far from a common consensus or a holistic picture (Boch et al. 2013, Schulze et al. 2015). Instead, there is a controversially fought debate on the general direction of management effects, positive or negative. In essence, researchers are divided on the questions how forests develop after management cessation and whether silvicultural interventions can have facilitative effects on diversity. The first perspective argues that unmanaged forests form monotone and uniform beech stands of low light and biodiversity, as they lack medium to large natural disturbances (particularly megaherbivores and fires). These would naturally open up the forest and act as facilitators of biodiversity (Bengtsson et al. 2000, Bauhus et al. 2009, Boch et al. 2013, Schulze et al. 2015). Therefore, it would need silvicultural practices to mimic these disturbances (Bauhus et al. 2009, Boch et al. 2013, Schulze et al. 2015). It is indeed true that beech stands with ceased management form homogeneous formations with initially low biodiversity (Ellenberg & Leuschner 1996). But it is imperative to mind that beech trees gain major ecological relevance as late as 200 years of age (much after their silvicultural 'maturity'), particularly for so called '*Urwald relict species'* (habitat specialists confined to old-growth forests, Schmidl & Bußler 2004, Moning & Müller 2009). Hence, pure diversity indices with no regard for the natural history of species might not capture the relevance of unmanaged forests for biodiversity. Furthermore, following the *shifting mosaic model*, we could expect high beta diversity on the larger scale. The model states that natural forests can be separated into patches of different successional stage. Upon reaching a climax state, a patch will inevitably experience a disturbance event (tree collapse, forest fire, etc.), which sets succession back to a previous state (cyclic succession, Ellenberg & Leuschner 1996, also compare '*National parks'* and '*Wilderness areas'* in **Figure 2**).

Concerning empirical results of forest management effects on biodiversity, there has been slight taxonomic bias towards herbs, vascular plants in general, and xylophagous insects (reporting mostly negative effects, Müller et al. 2008, Paillet et al. 2010, Schulze et al. 2015), and we still know little as to how woody plant communities develop when management ceases. Furthermore, the dual effects of silviculture and forest fragmentation remain elusive. The same is true for effects of forest fragmentation on herbivores and their interactions with their plant hosts. This thesis will contribute in illuminating these questions, as detailed in the following subsection.

AIMS AND OVERVIEW

Aims

Human modification of natural landscapes is one of the most pivotal drivers of global homogenization of species diversity and interactions, with particular importance for plants and herbivores. Yet, following decades of research on the ecosystematic effects of forest fragmentation in exotic biomes, we know more about what is happening in tropical forests than in Central European ones. Deforestation of European temperate forests is particularly old and extensive, yet the existing literature on the effects on plants, herbivores, and their interactions is scarce at best. Furthermore, human disturbance in Central European forests additionally manifests in silvicultural management, which is likely to have interacting effects with fragmentation. But while management implications for forest ecosystems have a notable tradition in the non-English and nonscientific forestry literature, the topic is still rising in international scientific research. It is hence of elementary importance to shed light on how these two aspects of human forest modification affect one of the most pivotal parts of ecosystems: plant-herbivore interactions. This thesis therefore aims to investigate how human forest modification alters the diversity, community composition, and trait manifestation of plants and insect herbivores (in the understory and the canopy), and how it affects the structure of their interactions and their food web robustness against secondary disturbances, such as climate change. The following **Chapters 2-5** serve this purpose, each addressing specific aspects outlined above. The final **Chapter 6** will then synthesize the central results, discuss the main patterns within a conceptual framework, contextualize the unique role of fragmented Central European forests by exploring whether they are suitable future projections for biomes under current deforestation, and finally utilize emerging insights from this thesis to provide recommendations for application for conservationists, foresters, and decision makers.

Overview of the core chapters

Chapter 2: analyzes the interactive effects of forest fragmentation and silviculture on the diversity and community composition of woody plant species in the hyperfragmented and differently managed Northern Palatinate highlands, and demonstrates which microclimatic plant requirements are proliferated in the different forest habitats.

Chapter 3: transfers the study to the next trophic level by investigating the effects of forest fragmentation on herbivore diversity and community structuring. This will be achieved by demonstrating the repercussions of direct habitat effects and the more indirect effects of fragmentation via changes in vegetation diversity and herbivore specialization.

Chapter 4: shifts our attention from the understory to the '*high frontier*': First, it will describe the immense abundance and species richness of arboricolous arthropods found in the treetops. Then it will explore if forest edge effects translate from the understory into the canopy, as tree crowns represent a '*horizontal edge*' themselves. Finally, it will characterize the natural history of selected identified species, focusing on those with particular conservation value.

Chapter 5: will mathematically synthesize empirically attested interactions between plants and herbivores into the conceptual framework of interaction networks and then analyze how their network topology is affected by forest fragmentation. As fragmentation affected habitats are more strongly coined by heat-adapted plants, this chapter will further investigate how the stability of plant-herbivore interaction networks in (un)fragmented forests will be differently affected by climate change via simulation of climate change-based extinction cascades. Finally, this chapter will relate network topology to network stability under climate change and briefly discuss emerging consequences for conservation.

In order to incorporate the factors of silviculture and forest fragmentation as driving agents of plant, herbivore, and interaction diversity, it needs an appropriate study region. The following subsection will concern with this issue by presenting the hyperfragmented Northern Palatinate highlands as a model study landscape.

THE NORTHERN PALATINATE HIGHLANDS

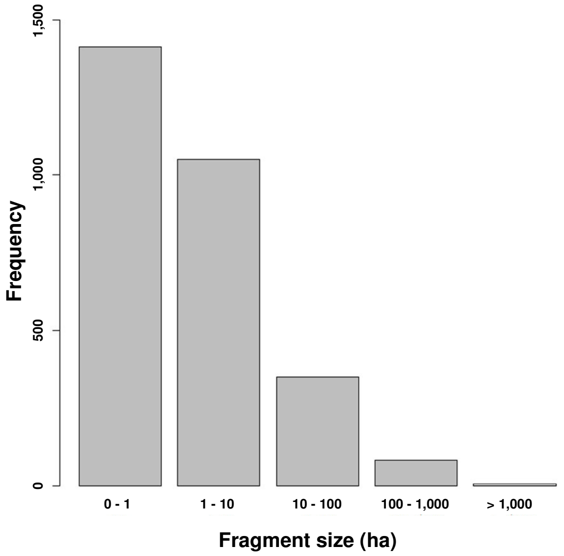

Figure 3: Distribution of fragment size classes. Small forest fragments dominate, with only 3.1% of fragments exceeding 1 km^2.

While deforestation in Germany is extensive (as already described), the spatial distribution is rather heterogenous. For instance, forest cover across the federal states ranges from 11% (Schleswig-Holstein) to 42% (Rhineland-Palatinate), with a German mean of 31%. Selection of a study landscape of representative fragmentation degree that simultaneously incorporates extensive silviculture is therefore pivotal. The '*Northern Palatinate highlands*' (49° 36' N and 7° 44' E) are an ideal choice for study, because of their pronounced fragmentation and comprehensive management, and because of the existence of unmanaged natural forest reserves.

The landscape is a low, undulating mountain range (250 – 687 m asl) covering an area of 1,556.4 km^2 and is situated between Kaiserslautern in the south and the Nahe River in the north (**Figure 5**, Naturräumliche Gliederung von Rheinland Pfalz 2010). It is characterized by a temperate Central European climate under oceanic influence (MAP: 800 mm; MAT: 9.4°C, 1970-2010, Deutscher Wetterdienst 2013). Geologically, sand- and siltstones of Permian origin dominate, interrupted by igneous hilltops of volcanic descent, such as rhyolite and andesite (MULEWF 1994). The Permian rocks provide fertile soils, hence deforestation occurred mainly in the valleys and hills were kept forested. Agriculture encompasses pastures, meadow orchards, cereals, and rape. There is no comprehensive historic documentation on the spatiotemporal deforestation in the Northern Palatinate highlands, but if we take the adjacent Palatinate Forest as a rough indicator, we can assume that most forest clearance occurred in the High Middle Ages (Geiger 1987, Keddigkeit 1987).

The resulting fragmentation is extensive. While Rhineland Palatinate has the proportionally highest forest cover in Germany (42%. MUF 2002), the Northern Palatinate highlands (34%) are close to the German average (31%). The

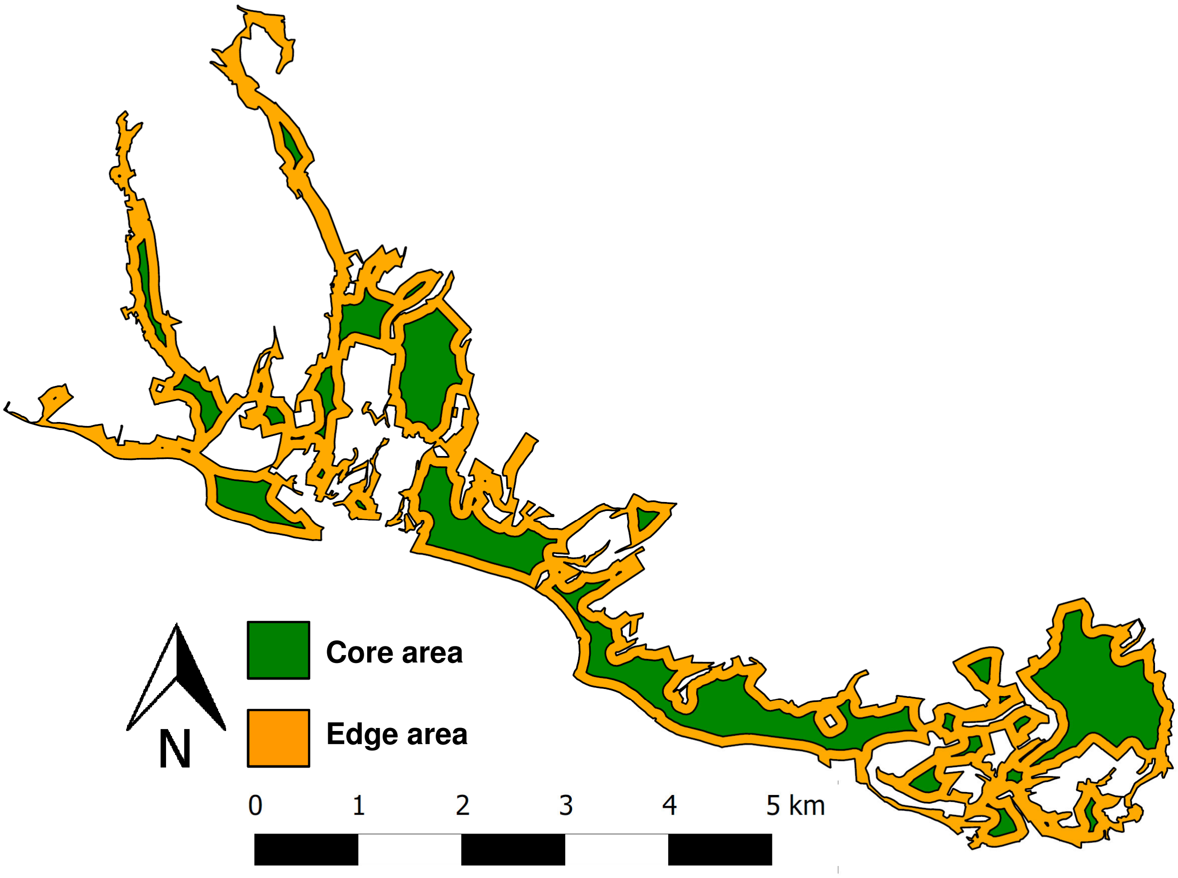

Figure 4: Forest fragment in the Northern Palatinate highlands with most complex form, i.e. most deviating from a circle. The strong irregularity causes the separation of the core area into 35 individual areas, assuming an edge depth of 100 m. Modified from Paul (2015).

study landscape comprises over 2,900 forest fragments, ranging from 0.1 to 5,616 ha (Paul 2015). Patch area roughly follows a power law distribution, with about 85% of fragments being smaller than 10 ha and only contributing 8.5% to the total forest area (**Figure 3**, Paul 2015). The total length of forest edges exceeds 5,700 km. This determines a pronounced scarcity of core areas. If we assume an edge depth of 100 m (Laurance & Lovejoy 2002), core areas constitute a mere 41% of the total forest area. Shape complexity is further responsible for high within-patch fragmentation of core areas. For illustration, the patch with the most complex form consists of 35 individual core areas separated by edge zones (**Figure 4**). Furthermore, 86% of all patches (2,497) are left with no core area at all (Paul 2015). Hence, most core forest can be found in the seven largest forest tracts (> 1,000 ha), which are ideal candidates as control forests. They are largely concentrated at the Königsberg near Wolfstein and the Donnersberg massif (the highest elevation in the study region, 687 m asl) near Kirchheimbolanden (Paul 2015).

Forest ownership, forest type, management regime, and patch size are partly interrelated. Small forest fragments are typically composed of deciduous mixed forests and are often owned privately (**Table 1**). Larger forest tracts often are a mosaic of different ownerships (mostly private, state-, and municipality-owned) and forest forms, including age class and old coppice forests. Privately owned stands vary wildly in management regimes, as applied interventions are often arbitrary, and may contain coppices. Management intensity is also dependent on parcel size and seclusion. Small parcels which are hard to reach are only rarely used for wood extraction. Hence there are private forests with a very low management intensity. State-owned forests follow federal guidelines for sustainable close-to-nature forestry (Landeswaldgesetz Rheinland-Pfalz 2000), but still mostly consist of age class forests (both, deciduous and coniferous). Across the Northern Palatinate highlands, there are four natural forest reserves, where no silvicultural intervention was performed since 1972. They are mostly established to protect rare forest formations, such as *Fraxino-Aceretum* associations in ravines or *Luzulo-Quercetum petraeae* on steep slopes with shallow soils (e.g. in the reserve Wildensteinertal). Yet, they also contain *Carpino-Fagetalia* mixed forests in between, which are comparable to the surrounding managed forests.

From this landscape configuration we can derive a conceptual framework to address the effects of human forest modification on plants, herbivores, and their interactions. Small fragments serve to study fragmentation effects *per se*, i.e. isolation and area effects. Edges of large control forests (> 1,000 ha) allow the study of edge effects, with the interior of these forests as control. To distinguish management effects within these continuous control forests, natural forest reserves, as well as individual private forests represent unmanaged stands. Following this framework, an initial system of permanent study plots was established in 2008 by Dohm and Barge (Barge 2009, Dohm 2009) and repeatedly extended, leading to a current total of 57 plots (**Table 1**, **Figures 5**, **6**). These sites were used in this thesis to answer the emerging questions formulated in the following chapter.

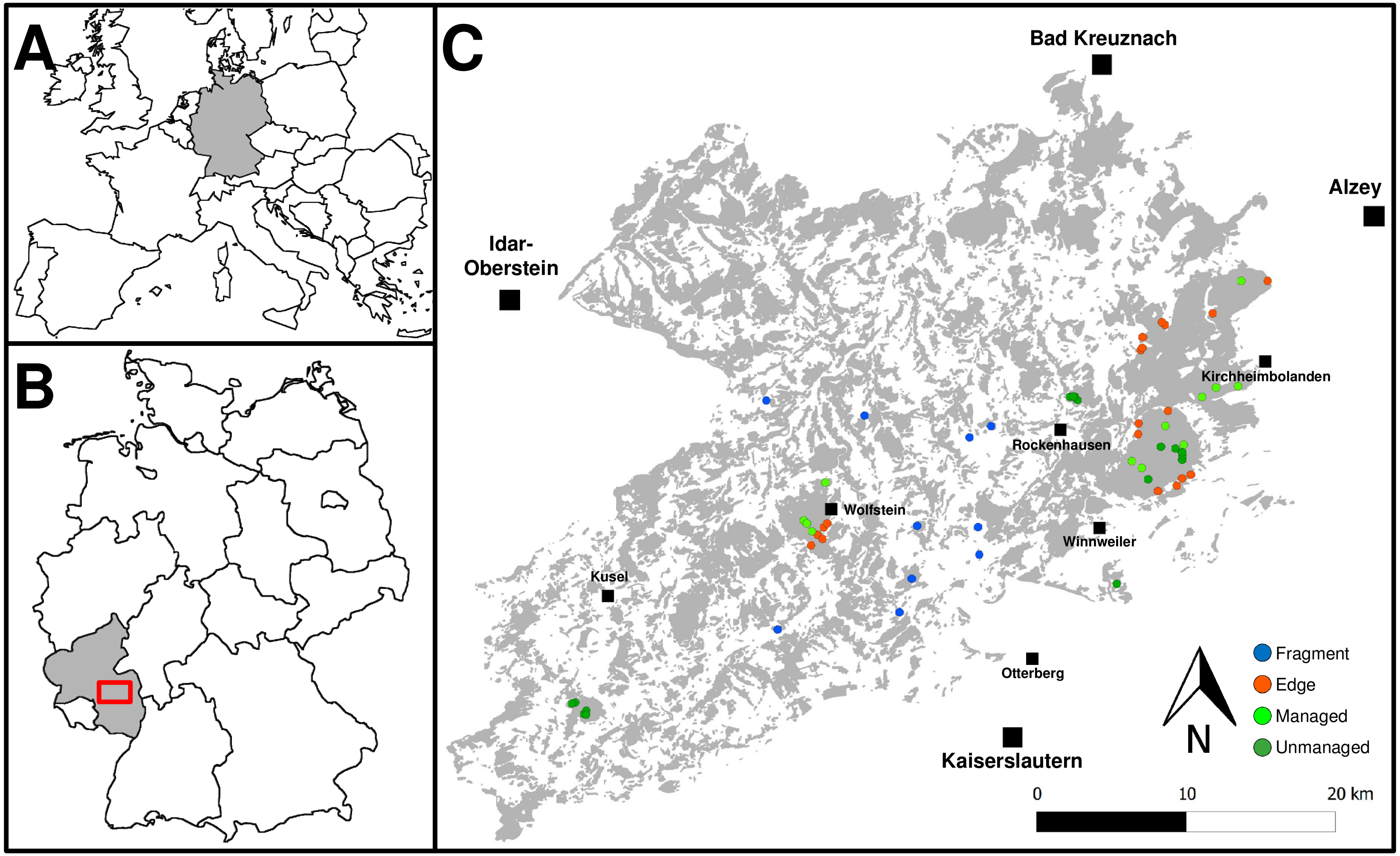

Figure 5: Geographical localization of study sites and landscape, with respect to Europe A and Rhineland-Palatinate, SW Germany B. The Northern Palatinate highlands **C** encompass > 2,900 forest fragments (grey polygons). Situated within these remnants are the individual 57 study plots (circles), divided in small forest fragments (blue), edges (orange) of continuous control forests (> 1,000 ha), managed interior forests (light green), as well as unmanaged ones (dark green). Larger municipalities are divided in larger and smaller than 10,000 inhabitants (larger/smaller black boxes).

Figure 6: Impressions from the Northern Palatinate highland and the chosen types of forest habitats. A The high degree of forest fragmentation, as well as the embedding of fragments within the anthropogenically used matrix is easily perceivable. **B** Managed forests are often composed of similarly-aged stands of few tree species. Note the little abundance of dead wood and the occurrence of stumps as sign of frequent wood extraction. **C** Unmanaged forests, on the other hand, consist of trees of differing age classes with high amounts of accumulating dead wood. **D** Forest edges, as the interface to the surrounding landscape, typically are open and light habitats. Note the belt of light-loving shrubs concluding the forest.

Table 1: Formal classification of study plots. Plotnames starting with '*Fog*' were subjected to fogging **(Chapter 4**). Plots spanned the described habitats, i.e. small fragments, edges of large control forests, managed interior of large control forests, and unmanaged ones. Plot placement incorporated districts of four forestry departments. Public ownership dominated, particularly in interior forests. '*NFR*' designate natural forest reserves.

#	Plotname	Habitat	Forestry District	Ownership	#	Plotname	Habitat	Forestry District	Ownership
1	F01	Fragment	Otterberg	Municipality	30	ZK11	Managed	Kusel	State
2	F02	Fragment	Otterberg	State	31	ZK13	Managed	Kusel	State
3	F04	Fragment	Otterberg	State	32	ZK14	Managed	Kusel	State
4	F05	Fragment	Kusel	Private	33	ZK16	Managed	Kusel	State
5	F14	Fragment	Otterberg	Private	34	ZK21	Managed	Donnersberg	State
6	F15	Fragment	Otterberg	Private	35	ZK23	Managed	Donnersberg	State
7	F18	Fragment	Donnersberg	State	36	ZK24	Managed	Donnersberg	State
8	F31	Fragment	Donnersberg	Private	37	ZK25	Managed	Donnersberg	State
9	F33	Fragment	Kusel	State	38	ZK31	Managed	Donnersberg	State
10	F34	Fragment	Otterberg	Municipality	39	ZK32	Managed	Donnersberg	State
11	RK11	Edge	Kusel	Private	40	ZK36	Managed	Rheinhessen	State
12	RK12	Edge	Kusel	Private & Municipality	41	ZK37	Managed	Donnersberg	State
13	RK13	Edge	Kusel	Private	42	UWK1	Unmanaged	Donnersberg	State/NFR
14	RK14	Edge	Kusel	Private & Municipality	43	UWK2	Unmanaged	Donnersberg	State/NFR
15	RK24	Edge	Donnersberg	State	44	UWK3	Unmanaged	Donnersberg	State/NFR
16	RK26	Edge	Donnersberg	State	45	UWB1	Unmanaged	Donnersberg	State/NFR
17	RK27	Edge	Donnersberg	State	46	UWW1	Unmanaged	Donnersberg	State/NFR
18	RK28	Edge	Donnersberg	State	47	UWW2	Unmanaged	Donnersberg	State/NFR
19	RK32	Edge	Donnersberg	State	48	UWW3	Unmanaged	Donnersberg	State/NFR
20	RK33	Edge	Rheinhessen	State	49	UWW4	Unmanaged	Donnersberg	State/NFR
21	RK35	Edge	Donnersberg	State	50	UWH1	Unmanaged	Kusel	Private
22	RK36	Edge	Donnersberg	State	51	UWH2	Unmanaged	Kusel	Private
23	FogRK11	Edge	Kusel	Private	52	UWH3	Unmanaged	Kusel	Private
24	FogRK26	Edge	Donnersberg	State	53	UWH4	Unmanaged	Donnersberg	Private
25	FogRK27	Edge	Donnersberg	State	54	FogUWK3	Unmanaged	Donnersberg	State/NFR
26	FogRK28	Edge	Donnersberg	State	55	FogUWW3	Unmanaged	Donnersberg	State/NFR
27	FogRK32	Edge	Donnersberg	State	56	FogUWH1	Unmanaged	Kusel	Private
28	FogRK33	Edge	Rheinhessen	State	57	FogUWH3	Unmanaged	Kusel	Private
29	FogRK36	Edge	Donnersberg	State					

Chapter 2

Effects of forest fragmentation and management on woody plant communities in Central European beech forests

View from the ridge of the natural forest reserve *Wildensteinertal* (Donnersberg) into the reserve itself and the fragmented Northern Palatinate highlands beyond. The forest has not experienced any human influence since 1972.

INTRODUCTION

At present, globally, the most severe anthropogenic disturbances on forest ecosystems are forest fragmentation (Saunders et al. 1991, Hagen et al. 2012) and silviculture (Bengtsson et al. 2000, Crowther et al. 2015).

Forest fragmentation (mainly acting via habitat reduction, isolation, and edge effects, Fahrig 2003) generally has detrimental effects on a wide range of ecological parameters, such as loss and/or homogenization of biodiversity, species interactions, functional traits, and ecosystem functioning, with ensuing ecosystem destabilization (Didham et al. 1998, Bengtsson et al. 2000, Wirth et al. 2008, Hagen et al. 2012, Valladares et al. 2012). These phenomena are particularly well described in tropical latitudes with recent and active deforestation, e.g. the northeastern Atlantic Forest of Brazil. There, diminished core areas suitable for hyperdiverse shade adapted forest interior floras (with many so called '*loser species*', Tabarelli et al. 2012) are surrounded by taxonomically and functionally impoverished edge floras consisting of few climatically adapted pioneers (so called '*winner species*', Tabarelli et al. 2008, 2012).

Fragmentation effects in ecoregions of much more historic deforestation (such as Central Europe) are less well researched and are hardly mentioned in standard forest ecology textbooks (Wirth et al. 2009a, Bartsch & Röhrig 2016). In addition, in a comprehensive review by Harper et al. (2005) only two of the 44 studies were on forest fragmentation in temperate Europe, and none of them specifically addressed the woody flora or incorporated management effects. Hence, we are lacking evidence as to how forest fragmentation acts as selective force on plant diversity, community composition, and certain functional plant traits. However, vegetational patterns along latitudinal gradients offer insights: tropical and temperate floras are remarkably different in their proportional species richness of shade adapted vs. light demanding species. In tropical biomes temperature is not a limiting factor, but may cause harsh microclimatic conditions in open habitats (e.g. forest edges, Laurance & Lovejoy 2002). Hence, the pool of light demanding pioneers is much poorer than the pool of shade adapted species in hyperdiverse forest interiors (Laurance et al. 2006, Tabarelli et al. 2012). In temperate biomes, however, closed forests are limited by energy regimes (light and temperature), and open habitats exhibit much more lenient climatic conditions, leading to relatively higher richness in light/temperature demanding woody plant species (Landolt 1977, Whittaker et al. 2006). Edge promotion and further anthropogenic facilitation in the cultural landscape created such open habitats suitable for these *edge* species. This is turn increased woody plant alpha diversity, hence affecting community composition (Hermy et al. 1999, Flückiger et al. 2002, Honnay et al. 2002) and challenging the general pattern, '*the larger the forests are, the higher the biodiversity they contain*' (Duelli et al. 2002).

Silvicultural management is an old, pervasive and intrinsic feature of Central European forests. Use began as early as the antique, reached maximum deforestation in the Middle Ages, and left only 0.2% of forest cover undisturbed (Hannah et al. 1995, Williams 2000, Wirth et al. 2009a). Its potentially disastrous impact was well demonstrated with the detrimental effects of spruce monocultures on manifold biotas, ecological functions, and services in the last century (Emmer et al. 1998, Hahn & Fanta 2001). Yet, the resulting need for further research is aggravated by several aspects, e.g. the variety of historic and present management policies (Hahn & Fanta 2001), or classification difficulties due to very specific on-site choices by foresters. But the largest aggravation is the blatant lack of unmanaged, pristine control forests, as even large-scale research projects fail to detect basic old-growth features in unmanaged forests (e.g. higher amounts of coarse woody debris, CWD, Blaser et al. 2013). Therefore quantitative variables which integrate multiple old-growth attributes might outperform categorical management classifications (Bauhus et al. 2009, Schall & Ammer 2013). Effects on vascular plant diversity, their community structuring and trait facilitation mainly depend on the management regime, resulting disturbance dynamics (e.g. canopy gaps), and hence changes in moisture and light climates (Aude & Lawesson 1998, Decocq et al. 2005, Paillet et al. 2010, Boch et al. 2013, Duguid & Ashton 2013). Yet, research usually focused on the herb layer, and much less is known about the particular response of woody plant species regarding their biodiversity, community composition, and functional trait signature. Managed forests should show decreased woody plant alpha and beta diversity as well high levels of shade adaption, because even-aged cultivation of selected tree species constrains species richness, enhances homogeneity over large areas and favors shade adapted tree species (Hahn & Fanta 2001, Decocq et al. 2005). Conversely, unmanaged forests progressively acquire old-growth features (e.g. natural disturbance dynamics), in turn promoting woody plant diversity and trait variability (e.g. in microclimatic requirements) (Bauhus et al. 2009, Brunet et al. 2010).

Taken together, I expect fragmentation and cessation of management to increase woody plant alpha diversity, mainly via edge promotion, old-growth gap dynamics, and release from tree species selection by foresters. This should result in increased light transmission, detectable in promotion of light demanding species in the communities, increased diversity and microclimate related plant traits. This is the first study on the conjoined effects of European forest fragmentation and management on woody plant communities. To address this issue, I censused over 4,000 tree/shrub individuals in 57 plots located in small forest fragments, edges, as well as managed and unmanaged continuous forests in a hyper-fragmented forest landscape in SW Germany and used integrative indices for holistic quantification of fragmentation, edge, and management effects as well as radiation regime requirements.

METHODS

Study Landscape, Sites, And Vegetation Census – The study landscape is located in the Northern Palatinate highlands (49° 36' N and 7° 44' E), a low, undulating mountain range (250 – 687 m asl) of Permian origin covering an area of 1,556.4 km^2 in SW Germany. It is characterized by temperate Central European climate under oceanic influence (MAP: 800 mm; MAT: 9.4°C, 1970-2010, Deutscher Wetterdienst 2013). I studied deciduous, broad-leaved forests, phytosociologically classified as *Carpino-Fagetalia* mixed forests with varying transitional degrees of *Fagion* and *Carpinion betuli* stands. Extensive deforestation in the Middle Ages occurred mainly in sand and siltstone-dominated valleys, while the agriculturally less valuable igneous hilltops were mostly forested. This has led to a landscape of hyper-fragmented forests, embedded in a matrix of cultivated fields, pastures and meadow orchards. Forest cover of this landscape (34%) is representative for Germany (31%, MUF 2002). Despite its high fragmentation degree with over 2,900 forest fragments ranging from 0.1 to 5616 ha (ca. 85% of them < 10 ha) and a total edge length of over 5,700 km, the region still harbours large forest tracts exceeding 1,000 ha.

Study sites were chosen from four habitat types differently affected by forest fragmentation and management: (i) *Small forest fragments* (n = 10): ranging between 1.6 and 176.2 ha and entirely surrounded by matrix. (ii) *Forest edges* (n = 19): peripheral areas within 50 m of the border of large forest tracts (continuous control forests, the three largest forest tracts in the study region, 1,155, 3,537 and 5,289 ha). (iii) *Managed forest interior* (n = 12): core areas of control forests beyond 100 m of the border and without detectable edge influence. Despite varying management regimes, policies, and small-scale choices by foresters, management practices can generally be summarized by age class cultivation. (iv) *Unmanaged forest interior* (n = 16): core areas of large forest tracts beyond 100 m of the border and without detectable edge influence. These sites include natural forest reserves (state property, unmanaged since 1972), as well as privately owned forests. The latter were preselected on the criteria of seclusion, (small) property size and after visual inspection (e.g. regarding CWD amounts) to minimize the probability of forest use. Low levels (mean wood extraction < 4 m^{3}ha^{-1}a^{-1}) or absence of management were verified via personal interviews with forest owners. Time since last wood extraction varied (29 ± 25 a, mean ± sd) and was not available for two out of six sites. Fragment, edge, and managed plots (20 x 50 m; 0.1 ha) were chosen at random across the study region. This design reflects the landscape configuration available to us and follows similar studies (Girão et al. 2007, Valladares et al. 2012). Inter-plot distance ranged from 0.1 to 70.1 km with 18.8 ± 14.0 km (mean ± SD). In 2013, within each plot all woody plant individuals > 1.3 m height and with DBH > 1 cm were identified to species level, totalling 4,139 plant individuals from 34 species and 15 families.

Index Generation – Indices for anthropogenic disturbances (fragmentation, edge, and management index), as well as for community wide radiation requirements in forest stands (henceforth *radiation regime index*, RRI) were created following Martorell and Peters (2005) and as used e.g. by Ribeiro et al. (2016). This was done by first normalizing all explanatory variables related to a given index and then performing a principal component analysis (PCA) with them. The plot scores on the first PCA axis are then rescaled to range from 0 (low disturbance/radiation regime) to 100 (high disturbance/ radiation regime), hence generating the index in question. Further information on how the different variables were measured can be found in the supplementary.

Fragmentation index (FI)

Metrics used to create the fragmentation index span those related to fragment size and shape (fragment area (ha), core area (ha), perimeter/area ratio (m^{-1}) and shape index) and isolation (proximity index). Core area is defined as the remaining forest area assuming a pertinent edge buffer of 100 m (Broadbent et al. 2008). The shape index (SHAPE, **Equation 1**) is the deviation of a forest fragment shape from a perfect circle (SHAPE = 1) with

Equation 1 $SHAPE = \frac{p}{2\sqrt{\pi a}}$

and p and a being the perimeter and the area of a given fragment. The proximity index contextualizes a forest fragment in its surrounding neighborhood (here 1,000 m buffer) by both regarding area and distance of its surrounding forest patches and is hence a measure for patch isolation (Gustafson & Parker 1994, Lang & Blaschke 2007). High values indicate high patch integration. Axis 1 of the PCA (FI before rescaling) explained 66% of the variation of these variables and was significantly correlated with all of them (mean R^2 = 0.86 and mean $p < 0.001$***).

Edge index (EI)

The edge index incorporates the distance of a plot to the nearest forest edge (m), as well as the relative forest cover in a 100 m buffer around it (%). Axis 1 of the PCA explained 79% of the variation of these variables and was significantly correlated with all of them (mean R^2 = 0.87 and mean $p < 0.001$***).

Management index (MI)

The management index consists of variables representing past logging events (number of stumps per 0.1 ha), forest ownership/classification (either public or private ownership, or natural forest reserve (then also in public ownership)), amounts of coarse woody debris (CWD, including lying CWD (m^3/ha), standing CWD (m^3/ha) and stump volume (m^3/ha)) as well as unextracted living biomass (basal area of trees (m^2/0.1 ha)). Axis 1 of the PCA explained 48% of variation of these variables and was significantly correlated with all of them (mean R^2 = 0.52 and mean $p < 0.001$***).

Radiation regime index (RRI)

Thermophily, photophily, and xerophily individually resemble specific niche requirements of plants, but are commonly dependent on site-specific radiation regimes and hence are highly autocorrelative. Hence, in order to quantify radiation regime requirements of a plant community, I integrated these three aspects into a synthetic index, using Ellenberg’s indicator values (EIVs, Ellenberg & Leuschner 1996), i.e. Ellenberg light (ranging from 1/low to 9/high light conditions), temperature (ranging from 1/cold to 9/heat adaption), and moisture (ranging from 1/dry to 12/submersed conditions). Plotwise EIVs (PEIV) were calculated similarly to Meyer et al. (2013) by first multiplying species dominance in a given plot with the corresponding EIV found in the literature (Ellenberg & Leuschner 1996). Then the sum over these products gives the PEIV (**Equation 2**), where i is the enumerator of all plant species in a plot n and D_i is their individual dominance.

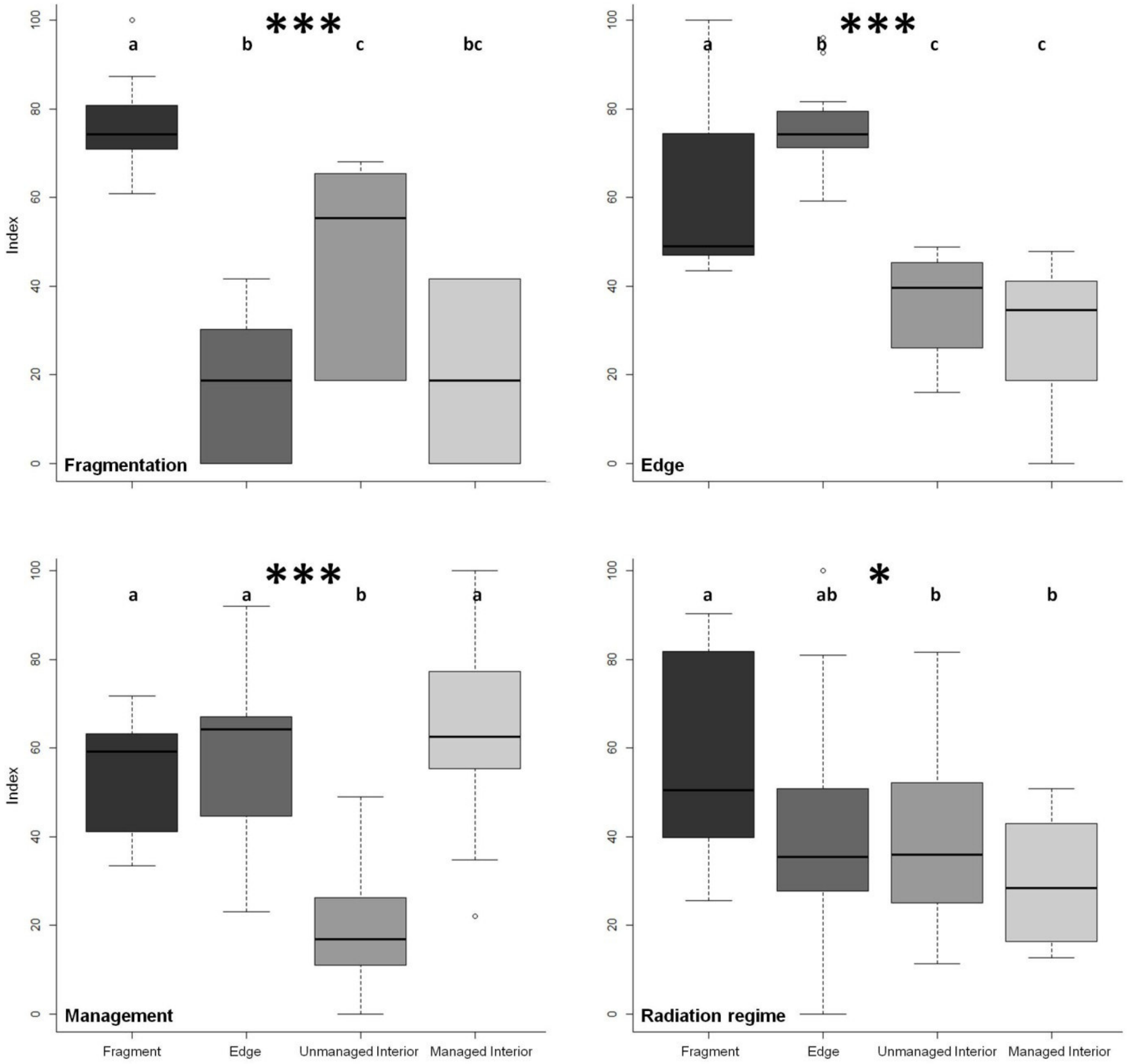

Figure 1: Habitat-wise comparison of all anthropogenic disturbance indices, as well as the radiation regime index (RRI). Edge and management index and RRI: one-way ANOVA with pairwise t-test as posthoc test without adjustment. Fragmentation index: Kruskal-Wallis test with Nemenyi as posthoc tests without adjustment.

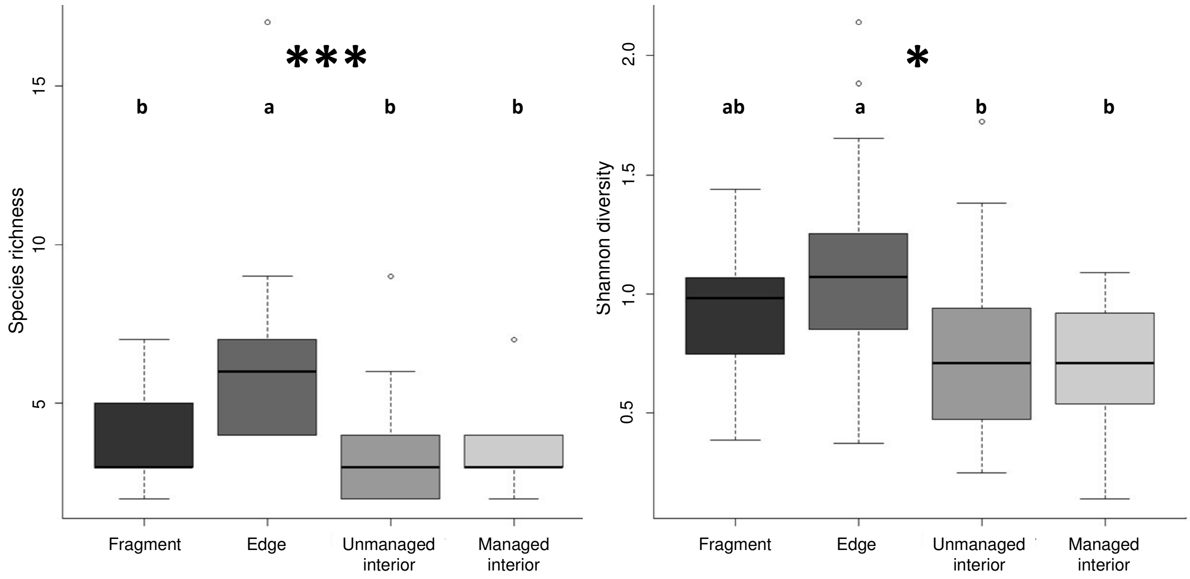

Figure 2: Effects of anthropogenic disturbance (forest fragmentation and silvicultural management) on species richness and diversity of woody plant species in the Northern Palatinate highlands. Left: Species richness (ANOVA of log-transformed richness data, $F_{(53,3)} = 7.952$, $p < 0.001^{***}$, untransformed data is shown). **Right:** Shannon diversity (ANOVA, $F_{(53,3)} = 3.602$, $p < 0.05^{*}$). Differing anthropogenic influences represented by: small forest fragments, edges of large forests, unmanaged interior of large forests, and managed interior of large forests. Group-wise differences are indicated by different letters (pairwise t-tests as posthoc tests).

Any given PEIV thus represents the overall plant community in a given plot in terms of thermophily, photophily, or xerophily, respectively.

Equation 2 $PEIV = \sum_{i=1}^{n} D_i \, EIV_i$

Plant species with EIVs given as '*indifferent*' were left out of the calculation (6 for Ellenberg temperature and 11 for Ellenberg moisture) and only contributed 13.7% and 13.8% to the data set in terms of abundance. Axis 1 of the subsequent PCA explained 55% of variation of the three PEIVs and was significantly correlated with all of them (mean $R^2 = 0.55$ and mean $p < 0.01^{**}$).

Data Analysis – All analyzes were performed with the programming language *R* (R Core Team 2015).

To evaluate the performance of aforementioned indices (fragmentation, edge, and management index, as well as RRI), I made habitat-wise comparisons, employing one-way ANOVAs where appropriate, and Kruskal-Wallis tests where ANOVA-assumptions could not be met with transformations.

Furthermore, habitat-wise differences in species richness and Shannon diversity were assessed using one-way ANOVAs. Fragmentation, edge and management effects on tree diversity (Shannon index) and on RRI were assessed using multiple linear regression with fragmentation, edge, and management indices as explanatory variables and Shannon index and RRI as response variables. Optimal model selection was performed with the *step* function. In cases where more than one explanatory variable was included in the model, partitioning (relative importance) of global R^2 was assessed with the *relaimpo* package following Grömping (2006) using the *lmg* metric. As the order in which explanatory variables are entered into the model is non-trivial for calculation of their relative importance, obtained partial R^2 values are an estimate. Hence, I report the mean and 95% CI of each partial R^2 for each variable based on 1,000 bootstrap-runs (function *boot.relimp*).

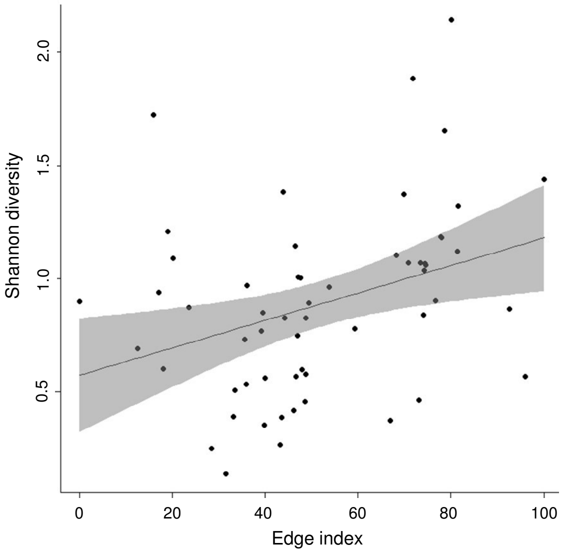

Figure 3: Intensity of edge effects (edge index) promotes Shannon diversity of woody plant species in the Northern Palatinate highlands. Linear regression (Slope = 0.006, SE = 0.002, $F_{(55,1)}$ = 7.264, $p < 0.01^{**}$, R^2 = 0.12), black line and grey banner represent the running mean and 95% CI, respectively.

Sufficiency of sampling intensity was assessed by calculation of saturation levels of species area curves, assuming asymptotic behavior, following Moreno & Halffter (2000).

Community segregation across forest habitats was analyzed using similarity values in a non-metric multidimensional scaling (NMDS, Bray-Curtis dissimilarity of square-root transformed abundance data, function *metaMDS*, vegan package, Oksanen et al. 2015) and performing an ADONIS permutation test (999 permutations) with forest habitat as a grouping variable. As a post hoc test I performed pair wise ADONIS procedures and adjusted p-values for multiple testing (Bonferroni-correction). To illustrate how community composition is structured by radiation-related functional traits, I supplemented a non-metric multidimensional scaling ordination (NMDS, Bray-Curtis dissimilarity of square-root transformed abundance data, function *metaMDS*, vegan package) with a heat map in which the RRI scores of sites correspond to colour-coding (low to high radiation conditions: blue – green – yellow – orange – red). Radiation/color interpolations between sites were calculated with *interp* function in the *akima* package (Akima & Gebhardt 2015).

Habitat wise comparison of beta dispersion was achieved similarly to Anderson et al. (2006) by measuring the distances of sites spanning the convex hull of a habitat in the NMDS ordination to their centroid (one-way ANOVA). I chose to use the convex hull because I wanted to compare the maximum spread in community dissimilarity amongst habitats.

Identification of indicator species for certain habitats was performed using a Dufrêne-Legrende indicator species analysis in the *labdsv* package (Roberts 2015). Indicator values (IV) range from 0 (no habitat association) to 1 (perfect habitat association).

RESULTS

As expected, forest habitats were exposed to different levels of anthropogenic disturbance (**Figure 1**), with managed and unmanaged forest habitats exhibiting the major differences relative to forest edges and fragments, particularly in terms of edge effects and radiation. Furthermore, unmanaged forest indeed displayed substantially lower management intensity.

Across these four habitats a total of 4,139 plant individuals from 34 species and 15 families were recorded. At plot level, forest edges supported more enriched and diverse assemblages (**Figure 2**). Precisely, woody plants in forest edges were twofold more speciose as compared to both unmanaged and managed forests. Accordingly, forest edge effects were positively related to woody plant diversity in the Northern Palatinate highlands (R^2 = 0.12, **Figure 3**). However, there was neither a major influence by fragmentation effects *per se* nor by silviculture.

Moving to habitat-scale, my sampling effort did not capture a total picture of the woody plant flora across the forest habitats of Northern Palatinate highlands, since sampled flora of small forest fragments, edges, and of managed and unmanaged interior forests was represented by 65%, 73%, 79%, and 59% of expected species (20, 43, 15, and 29). However, there was further evidence for enriched edge floras, as species richness in forest edges was 103% and 77% higher than in managed and unmanaged interior forests and 77% higher than in small forest fragments, when rarefied to same sample size (n = 10, **Figure 4**).

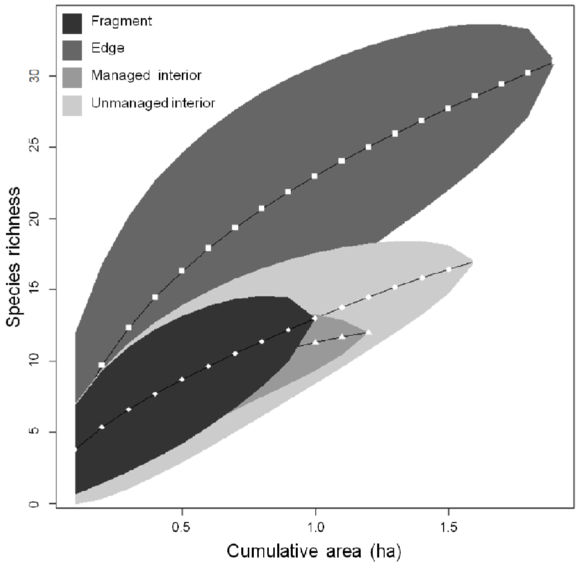

Figure 4: Effects of anthropogenic disturbance (forest fragmentation and silvicultural management) on woody plant species richness in the Northern Palatinate highlands: small forest fragments, forest edges of large control forests, and managed and unmanaged interior forests. Species richness is plotted against cumulative plot area (0.1 ha). White symbols and black line: running mean of 100 iterations. Grey polygons: 95th percentile.

Forest habitats also differed in terms of plot-level taxonomic composition (**Table 1**), despite a certain overlap in the NMDS ordination (**Figure 5**). Community differences included fragmentation-affected vs. interior forests and managed vs. unmanaged. Furthermore, there was striking evidence for biotic homogenization, as managed communities clearly converged in the NMDS ordination. This pattern was further confirmed by on average 35% higher beta dispersion of unmanaged woody plant communities over managed ones (one-way ANOVA, **Figure 5**). The highest levels of heterogeneity were found in forest edge communities (122% larger than

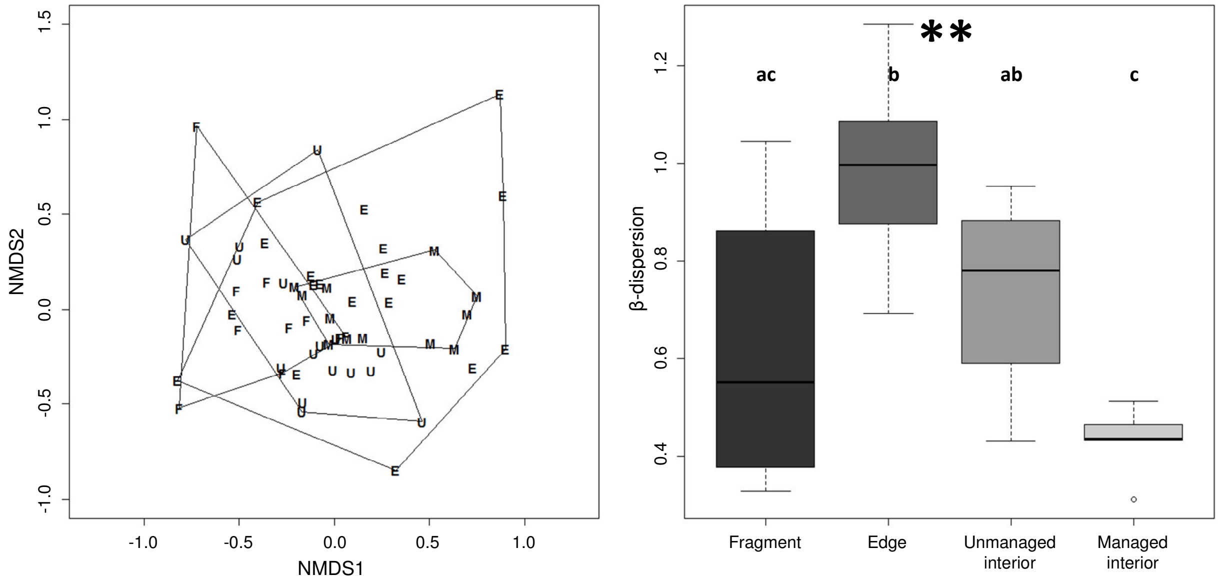

Figure 5: Effects of anthropogenic disturbance (forest fragmentation and silvicultural management) on segregation and homogenization of woody plant communities in the Northern Palatinate highlands. Left: NMDS ordination based on square-root transformed Bray-Curtis similarities of woody plant communities (stress = 0.18). Polygons encompass plots of a specific forest habitat (F: small forest fragments, E: edges of large forests, U: unmanaged interior of large forests, and M: managed interior of large forests). **Right:** Beta dispersion of the woody plant communities, measured as the distance of the hull plots in the NMDS space to the polygon centroid (box-cox-transformation; ANOVA, $F_{(14,3)} = 5.638$, $p < 0.01^{**}$; untransformed data is shown).

managed interior forests), indicating large compositional variability. Cross-habitat taxonomic differentiation was more related to occurrence of rare species (e.g. high occurence in forest edges) than to changes on the relative contribution of dominant species (**Figure 6**).

Moving to functional signature, plot-level taxonomic composition was found to be entirely shaped by the prevailing radiation regimes (**Figure 7**), as there was strong indication for the corresponding index to be an explanatory variable for community distribution from one extreme point in the NMDS ordination to the other. In other words, plots that were very different in terms of taxonomic composition were also very likely to be different in their radiation regime patterns. Furthermore, plot degree of thermo-, photo-, and xerophily significantly increased with increasing intensity of fragmentation and edge effects (multiple linear regression, global $R^2 = 0.35$, **Table 2**). Forest management had no effect, as the management index was excluded from the model in the stepwise selection process. In synthesis, managed interior forests were coined by shade-adapted communities, while unmanaged and (even more) edge floras exhibited the widest variability in radiation regime requirements. Woody floras in small fragments displayed the overall largest levels of thermo-, photo-, and xerophily. These findings are further highlighted by the natural history of identified habitat indicator species (Dufrêne-Legendre analysis). *Sambucus nigra* is a shrub with a large amplitude of light compatibility and is hence an indicator species for small forest fragments under varying influence of edge effects (IV = 0.30, $p < 0.01$**). Furthermore, all three edge indicator species are well known thermophilous and/or photophilous trees and shrubs of open habitats (*Prunus avium*, IV = 0.30, $p < 0.05$*; *Prunus spinosa*, IV = 0.26, $p < 0.01$**; *Sorbus aucuparia*, IV = 0.21, $p < 0.05$*). Finally, indicator species of managed interior forests were typical trees of commercial silviculture with either pronounced shade tolerance (e.g. *Fagus sylvatica*, IV = 0.37, $p < 0.01$**) or cold tolerance (*Larix decidua*, IV = 0.27, $p < 0.05$*).

Table 1: Effects of anthropogenic disturbance (forest fragmentation and silvicultural management) on compositional community segregation of woody plant species in the Northern Palatinate highlands (ADONIS test, 999 permutations, square-root transformed Bray-Curtis similarities). As a post hoc test, pairwise combinations of all four forest habitats (forest fragments, edges, managed interior, unmanaged interior) were tested and p-values adjusted by Bonferroni procedure.

	R	p
Global comparison	**0.16**	**< 0.001*** **
F - E	0.08	0.078
F - M	**0.19**	**< 0.05***
F - U	0.08	0.528
E - M	0.06	0.396
E - U	**0.12**	**< 0.01****
M - U	**0.17**	**<0.01****

F: fragment, E: edge, U: unmanaged interior, M: managed interior.

Table 2: Forest fragmentation and edge effects on radiation regime requirements (radiation regime index) of woody plant species in the Northern Palatinate highlands.

Anthropogenic disturbance index	Slope ± SE	p	R^2_{global}	R^2_{RI} ± 95%CI
fragmentation-index	0.426 ± 0.085	**< 0.001*** **	0.35	0.31 ± 0.06
edge-index	0.220 ± 0.102	**< 0.05***		0.17 ± 0.06

SE: standard error. R^2_{global}: R^2 of the whole model. R^2_{RI}: relative importance of individual variables. CI: confidence interval.

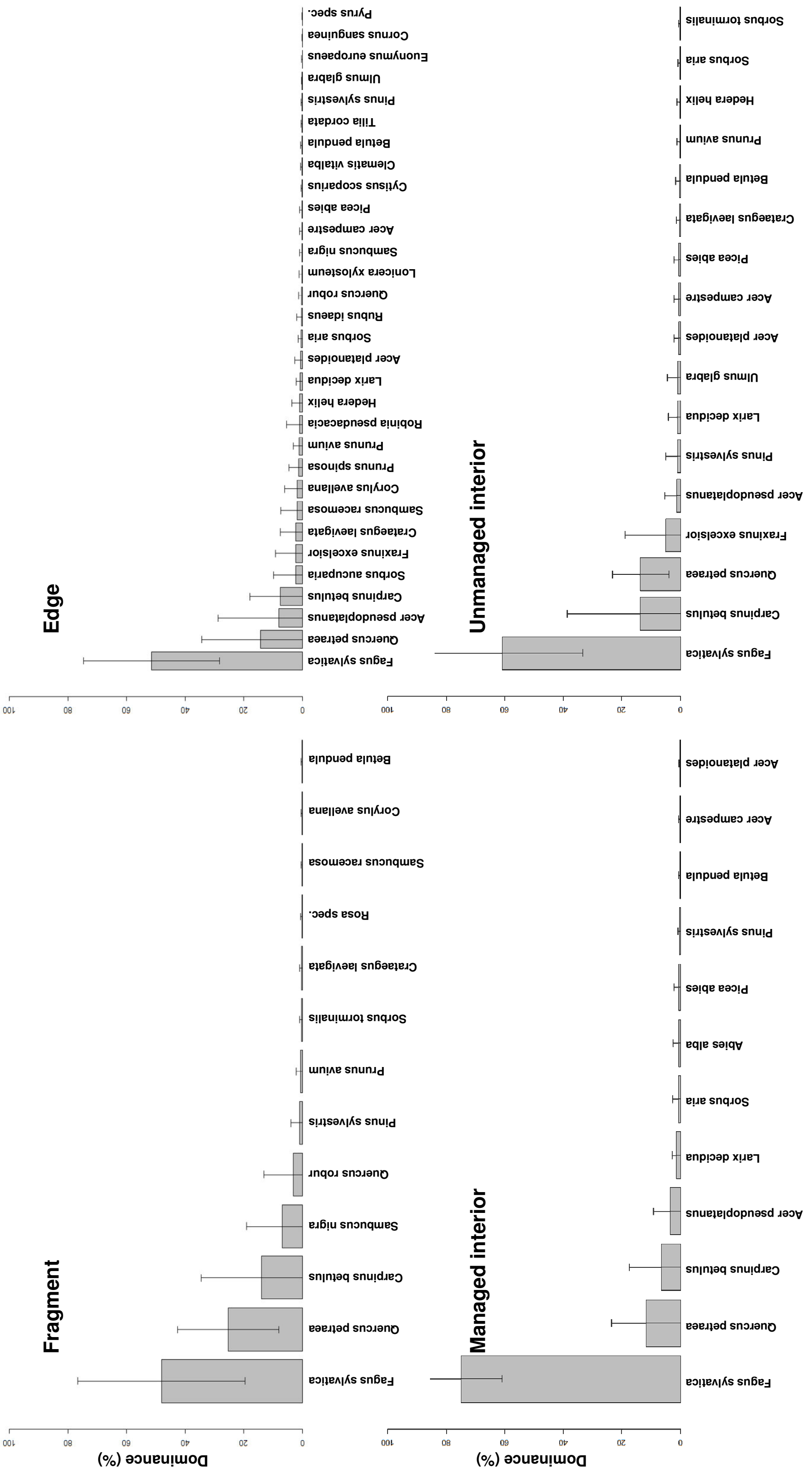

Figure 6: Effects of anthropogenic disturbance (forest fragmentation and silvicultural management) on the dominance distribution of woody plant species in the Northern Palatinate highlands.

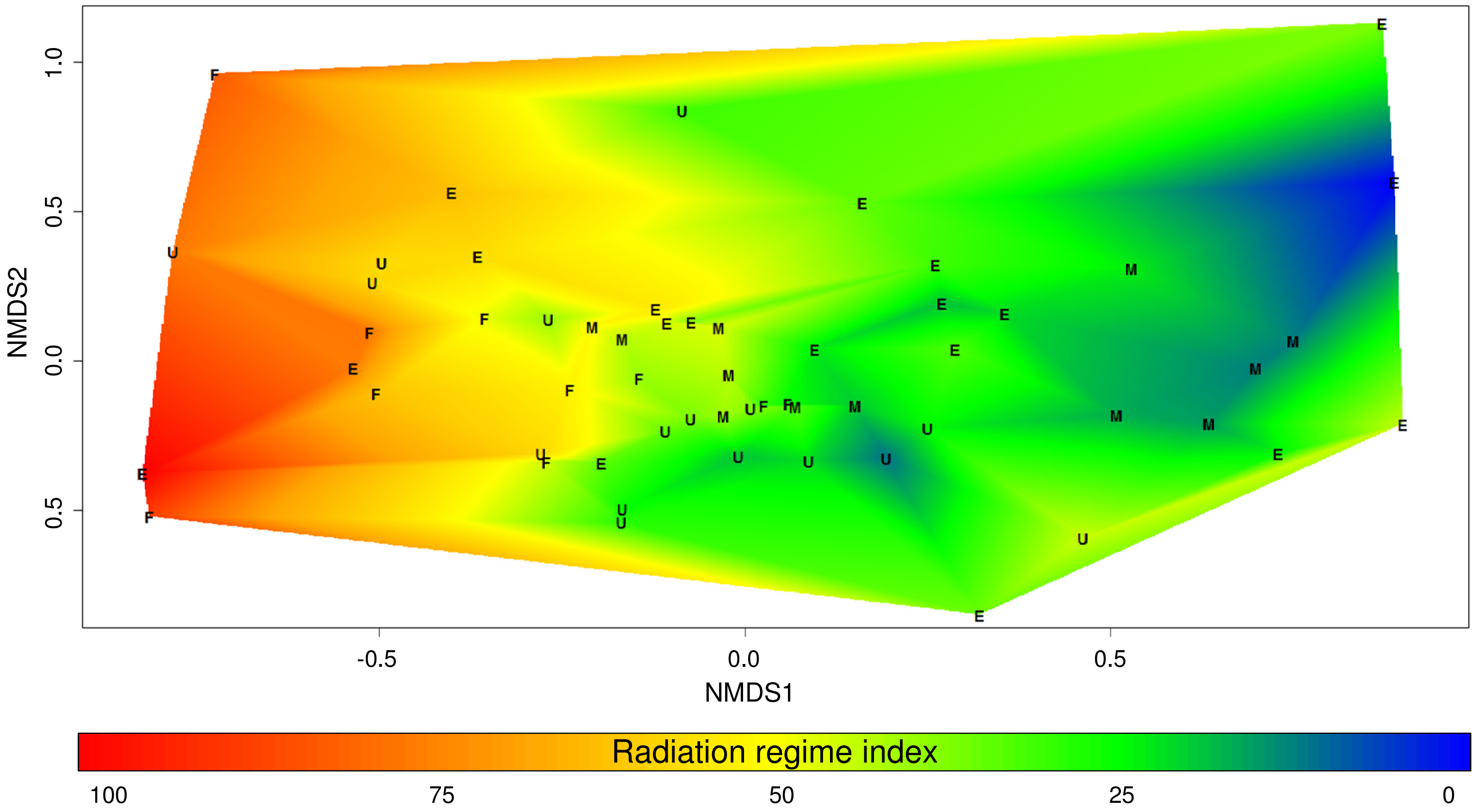

Figure 7: Prevailing radiation regimes shape community structuring of the woody flora in the Northern Palatinate highlands. NMDS ordination (identical to **Figure 5**, square-root transformed Bray-Curtis similarities, stress = O. 18) was superimposed with the radiation regime index (RRI) by interpolating the color-coded RRI between site-specific communities (letters). Red hues indicate thermo-, photo-, and xerophilic communities, blue hues vice versa. F: small forest fragments, E: forest edges, M: managed forest interior, U: unmanaged forest interior.

DISCUSSION

The general consensus on effects of forest fragmentation on plant assemblages is a promotion of heat/light adapted pioneer species via (Laurance & Lovejoy 2002, Laurance et al. 2006, Tabarelli et al. 2012). However, the patterns and processes in (Central European) temperate forests and their interaction with silvicultural management are far less well understood. Most temperate studies focused either on edge effects, species-level responses, or on communities without considering functional traits or forestry impacts (Palik & Murphy 1990, Meiners & Pickett 1999), which has limited our comprehension about biological dynamics in these human-modified landscapes. Here I contribute in illuminating this matter by reporting positive influence of forest fragmentation and cessation of management on plant biodiversity, mainly driven by plant-specific radiation regime requirements. Specifically, forest edges supported higher plant diversity (including more rare species) and beta dispersion, with high variability in radiation regimes, as opposed to simplified and shade-adapted plant assemblages in interior forests. Hence, I was able to identify several taxonomic associations typical of forest edges, e.g. *Sambucetum racemosae*, *Crataego-Prunetum spinosae* and *Rubo fruticosi-Coryletum avellanae* (Schubert et al. 1995). Unmanaged forests, while not more species rich than their counterparts, showed first signs of old-growth formation via higher beta diversity and slightly higher radiation regimes. Diversity of small forest environmental filtering, often allowing only a small, resistant set of species to prevail, with subsequent biotic homogenization
fragments was nearly as high as forest edges, while the lack of core area was reflected in more heat/light/drought-adapted communities. Collectively, these uncovered patterns reinforce the notion that establishment of forest edges, and to a lesser degree cessation of management, represent major drivers of forest-related plant communities in terms of structure and spatial organization, as well as in terms of biodiversity persistence in human-modified landscapes.

In tropical forests, the human modification of landscapes, i.e. forest-use, but most importantly fragmentation and edge proliferation, have been identified as major forces reorganizing plant assemblages at multiple spatial scales, including homogenization at regional level (Laurance et al. 2006, Tabarelli et al. 2008, Lôbo et al. 2011). These assemblages usually lack functional groups typical for old-growth floras while a small set of light-loving, disturbance adapted species tend to proliferate, resulting in a winner/loser species replacement (Girão et al. 2007, Santos et al. 2008, Tabarelli et al. 2012). For instance, large trees, ferns, aroids and calatheas represent emblematic plant groups experiencing decline and eventual extirpation across tropical edge-affected habitats (Laurance et al. 2000, Lima et al. 2015). For temperate forests, however, the picture is a little different. Concerning fragmentation effects, the empirical data basis is still sketchy. However, the small yet growing body of research points towards high biodiversity in forest edges with pronounced light-adaption (Flückiger et al. 2002, Honnay et al. 2002, Meiners & Pickett 1999), which has also been more frequently reported in non-scientific, non-English, and/or applied forestry literature (Coch 1995, Flückiger et al. 2002). Also, the conjunction of edge effects, high plant beta diversity, and resulting variety in radiation regime requirements agrees well with similar findings, where heterogeneous biotic responses in edges were attributed to differing edge structuring (Meiners & Pickett 1999, Marchand & Houle 2006). Concerning effects by silviculture, my results contribute to the current debate on the relationship between forest management and biodiversity. One position states that it needs silvicultural practices as disturbances to promote biodiversity, or otherwise monotone beech stands would develop (Hobi et al. 2015, Schulze et al. 2015). However, my findings lend support for the notion of beneficial effects on plant communities in unmanaged forests, as demonstrated by noticeably higher beta diversity (Paillet et al. 2010, Duguid & Ashton 2013).

From the variety of factors potentially responsible for the observed biotic patterns across (un)fragmented and (un)managed forest systems, I deem two main drivers most pivotal: anthropogenic alterations of microclimates, which in turn partly interact with silvicultural impacts.

Concerning forest edges, as described, plant communities showed functional trait signatures in radiation regime requirements similar to tropical communities, although patterns of biodiversity were completely reversed. This complex might be unravelable by referring to (i) a latitudinal shift in proportional species richness of edge vs. interior species, (ii) an enforced small scale of ecotone effects and (iii) silvicultural best practice regulations. (i) Although to my knowledge not documented in synthesis (and therefore a promising future research topic), there are individual indications for a shift from proportionally poor edge vs. interior species pools at low latitudes towards relatively richer pools in temperate biomes. This might be explicable with relationships between latitudinal richness gradients and functional traits related to light, temperature and moisture requirements/sensitivities (Hawkins et al. 2003, 2014). In tropical biomes species richness depends more on water availability, as energy (light and temperature) is a far less limiting factor (Hawkins et al. 2003), hence the described edge/interior diversity gradient (Peña-Claros 2003, Tabarelli et al. 2008). In temperate biomes, however, energy availability sustains biodiversity, as plants need to cope with seasonality and energy intake maximization (Whittaker et al. 2006, Shiono et al. 2015). Hence, closed, energy-limited interior forests sustain few shade-adapted plant species, whereas open habitats maintain high biodiversity (Bartish et al. 2010). (ii) Woody plant alpha diversity in forest edges might further benefit from completion of edge species (e.g. blackthorn, *Prunus spinosa*, also an indicator species in my study) immediately adjacent to the forest margin with forest species (e.g. beech, *Fagus sylvatica*, indicator species for managed forests) close behind. The transition zone between high forest and (agricultural) matrix is usually purposely kept very small to maximize usability of both habitats (Coch 1995, Bartsch & Röhrig 2016). Although the width varies, the first commercially used trees usually appear within the first ten meters from the edge (personal observation). This is well within the zone of noticeable edge effects (Matlack 1993, Harper et al. 2005) and in agreement with reported edge depths in Switzerland (observed average of 4.7 m vs. proposed ideal of 25m - 40 m, Krüsi et al. 1996). (iii) Best practice of forestry institutions aims at promotion of taxonomical richness and structural complexity. Less common tree species are spared, while late successional species are felled, which in turn promotes habitat openness and sets back succession (Coch 1995, Bartsch & Röhrig 2016). This also helps to explain the occurrence of many rare species in forest edges in my study. Furthermore, forestry-related structural edge heterogeneity might have benefited the found variety in radiation regimes and biotic response heterogeneity (Meiners & Pickett 1999, Marchand & Houle 2006).

Adopting this rationale on the structuring of edge communities, I would also expect diverse plant assemblages inhabiting small forest fragments, since fragment area usually correlates positively with presence of edge-affected habitats (Saunders et al. 1991, Fahrig 2003). Indeed, my edge and fragmentation indices both positively affected radiation regimes. Although small fragment communities witnessed a promotion of light adapted edge species, unlike forest edges in large forest tracts, they were not as much complemented by interior species (such as *F. sylvatica*), because they were physically apart from interior habitats (Laurance 2008). Thus, although fragments experienced warmest/ brightest microclimates, fragment assemblages were not as species rich and heterogeneous as edge floras.

Surprisingly, managed forest stands differed little from unmanaged forests in terms of species richness or diversity at plot level. However, I found striking differences in beta diversity and to a lesser degree in radiation regimes, with unmanaged forest communities being much more constrained/ homogenized, with slightly higher shade/cold tolerance. Missing differences might be attributable to young age of unmanaged control forests, which are still developing old-growth features. On the other hand, the found contrast concerning beta diversity and radiation regimes could possibly arise from silvicultural species selection in managed habitats, and from first indications of natural forest formation in unmanaged ones. The lack of primary forests as adequate controls is certainly one major bias this study shares with many others addressing management effects in Central Europe (Wirth et al. 2009a). The natural reserves chosen as substitutes have following shortcomings. Central European forests (including reserves) lack primal and substantial disturbance regimes that are associated with natural forests, e.g. megaherbivores (due to extinction) or forest fires (due to human control) (Bengtsson et al. 2000, Bauhus et al. 2009). Furthermore, forest reserves usually are relatively young (here 40 a), which often results in nonsignificant, or even reversed patterns (Blaser et al. 2013). For illustration, the full forest development cycle initiated in an individual gap takes 200-300 years (Brunet et al. 2010). Concerning species choice as driver of community homogenization and low radiation regime requirements, I want to call to attention that foresters primarily cultivate few profitable tree species, which intrinsically limits the available species pool (Kuennecke 2008, Schulze et al. 2015). Among 85 tree species in Central Europe, only 28 are commercially used (Schulze et al. 2015) and only 4 genera constitute 73% of Germany's forests (Bundeswaldinentur 2012). Similarly, in my study 93% of individuals in managed forests were either beech, oak, or hornbeam. Furthermore, many of these commercially valuable species display pronounced shade/cold tolerance, such as beech (*F. sylvatica*) and European larch (*L. decidua*), which also were indicator species for managed forests in this study. This selective practice acts like a filtering mechanism, hence heavily constricting community composition and contradicting notions that argue in favor of silviculture as biodiversity facilitator via anthropogenic disturbances (Schulze et al. 2015). Contrastingly to this anthropogenic homogenization, greater beta dispersion in unmanaged forests might be first indications of successful management release: localized natural disturbances (e.g. treefall gaps) open the habitat and individual stands develop according to site conditions (Bauhus et al. 2009). This is further supported by slightly higher variability in radiation regime requirements and by 23% lower dominance of highly shade tolerant beech in unmanaged forests. Additionally, I found further indications for natural forest formation: dead wood, a key feature of old-growth forests (Wirth et al. 2009b), was 88% higher in unmanaged stands (72.1 m^3/ha), compared with managed ones (38.3 m^3/ha, supplementary).

Several relevant implications emerge from my observed patterns and presumed processes, particularly for future research. For one, my findings reveal potentially cascading effects for other ecosystem components, such as alterations in energy fluxes and biodiversity turnover via changes in herbivory (e.g. caused by increased leaf palatability in edges) or predation rates (Wirth et al. 2008, Martinson & Fagan 2014). Further implications highlight the individuality of forest ecosystems when faced with fragmentation. This is best illustrated by completely reversed edge/interior biodiversity patterns, compared to e.g. tropical biomes. Concerning managed forests, my results contribute to the current debate on silviculture effects on forest biodiversity. Specifically, they challenge current views predicting unmanaged beech forests to form monotone and uniform beech stands of low light and biodiversity in the absence of silvicultural practices, which would mimic natural disturbances, and hence facilitate biodiversity (Bauhus et al. 2009, Boch et al. 2013, Schulze et al. 2015). In contrast, for my study system dominated by age class forestry (the most widespread forestry type in Europe, Schulze et al., 2015), I found clear signals for a release from community and trait constraints, further supporting the notion of higher biodiversity in unmanaged forests (Paillet et al. 2010, Duguid & Ashton 2013). Hence, the necessity arises to further investigate the effects of differing management regimes, with particular emphasis on the role played by accompanying disturbance dynamics. Furthermore, as long as forest reserves remain relatively young, quantitative indices should earn preference over categorical classifications (Schall & Ammer 2013). Applied to biodiversity conservation and forest management, my uncovered patterns suggest that certain human disturbances, particularly establishment of forest edges, increment the conservation value of human modified landscapes as complementary habitats, all the more while near-natural forests are still developing.

In synthesis, this paper contributes to the scarcely studied field of forest fragmentation in Central Europe and its interplay with forest management. First, I exhibit the role of forest edges and small fragments as anthropogenically coined biodiversity reservoir for woody plants in a cultural landscape. These contrasts to many studies from other biomes are explicable by biogeographical effects on natural species pools and large-scale interferences by silviculture. Hence, forest fragmentation cannot be easily generalized across biomes. Cessation of forest management led to increased beta diversity and variability in radiation regime requirements. The interplay of forest fragmentation and management demonstrates the unique position of European beech forests, highlights the importance of fragmented habitats for biodiversity (at least in the current cultural landscape), and supports published insights that management release leads to increased biodiversity. Yet, further studies are needed, as forest fragmentation in Central Europe is far from being fully understood and as management effects on biodiversity are still intensively debated.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY

Data basis for calculation of integrative indices

Table S1: Breakdown of used integrative indices into their ecological components and representative variables and how these were measured. R^2 and *p*-values result from Spearman rank correlations of each respective variable with the first PCA axis generated by all variables of an individual index.

integrative index	ecological component	measured variable	R^2	p	measurement
fragmentation index	fragment area and shape	area (ha)	0.99	< 0.001***	ESRI Arc GIS 10.1 + extension *vLATE*
		core area (ha)	0.99	< 0.001***	ESRI Arc GIS 10.1 + extension *vLATE*
		perimeter/area ratio (m^{-1})	0.89	< 0.001***	ESRI Arc GIS 10.1 + extension *vLATE*
		SHAPE index	0.98	< 0.001***	ESRI Arc GIS 10.1 + extension *vLATE*
	fragment integration	proximity index	0.41	< 0.001***	ESRI Arc GIS 10.1 + extension *vLATE*
edge index	edge influence	distance to forest margin	0.96	< 0.001***	ESRI Arc GIS 10.1 + extension *vLATE*
		forest buffer	0.79	< 0.001***	ESRI Arc GIS 10.1 + extension *vLATE*
management index	past logging events	number of stumps per 0.1 ha	0.80	< 0.001***	census within a 20 m x 50 m plot
	management type	state foresters; private; natural forest reserve	0.53	< 0.001***	classification after personal communication with forestry departments, the reasoning being that management intensity decreases from state forests over privately owned forests to unmanaged reserves.
	coarse woody debris (CWD)	lying logs (m^3/ha)	0.24	< 0.001***	line intersect method following Marshall et al. (2000)‡ using 3 transects à 100 m leaving the plot and censusing all lying CWD pieces > 10 cm.
		standing snags (m^3/ha)	0.56	< 0.001***	volume of all standing dead tree individuals (dbh > 10 cm) within the 20 m x 50 m plot was calculated and added assuming an idealized shape of a frustum of a cone.
		stumps (m^3/ha)	0.83	< 0.001***	volume of all stumps (diameter > 10 cm) within the 20 m x 50 m plot was calculated and added assuming an idealized shape of a frustum of a cone.
	unextracted living biomass	basal area (m^2/0.1 ha)	0.15	< 0.01**	basal area of each tree/shrub individual (dbh > 1 cm) within the 20 m x 50 m plot was summed.
radiation regime index	light adaption	plotwise indicator value for light	0.72	< 0.001***	see Ellenberg & Leuschner for documentation of the values and the method section of this paper for index calculation
	temperature adaption	plotwise indicator value for temperature	0.80	< 0.001***	
	moisture adaption	plotwise indicator value for moisture	0.12	< 0.01**	

‡ Marshall PL, Davis G, & LeMay VM 2000. Using line intersect sampling for coarse woody debris. Forest Research Technical Report. 37 pp.

Habitat-wise comparison of coarse woody debris (CWD)

Total amounts of CWD (standing and lying CWD, as well as stump volume, **Table S1**) were compared between unmanaged and managed interior forests employing a t-test. CWD in unmanaged forests was 88% higher (72.1 m^3/ha), than in managed stands (38.3 m^3/ha, t = 2.6734, df = 25.947, $p < 0.05$*).

Chapter 3

Edge effects and trophic specialization facilitate diversity of insect herbivores in fragmented temperate forest landscapes

White satin moth (*Leucoma salicis*, *Lymantriidae*), a polyphagous herbivore, with a preference for aspen, *Populus* spp. and willow, *Salix* spp. (here on beech, *Fagus sylvatica*). This specimen was spared from being analyzed, as it foraged just outside the study plot.

INTRODUCTION

Evidently, across terrestrial ecosystems, forest fragmentation is among the most severe forms of anthropogenic disturbance, affecting biodiversity, species interactions, ecosystem functions and services (Saunders et al. 1991, da Silva & Tabarelli 2000, Laurance & Lovejoy 2002). Particular attention should be paid as to how forest fragmentation affects insect herbivores: They are extremely species rich, harbor the bulk of consumer biomass, and are further fundamental functional determinants of structure and throughput of energetic pathways, due to their high variability in host selectivity (Price 2002, Novotny et al. 2006, Valladares et al. 2012). Although our understanding is far from being complete, there are several evidences that forest fragmentation affects insect herbivores in multiple ways, particularly directly via changes in abiotic conditions, and indirectly via bottom-up effects (Wirth et al. 2008, Valladares et al. 2012). Insect herbivores (as ectotherms) are likely to benefit from higher energy inputs from forest edge proliferation via increased metabolic rates and decreased mortality, in turn increasing herbivory rates (Matlack 1993, Emmerson et al. 2005, Wirth et al. 2008, Lindner et al. 2010, Traill et al. 2010). Furthermore, edge microclimates are known to typically simplify plant communities in their diversity, composition, and functional traits towards pioneer assemblages, with pivotal importance for their herbivores (Laurance et al. 2006, Tabarelli et al. 2008). For one, such pioneer species offer leaf material of higher palatability, which increases herbivory, particularly by generalist herbivores (Urbas et al. 2007, Wirth et al. 2007). Furthermore, impoverishment in plant diversity and community composition alter/constrain host availability, which affects specialized herbivores the most (Steffan-Dewenter & Tscharntke 2000, Cagnolo et al. 2009), in turn promoting generalist herbivores to '*winner*' species in this scenario (Steffan-Dewenter & Tscharntke 2000, Wirth et al. 2008). These shifts in fundamental niche breadth might have potentially cascading effects on food-web stability and hence ecosystem functionality, pointing towards the importance of bottom-up effects on herbivores during forest fragmentation (Blüthgen & Klein 2011, Valladares et al. 2012).

For temperate ecosystems, there are hardly any insights on how forest fragmentation affects diversity, community composition, or trophic specialization of insect herbivores, although the existing evidence points towards partly different responses (van Halder et al. 2010). For this I have to address microclimate, as well as vegetation patterns and resulting host availability. First, there is evidence that herbivores strongly benefit from lenient edge conditions concerning herbivore abundances, diversity and consumption rates, as edges represent a release from energy-constraining interior conditions (MacGarvin et al. 1986, Lavallée et al. 1996, Cappuccino & Martin 1997, van Halder et al. 2010). Second, woody plant floras likewise show increased alpha and beta diversity in forest edges through large natural pools of edge species and silvicultural facilitation, while interior floras are biologically homogenized by foresters (Krüsi et al. 1996, Honnay et al. 2002, Bartsch & Röhrig 2016). Due to the high average dependence of insect herbivores (particularly specialists) on host plant availability, edge habitats are likely to similarly increase herbivore diversity, especially if herbivore assemblages are specialized (Haddad et al. 2001, 2011, Lewinsohn & Roslin 2008). High average trophic specialization in fragmented forest habitats is indeed plausible, as with increasing plant richness specialist herbivores accumulate more species in the community than generalists (Novotny et al. 2010), presumably due to decreasing competitive pressure (Haddad et al. 2001). Conversely, commercial tree species dominating the floristically poor forest interior (e.g. beech, *Fagus sylvatica*) naturally associate with few specialist herbivores (Sprick & Floren 2008, Schulze et al. 2015). Furthermore, fragmentation, trophic niche differentiation of herbivores, as well as host plant composition are likely to determine herbivore community composition (Crist et al. 2006, Novotny et al. 2010).

Hence, in summary, I expect to see opposed patterns of diverse, specialized, and variable herbivore communities in fragmentation affected forest habitats versus impoverished, generalist, and simplified communities in the forest interior. The assumed key drivers are abiotic and bottom-up effects. To answer this, I sampled live herbivores in 36 study sites in two sampling campaigns across a hyperfragmented forest landscape (1,500 km², > 2,900 fragments) in SW Germany, totaling > 200 h of sampling and used integrative indices for holistic quantification of fragmentation and edge effects.

METHODS

Study Landscape – The Northern Palatinate highlands are a low, undulating mountain range (250 – 687 m asl) of Permian origin covering an area of 1,556.4 km² in SW Germany. It is characterized by a temperate Central European climate under oceanic influence (MAP: 800 mm; MAT: 9.4°C, 1970-2010, Deutscher Wetterdienst 2013). Studied forests are deciduous, broad-leaved woodlands, phytosociologically classified as *Carpino-Fagetalia* mixed forests with varying transitional degrees of *Fagion* and *Carpinion betuli* stands. Extensive deforestation in the Middle Ages occurred mainly in sand and siltstone-dominated valleys, while the agriculturally less valuable igneous hilltops remained forested. This has led to a landscape of hyper-fragmented forests, embedded in a matrix of cultivated fields, pastures and meadow orchards. Forest cover of the selected area (32%) of this landscape (1,010 km², 49° 36’ N and 7° 44’ E) is representative for Germany (31%, MUF 2002). Despite its high fragmentation degree, with over 2,900 forest fragments ranging from 0.1 to 5616 ha (ca. 80% of them < 10 ha) and a total edge length of over 5,700 km, the region still harbours large forest tracts exceeding 1,000 ha.

Study Sites – Permanent plots were established in 2008, which were selected for three habitat types that reflect fragmentation-induced and continuous forest conditions: (i) small forest fragments: ranging between 2.2 and 145.1 ha and entirely surrounded by matrix, reflecting effects of habitat loss and patch isolation with varying degrees of edge influence; (ii) forest edges: peripheral areas within 50 m of the border of large forest tracts (continuous control forests, the three largest forest tracts in the study region, 1,049, 3,512 and 5,616 ha), selected to address edge effects; (iii) forest interior: core areas of control forests beyond 100 m of the border, without detectable edge influence. For each habitat, twelve plots (20 x 50 m; 0.1 ha) were randomly chosen across the study region. This design reflects the available landscape configuration, that is, a severely fragmented region typical for Germany (Forest Europe 2011), including three large forest stands that could be adopted as control areas following similar studies (Girão et al. 2007, Valladares et al. 2012). Inter-plot distance ranged from 0.3 to 35.4 km with 13.9 ± 7.6 km (mean ± SD). All woody plant species > 1.3 m height were identified. Shannon diversity of woody plants significantly increased with increasing edge influence (ANOVA, $F_{(33,2)} = 13.21$, $p < 0.001$***), being highest in forest edges (1.52 ± 0.40, mean ± sd), followed by small forest fragments (0.93 ± 0.52) and forest interiors (0.56 ± 0.46).

Insect herbivores were sampled alive in the understory stratum (1.3 m – 2 m) of the plots during two field campaigns (May to August 2010 and August to September 2010). Foliage of each woody plant individual within reach was beaten, regardless of age class, over a funnel-shaped trap (supplementary, **Figure S1**). Sampling intensity totalled 207 h of beating and 1,353 woody plant individuals. Herbivore verification and separation from transient insect species was achieved by using no-choice feeding-assays and analyzing published host plant records of identified species. Insects were assigned to morphospecies and later identified to species level whenever possible (56%) using standard keys or experts (**Table S2**). Caterpillars were reared to adults, if possible, and then identified. Voucher specimens were deposited at the Natural Museum of Basel (*Psylloidea*) and at the department of Plant Ecology and Systematics at the University of Kaiserslautern (all other taxa).

Sampling adequacy, as well as habitat effects on herbivore species richness were evaluated using species area curves (100 iterations), as well as estimations of percental curve saturation following Moreno & Halffter (2000).

Index Generation – Indices for fragmentation and edge effects (fragmentation-, and edge-index) were created following Martorell and Peters (2005) and as used by Ribeiro et al. (2016): first, all variables related to a given index (see below) were normalized and then entered in a principal component analysis (PCA). The scores of plots on the first PCA axis are then rescaled to values ranging from 0 (low fragmentation/edge effects) to 100 (high fragmentation/edge effects), hence generating the index in question.

Fragmentation index

Metrics used to create the fragmentation index span those related to habitat loss (fragment area (ha), core area (ha), perimeter/area ratio (m^{-1}) and shape index), as well as patch isolation (proximity index). Core area refers to the remaining area of core forest within a forest patch assuming a pertinent edge buffer of 100 m (Broadbent et al. 2008). The shape index measures a fragment's deviation from a perfect circle (highest proportion of core forest to edge zone). The proximity index contextualizes a forest fragment in its surrounding neighbourhood (here 1,000 m buffer) by both regarding area and distance of its surrounding forest patches and is hence a measure for patch isolation (Gustafson & Parker 1994, Lang & Blaschke 2007). High values indicate high patch integration. Axis 1 of the PCA explained 71% of the variation of these variables and was significantly correlated with all of them (mean $R^2 = 0.85$ and mean $p < 0.001$***).

Edge index

The edge index incorporates the distance of a plot to the nearest forest edge (m), as well as the relative forest cover in a 100 m buffer around it (%). Axis 1 of the PCA explained 79% of the variation of these variables and was significantly correlated with all of them (mean $R^2 = 0.89$ and mean $p < 0.001$***).

Specialization index

Similarly to the calculation of site-specific biological indicator values (Meyer et al. 2013), site-specific trophic specialization of the herbivore community was calculated by first categorizing each herbivore species *i* into four degrees of trophic specialization Sd_i using published host plant ranges: 1 - zoophytophagous, 2 - polyphagous (feeding on plants of various families), 3 - oligophagous (feeding only within one plant family), and 4 - monophagous (feeding only within one plant genus) (**Table S2**). Specialization degrees 1 to 4 were then multiplied with the dominance values of each species in each plot (D_i). Summarizing all products within a plot then gives a plot-specific specialization value for the community (*SV*, **Equation 1**).

Equation 1 $SV = \sum_{i=1}^{n} D_i\, Sd_i$

Rescaling the values from 0 (lowest specialization degree) to 100 (highest specialization) gives the specialization index. Herbivore species of unclear specialization degree (e.g. morphospecies) were left out of the calculation, i.e. 52 taxa (38.5%) or 168 individuals (15.9%) of the data set, respectively. For three sites in one sampling campaign (4% of all plots) index calculation was impossible due to no remaining herbivores with known feeding mode. They were assigned the median index value (25).

Analysis Of Insect Herbivore Diversity – To access how forest fragmentation, average trophic niche breadth, and bottom-up factors affect herbivore diversity, I chose the fragmentation, edge, and specialization indices, as well as vegetation diversity (Shannon index) as explanatory variables. As herbivores were collected twice within each plot, namely in each of the two sampling campaigns, herbivore samples were not independent from each other. Hence, effects of aforementioned factors on herbivore diversity were analyzed by employing linear mixed models with *sampling campaign* as a random factor (package nlme, Pinheiro

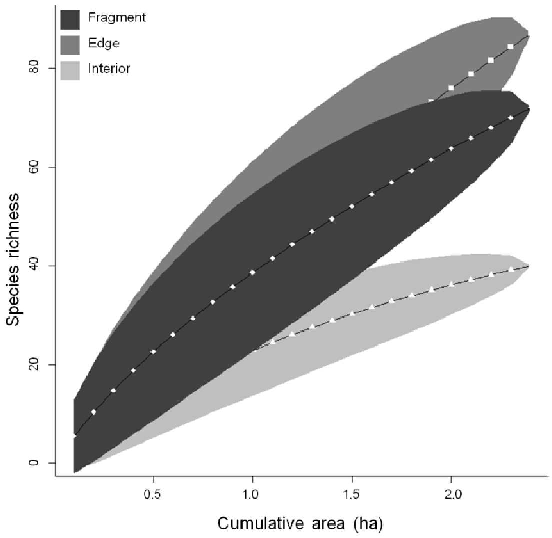

Figure 1: Herbivore species richness across three forest habitats differently affected by forest fragmentation: forest edges, small fragments, and interior of large control forests. Species richness is plotted against cumulative plot area (0.1 ha). White symbols and black line: running mean of 100 iterations. Grey polygons: 95th percentile.

et al. 2013). Variable selection and model optimization was achieved in a backwards stepwise fashion by creating the full model, followed by dropping each variable that did not significantly impair goodness of fit. (Marginal) R^2 values for the fixed effects were calculated following Nakagawa and Schielzeth (2013).

Parameters Structuring Herbivore Community Composition – To analogously assess if fragmentation, edge, and specialization index, as well as herbivore diversity and vegetation diversity are structuring components of herbivore community composition, they were included as explanatory variables in a stepwise variable selection process (function *ordistep*, *vegan* package, AIC-based, maximum of 1,000 iteration steps), in an analysis of redundancy (RDA, Hellinger transformed abundance data, with Euclidian distances, Legendre & Legendre 1998). *Sampling campaign* was partialled out before analysis as a conditional variable. Significance testing of the whole model and marginal terms, as well as computation of (adjusted) R^2 was performed using the *anova.cca* and *RsquareAdj.cca* function (*vegan* package, Legendre et al. 2011, Oksanen et al. 2015). R^2 of marginal terms were obtained by variance partitioning using the *varpart* function (*vegan* package).

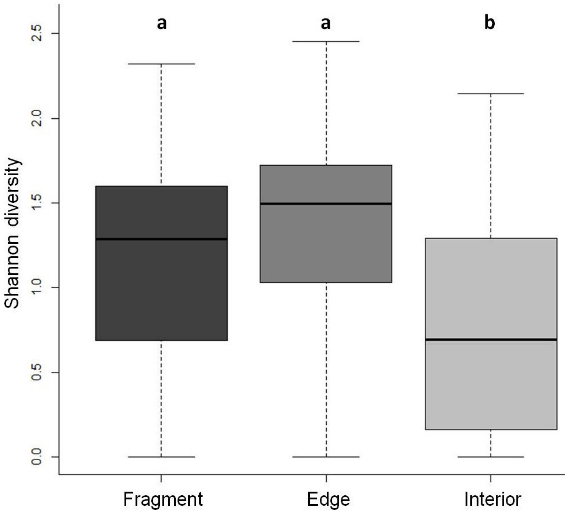

Figure 2: Effects of forest fragmentation on Shannon diversity of insect herbivores in the Northern Palatinate highlands. Linear mixed models with Shannon diversity as response variable, habitat as fixed factor, and sampling campaign as random factor. F test of the fixed effect: $F = 5.87_{(2,68)}$, $p < 0.01^{**}$. $R^2 = 0.14$ (Nakagawa & Schielzeth 2013). Post-hoc: simultaneous tests for general linear hypotheses, Tukey contrasts. Correction of p values: single-step method.

Data analysis was entirely performed in the programming language *R* (R Core Team 2015).

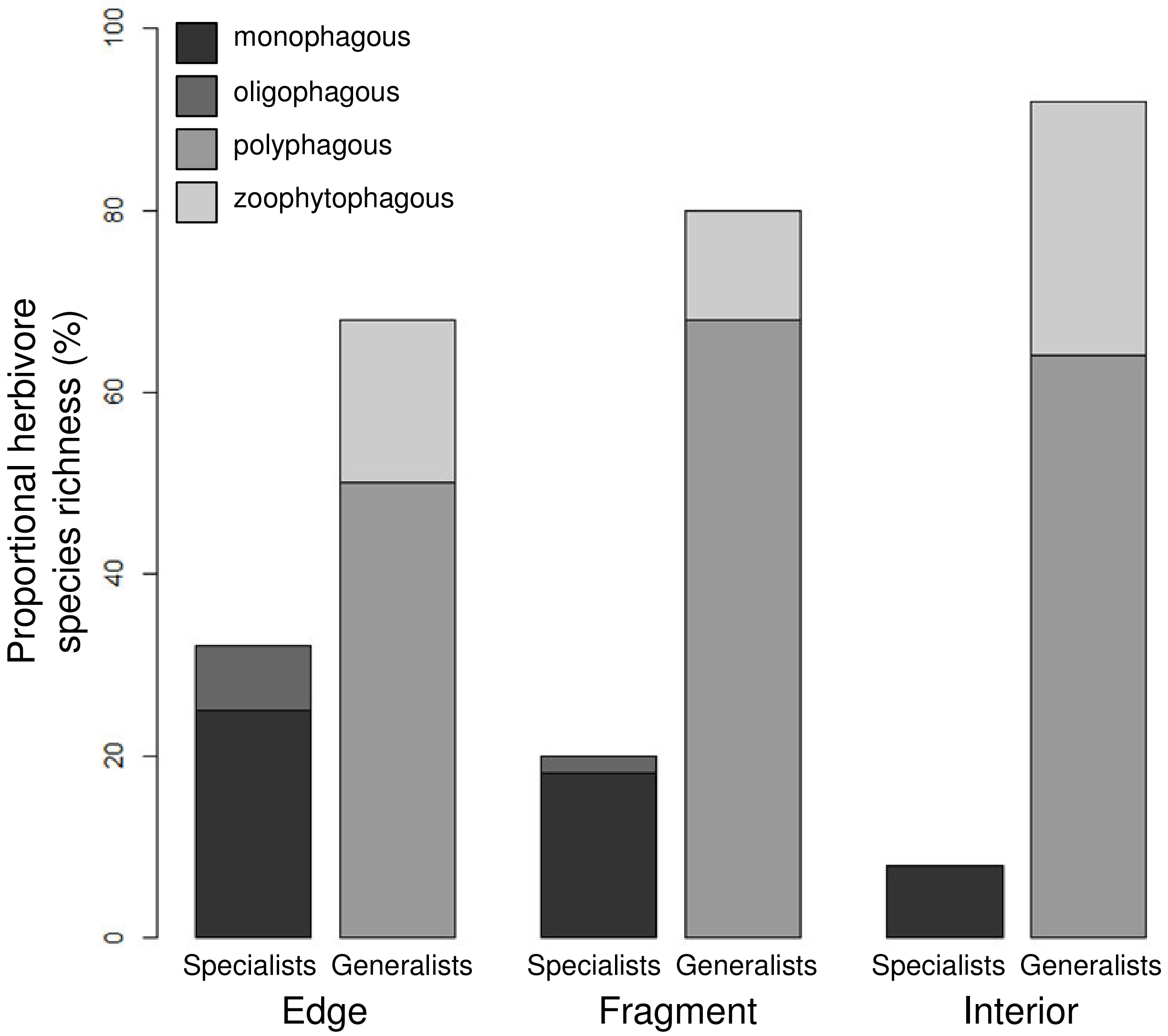

Figure 3: Fragmentation- and edge effects on the fundamental trophic niche breadth of insect herbivores in the Northern Palatinate highlands. Proportional species richness of different degrees of trophic specialization (mono-, oligo-, poly-, and zoophytophagous), classified into specialists and generalists, is depicted across three forest habitats: forest edges, small forest fragments, and interior of large control forests. Only taxa with verifiable niche breadth were considered (n = 82, 61% of all species).

RESULTS

I found a total of 1058 herbivores from 134 species and 28 families. As typical for entomological field studies, sampling intensity captured only a fraction of the total insect community. Assuming asymptotic behavior of the species-area curve, the herbivore fauna of forest edges, small fragments and interior forests was represented by 34%, 41%, and 47% of expected species (257, 175, and 86). Edge effects more than doubled herbivore species richness, as richness in forest edges was 118% higher than in interior forests and 21% higher than in small forest fragments (**Figure 1**).

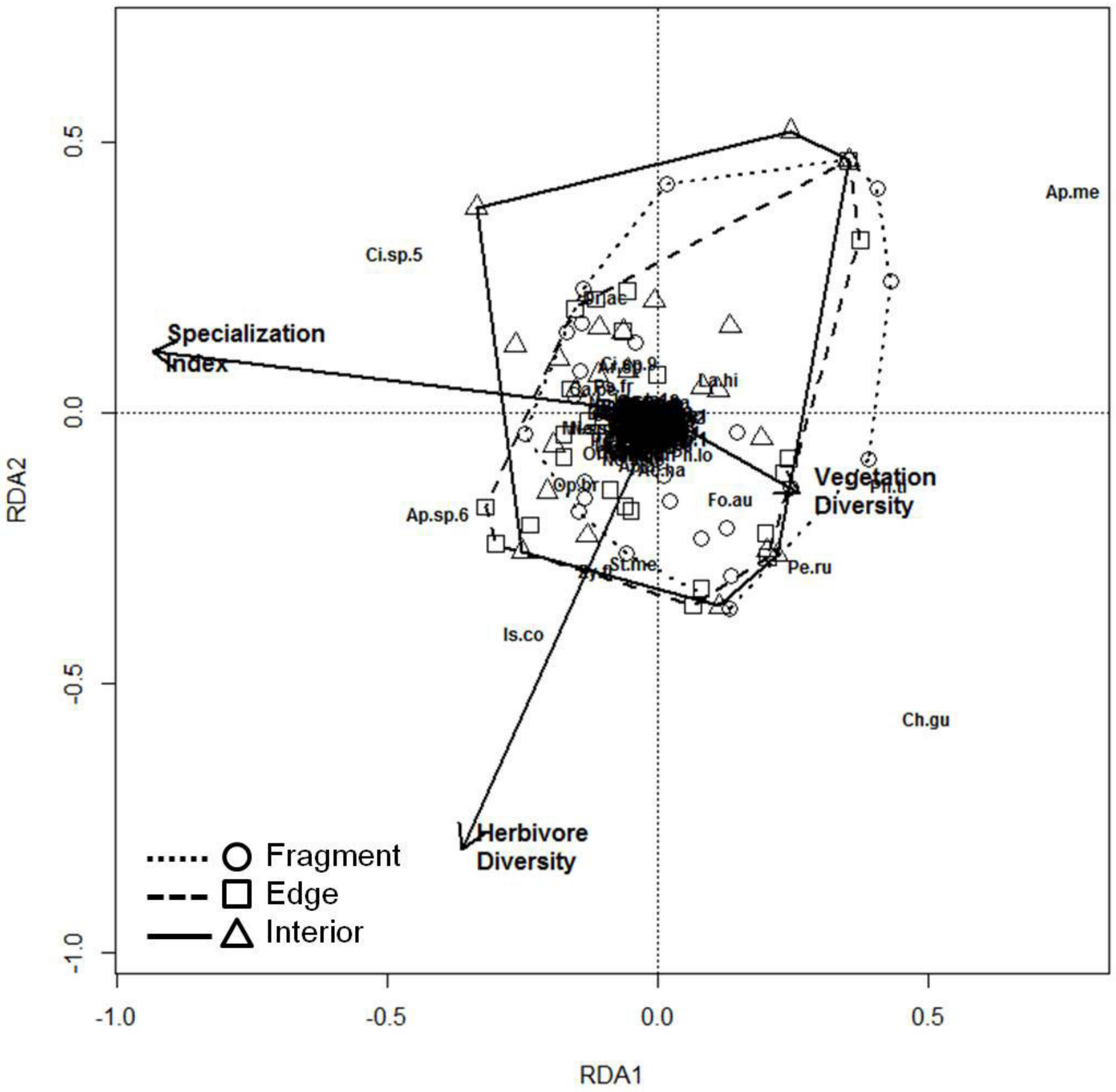

Figure 4: Effects of forest fragmentation, average trophic niche breadth, herbivore diversity, and bottom-up effects on community composition of insect herbivores in the Northern Palatinate highlands. Trophic niche breadth as measured by the specialization index and bottom-up effects represented by vegetation diversity of host plants. Symbols and lines indicate study plots, habitat affiliation and maximal community spread of a habitat in the RDA space, respectively. Four-letter codes abbreviate herbivore taxa. Length and orientation of arrows of explanatory variables represent relative explanatory power, as well as direction of community change along the respective variable. For RDA statistics, see **Table 2**.

Similarly, forest fragmentation, particularly edge effects, positively affected Shannon diversity of insect herbivores. In forest edges (1.4 ± 0.6) and in small forest fragments (1.2 ± 0.6) herbivore diversity was significantly higher (71% and 46%, respectively) than in the forest interior (0.8 ± 0.6) (**Figure 2**). Across forest habitats herbivore communities expressed high generality,

Table 1: Effects of edge intensity and degree of trophic specialization of herbivores on herbivore diversity in the Northern Palatinate highlands. Linear mixed models (df = 68) with sampling campaign as random factor. R^2 calculation following Nakagawa and Schielzeth (2013).

Fixed effect	Slope ± SE	p	R^2
Edge-index	0.011 ± 0.003	< 0.001***	0.31
Specialization-index	0.010 ± 0.003	< 0.001***	

SE: standard error

with 71% of herbivore taxa being either polyphagous or zoophytophagous. While the specialization index did not relate to either edge or fragmentation index (GLMM, not shown), there still were verifiable edge effects on trophic specialization degree amongst herbivores, with a fourfold increase in proportional species richness of herbivore specialists (being mono- and oligophagous) from interior forests (8%), over fragments (20%), to forest edges (32%) (Fisher's exact test, $p < 0.001$***, **Figure 3**).

Similarly, across the landscape, and regardless of habitat, intensity of edge effects as well as average degree of trophic specialization increased herbivore diversity ($R^2 = 0.31$, **Table 1**).

While the fragmentation index and vegetation diversity were excluded as explanatory variables in the variable selection process, there still were indications for a positive relationship between vegetation and herbivore diversity when only considering the first sampling campaign (linear regression, F test: $F = 10.67_{(1,34)}$, $p < 0.01$**, $R^2 = 0.24$). Vegetation and herbivore diversity, as well as the specialization index were (highly) significant, yet minor factors structuring herbivore communities (analysis of redundancy, $p < 0,001$***, $R^2 = 0.10$, **Table 2**). Forest fragmentation did not affect herbivore community composition, as both the fragmentation and edge index were excluded in the model selection process. This is further demonstrated by absence of apparent community homogenization or segregation across habitats, implying high community congruence (**Figure 4**).

DISCUSSION

In this study I analyzed how insect herbivore assemblages are affected by forest fragmentation and to what extent bottom-up effects and trophic specialization play a role. As expected, I saw a general edge/interior contrast, with edge effects increasing herbivore richness, diversity, and trophic specialization. Additionally, herbivore diversity was positively affected by trophic specialization and bottom-up effects (vegetation diversity). While neither fragment isolation nor edge effects were structuring components of herbivore community composition, there were significant, yet marginal effects from trophic specialization, vegetation diversity, as well as herbivore diversity. These results are partly in line with the existent literature, with some noticeable deviation, underlining the peculiar role of herbivores in fragmented Central European temperate forests. While there is extensive literature on effects of fragmentation on many taxonomic groups and ecological processes (including herbivory), insights into diversity and functional attributes of herbivore communities are limited (Laurance & Lovejoy 2002, Tscharntke et al. 2002, Wirth et al. 2008). However,

Table 2: Community composition of insect herbivores explained by average trophic niche breadth, herbivore diversity, and bottom-up effects. Trophic niche breadth as measured by the specialization index and bottom-up effects represented by Shannon diversity of woody host plants. Analysis of redundancy (RDA), n = 72. Factor *sampling campaign* was partialled out from the analysis as conditional variable.

Structuring component	$R^2_{marginal}$	$p_{marginal}$	R^2_{global}	p_{global}
specialization index	0.05	< 0.001***		
herbivore diversity	0.04	< 0.01**	0.10	< 0.001***
vegetation diversity	0.02	< 0.01 **		

R^2_{global}, p_{global}: R^2 and p-value of the whole model. $R^2_{marginal}$, $p_{marginal}$: R^2 and p-value of the marginal terms only.

there is evidence for increased herbivore abundance, richness, and diversity in fragmented forest habitats (MacGarvin et al. 1986, Lavallée et al. 1996, Cappuccino & Martin 1997, Barbosa et al. 2005). Furthermore, fragmentation-caused facilitation of specific *'winner'* species naturally promotes their corresponding functional traits, most notably trophic generality (Barbosa et al. 2005, Wirth et al. 2007, Meyer et al. 2009). This pattern is entirely opposed to higher specialization in forest edges, as documented here. However, overall generality was high (71% of all species), corroborating the notion of low host selectivity in temperate systems (Dyer et al. 2007). Nevertheless, this latitudinal pattern has been challenged in the past towards equally low host specifity at low latitudes and higher relevance of herbivore guild affiliation (Fiedler 1998, Novotny et al. 2002, 2006). High compositional congruence of herbivore communities across habitats, found in this study, contradicts both the generally reported pattern of biotic homogenization through forest fragmentation for various taxonomic groups and biomes (Laurance & Lovejoy 2002, Tabarelli et al. 2012), as well as existent evidence for compositional segregation of edge vs. interior herbivore communities (Barbosa et al. 2005).

When considering underlying mechanistic relationships, forest edges were observed to be the dominating factor of herbivore assemblages. To explain this, three partly interrelated mechanistic aspects are plausible. Arguably, edge effects acted directly/abiotically (via altered microclimates and habitat structure), and indirectly via edge responses of plant assemblages and subsequent alterations in herbivore specialization.

Warmer, sunnier microclimates in forest edges and small fragments might benefit ectothermic herbivores via longer activity periods, causing higher developmental and metabolic rates and lower mortality (Cappuccino & Martin 1997, Lindner et al. 2010, Tuff et al. 2016). Furthermore, warm and light edge conditions might increase palatability of plant tissues and saps via higher metabolite concentrations. Hence, several herbivore guilds may prefer exposed forest habitats, e.g. leaf chewers or phloem suckers (e.g. *Sternorrhyncha* and most *Auchenorrhyncha*) (Meyer et al. 2006, Wirth et al. 2008, Gamper et al. 2011). Following this notion, there was indeed evidence for edge preferences of adult leaf chewers and phloem suckers (linear mixed models, **Table S1**). Forest edges are inherently open habitats (as interfaces between forest and matrix) and form noticeably rich vegetation structures in temperate forests (Coch 1995, Duelli et al. 2002). Hence, they are prone to drastically alter dispersal dynamics (Boer 1990, Roland 1993). For instance, light, passive fliers (aeroplancton, e.g. many *Sternorrhyncha*) could benefit from wind-driven dispersal from edge to edge across the landscape, which enhances metapopulation stability (Boer 1990, Weidel 2008). In turn, edge-related facilitation of particular guilds and taxonomic groups could help to explain increased herbivore specialization, as certain guilds (e.g. phloem suckers) are noticeably host-specific (Dixon 1985). High structural complexity in forest edges might further benefit herbivores via high microhabitat availability/heterogeneity, as well as escape options from predators (Price et al. 1980, Coch 1995, Gols et al. 2005) and is caused by both silvicultural practices and high plant diversity (Coch 1995, Magura 2002, Honnay et al. 2002).

Plant diversity is in turn well known to increase herbivore diversity by their utilization of emerging trophic niches (Haddad et al. 2001, 2011, Lewinsohn & Roslin 2008). This is particularly true for specialized herbivores, as they are more likely to feed exclusively on one or few host species. This in turn facilitates trophic niche differentiation through decreasing niche overlap and hence reduces competitive pressure on specialist species (Lewinsohn & Roslin 2008). As both factors, herbivore specialization and (to a lesser degree) host plant diversity, were observed to be positively related to edge effect intensity, it can be assumed that the two act synergistically in increasing herbivore diversity in forest edges. Opposed to this, interior forests were significantly composed of species-poor plant assemblages with high dominance of commercially used tree species (supplementary). The most dominant, *Fagus sylvatica*, houses few specialist herbivores (e.g. only one weevil species, *Orchestes fagi*, *Curculionidae*) (Böhme 2001, Sprick & Floren 2008), hence further increasing the edge/interior contrast in herbivore diversity and specialization.

Interestingly, no direct influence of forest fragmentation on herbivore community composition was found, but instead of plant diversity, herbivore diversity, and specialization. This is surprising, as edges, or warmer temperatures in general, have been shown to drive herbivore community composition, typically towards homogenization (Barbosa et al. 2005, de Sassi et al. 2012). It therefore seems that herbivore species are much more dependent on biotic site conditions, as detailed above, and less on habitat identity.

These results and the assumed underlying patterns paint a fairly consistent picture of diverse and specialized herbivore assemblages in rich edge floras versus impoverished, generalist assemblages in poor, silviculturally-used interior floras, noticeably driven by the associated biotic factors. These findings challenge the familiar paradigm of biotic homogenization during forest fragmentation (Saunders et al. 1991, da Silva & Tabarelli 2000) and emphasize the need to individually characterize an ecosystem's distinct response to fragmentation. In the case of fragmented temperate forests, where the interior is extensively used and where open habitats pose a release from constraining energy limitations, fragmentation-affected habitats might act as biodiversity reservoirs in the cultural landscape. Emerging management implications for conservation and ecosystem functioning should take these conclusions into consideration. Concrete proposals could include facilitation of habitat openness and plant richness, e.g. by establishment of species mixtures in interior forests.

In synthesis, I demonstrated that forest fragmentation (particularly edge effects) drives diversity of temperate insect herbivores. Likewise, bottom-up effects and trophic specialization also distinctively participate in shaping herbivore diversity and community composition. As these biotic factors, in turn, are also affected by fragmentation, I can hypothesize that in temperate biomes forest fragmentation is the main driver of this interdependent system of forest biota and their interactions. A further pivotal aspect is that this study further contributes to the increasing evidence of positive influences of forest fragmentation in temperate systems. Across biomes it has been the general consensus that fragmentation leads to biotic homogenization (Saunders et al. 1991, da Silva & Tabarelli 2000). However, in the reality of extensively managed cultural landscapes, ecosystem margins (with comparatively lenient microclimates) may serve as biodiversity reservoirs, which potentially benefit from proactive management for conservation and ecosystem functionality (Duelli et al. 2002, Honnay et al. 2002).

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SUPPLEMENTARY

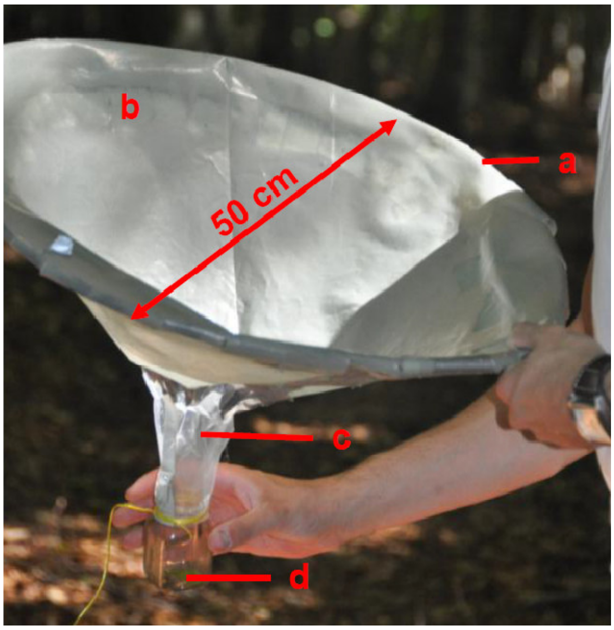

Figure S1: Design/dimensions of the sampling funnel used to collect insects via the foliage beating method. a Outer metal ring of 50 cm in diameter, covered with **b** a robust plastic foil. **c** Attached PE foil that leads to **d** the sampling jar.

Insect Sampling And Herbivore Verification – Knocked off insects were collected in a sample-jar attached to the bottom of a plastic-funnel attached to a metal ring of 50 cm in diameter with a slope of about 30° via a tube of PE-foil of 15 cm (**Figure S1**). Sampled vegetation per plant individual varied between half and full cover of the funnel.

Individually collected insects with chewing mouth parts were tested in no-choice feeding-assays to verify active herbivory. Insects were kept in an arena (50 ml PP tubes) with 10 – 20 mm² pieces of leaf material conspecific to the sampled host plant on the bottom and 2 cm² of moistened paper clips on the top to provide humidity. Leaf pieces were screened for chewing traces (positive interaction) 24 – 48 h after start. Insects with negative no-choice assays were excluded. As insects with sucking mouth parts (e.g. cicadas) usually do not show clear feeding traces in plant material, they were identified to species level and verified against whether published records of host plants included the sampled plant species. Wingless insects that belonged to exclusively herbivorous taxa (e.g. cicada nymphs) were not submitted to no-choice feeding-assays, but instead assigned to morphospecies levels and kept in the analysis, as they were most probably not tourists on the particular host plant. Caterpillars were reared to adults (in 50 ml PP tubes with moisture paper clips and plenty of source plant material), if possible, and then identified. Where final identification was impossible, morphospecies were assigned. Reared butterflies were conserved by pinning, about half of the caterpillars were frozen, and all other insects stored in 70% Ethanol. Using published host plant ranges, herbivores were classified into two levels of trophic specialization: specialists (not feeding on more than one plant family) and generalists (feeding on several plant families or being zoophytophagous) (**Table S2**).

Edge Effects On Beech Dominance – Decreasing dominance of beech (*Fagus sylvatica*) with increasing edge effect intensity was demonstrated via Spearman rank correlation of beech dominance and the edge index (see method section of main manuscript for index generation) (S = 10536, $p < 0.05$*, r = -0.36).

Habitat Preference Of Trophic Guilds – To assess edge affinity of particular trophic guilds, herbivores were classified into guilds according to feeding mode and life stage as follows:

Adult leaf chewers: mature folivorous herbivores (all beetles, *Coleoptera*), which are obligatory herbivores (no zoophytophagous species). **Larval leaf chewers:** immature folivorous herbivores, consisting of butterflies (*Lepidoptera*) and sawflies (*Symphyta*). **Phloem suckers:** herbivores feeding on phloem sap, including all *Sternorrhyncha* and *Auchenorrhyncha*. **True bugs:** All *Heteroptera* share the feature of feeding via their rostrum, identically to other members of the *Hemiptera*. But in contrast to phloem feeders, true bugs exhibit variety and diversity in food sources and are hence pooled in this guild. **Omnivore chewers:** similarly, this guild encompasses the same general feeding mode (chewing), but differs from the above guilds by not being obligatory herbivorous. Omnivores feed opportunistically on plant tissues, as well as prey and are hence subsumed in this guild. They consist of click beetles (*Elateridae*) and Earwigs (*Dermaptera*). Guild responses to edge effect intensity were entered into linear mixed models, with species diversity of a guild as a response variable, edge index as fixed factor (see method section of main manuscript), and sampling campaign as random factor (**Table S1**).

Table S1: Edge affinity of different trophic guilds of herbivorous insects in fragmented forests in the Northern Palatinate highlands. Linear mixed models (df = 69), with species diversity of guilds as response variable, edge index as fixed factor, and sampling campaign as random factor.

Guild-specific species diversity	Slope ± SE	p	R^2
Adult chewers	0.002 ± 0.001	**< 0.05***	0.07
Larval chewers	0.001 ± 0.002	> 0.05	0.00
Phloem suckers	0.007 ± 0.003	**< 0.01****	0.11
True bugs	0.001 ± 0.002	> 0.05	0.01
Omnivorous chewers	0.001 ± 0.001	> 0.05	0.02

Table S2: List of insect herbivores participating in plant-herbivore interaction networks in forest fragments, edges and forest interior. Degree of host plant specialization was categorized as follows: Monophagous (mono): Feeding on not more than one plant genus; oligophagous (oligo): Feeding on not more than one plant family; polyphagous (poly): Feeding on several plant families; omnivorous (omni): Feeding on plants as well as animals.

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	SD	Mean	SD	Mean	SD
Pogonocherus.hispidus	*Cerambycidae*	*Coleoptera*	poly	0.17	0.39	0.00	0.00	0.00	0.00
Andrion.regensteiniensis	*Curculionidae*	*Coleoptera*	mono	0.00	0.00	0.17	0.58	0.00	0.00
Barypeithes.sp.1	*Curculionidae*	*Coleoptera*	-	0.00	0.00	0.17	0.39	0.00	0.00
Coeliodes.transversealbofasciatus	*Curculionidae*	*Coleoptera*	mono	0.08	0.00	0.00	0.00	0.00	0.00
Curculio.glandium	*Curculionidae*	*Coleoptera*	oligo	0.25	0.62	0.00	0.00	0.00	0.00
Otiorhynchus.veterator	*Curculionidae*	*Coleoptera*	poly	0.00	0.00	0.17	0.58	0.00	0.00
Phyllobius.argentatus	*Curculionidae*	*Coleoptera*	poly	0.17	0.58	0.17	0.58	0.25	0.62
Phyllobius.pyri	*Curculionidae*	*Coleoptera*	poly	0.00	0.00	0.42	1.44	0.00	0.00
Polydrusus.cervinus	*Curculionidae*	*Coleoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Polydrusus.marginatus	*Curculionidae*	*Coleoptera*	poly	3.92	13.57	0.08	0.29	0.00	0.00
Polydrusus.mollis	*Curculionidae*	*Coleoptera*	poly	0.08	0.29	0.08	0.29	0.08	0.29
Strophosoma.melanogrammum	*Curculionidae*	*Coleoptera*	poly	0.17	0.39	0.58	1.00	0.25	0.45
Athous.haemorrhoidalis	*Elateridae*	*Coleoptera*	omni	0.00	0.00	0.08	0.29	0.00	0.00
Lagria.hirta	*Lagriidae*	*Coleoptera*	poly	0.83	1.64	0.33	0.65	0.33	1.15
Apterygida.media	*Forficulidae*	*Dermaptera*	omni	0.33	0.89	1.50	2.54	0.83	1.80
Chelidurella.guentheri	*Forficulidae*	*Dermaptera*	omni	3.00	5.56	2.50	3.12	1.25	2.26

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
Forficula.auricularia	*Forficulidae*	*Dermaptera*	omni	0.00	0.00	0.33	0.65	0.08	0.29
Hemiptera.sp.1	-	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Heteroptera.sp.1	-	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Psylloidea.sp.2	-	*Hemiptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Acanthosoma.haemorrhoidale	*Acanthosomatidae*	*Hemiptera*	poly	0.00	0.00	0.17	0.39	0.17	0.39
Aphidina.sp.2	*Aphididae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Aphidinae.sp.6	*Aphididae*	*Hemiptera*	-	0.50	1.17	0.08	0.29	0.75	2.05
Drepanosiphum.aceris	*Aphididae*	*Hemiptera*	mono	0.00	0.00	0.33	0.89	0.00	0.00
Drepanosiphum.sp.1	*Aphididae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Dysaphis.crataegi	*Aphididae*	*Hemiptera*	mono	0.08	0.29	0.00	0.00	0.00	0.00
Lachnus.roboris	*Aphididae*	*Hemiptera*	oligo	0.00	0.00	0.08	0.29	0.00	0.00
Myzocallis.carpini	*Aphididae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Periphyllus.testudinaceus	*Aphididae*	*Hemiptera*	mono	0.17	0.58	0.17	0.39	0.00	0.00
Aphrophora.alni	*Aphrophoridae*	*Hemiptera*	poly	0.00	0.00	0.25	0.87	0.00	0.00
Phyllaphis.fagi	*Callaphididae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.17	0.39
Tuberculatus.sp.1	*Callaphididae*	*Hemiptera*	oligo	0.00	0.00	0.08	0.29	0.00	0.00
Acericerus.sp.1	*Cicadellidae*	*Hemiptera*	mono	0.08	0.29	0.00	0.00	0.00	0.00
Alebra.sp.1	*Cicadellidae*	*Hemiptera*	poly	0.00	0.00	0.08	0.29	0.08	0.29
Arboridia.sp.1	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.17	0.58	0.00	0.00
Cicadellidae.sp.1	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.25	0.87	0.00	0.00
Cicadellidae.sp.10	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Cicadellidae.sp.11	*Cicadellidae*	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Cicadellidae.sp.13	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Cicadellidae.sp.14	*Cicadellidae*	*Hemiptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Cicadellidae.sp.2	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.17	0.58
Cicadellidae.sp.5	*Cicadellidae*	*Hemiptera*	-	0.58	0.79	0.42	1.44	2.17	6.89
Cicadellidae.sp.7	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.00	0.00	0.17	0.58

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	SD	Mean	SD	Mean	SD
Cicadellidae.sp.9	*Cicadellidae*	*Hemiptera*	-	0.33	0.78	0.00	0.00	0.00	0.00
Eurhadina.sp.1	*Cicadellidae*	*Hemiptera*	mono	0.08	0.29	0.00	0.00	0.00	0.00
Iassus.lanio	*Cicadellidae*	*Hemiptera*	mono	0.50	0.90	0.17	0.39	0.00	0.00
Ledra.aurita	*Cicadellidae*	*Hemiptera*	poly	0.25	0.62	0.08	0.29	0.25	0.45
Oncopsis.carpini	*Cicadellidae*	*Hemiptera*	mono	0.00	0.00	0.17	0.58	0.00	0.00
Ribautiana.sp.1	*Cicadellidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Typhlocyba.bifasciata	*Cicadellidae*	*Hemiptera*	poly	0.00	0.00	0.00	0.00	0.08	0.29
Zygina.angusta	*Cicadellidae*	*Hemiptera*	poly	0.33	1.15	0.00	0.00	0.00	0.00
Zygina.flammigera	*Cicadellidae*	*Hemiptera*	poly	2.17	3.74	0.33	0.89	0.17	0.58
Zygina.griseombra	*Cicadellidae*	*Hemiptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Cicadidae.sp.1	*Cicadidae*	*Hemiptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Tachycixius.pilosus	*Cixiidae*	*Hemiptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Issus.coleoptratus	*Issidae*	*Hemiptera*	poly	2.33	3.52	1.25	1.48	2.08	3.40
Lygus.pratensis	*Miridae*	*Hemiptera*	poly	0.17	0.39	0.00	0.00	0.00	0.00
Lygus.rugulipennis	*Miridae*	*Hemiptera*	omni	0.00	0.00	0.00	0.00	0.08	0.29
Megacoelum.infusum	*Miridae*	*Hemiptera*	omni	0.00	0.00	0.17	0.39	0.00	0.00
Miridae.sp.1	*Miridae*	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.33	0.89
Miridae.sp.10	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.08	0.29
Miridae.sp.2	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Miridae.sp.3	*Miridae*	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Miridae.sp.5	*Miridae*	*Hemiptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Miridae.sp.6	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Miridae.sp.7	*Miridae*	*Hemiptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Miridae.sp.8	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Miridae.sp.9	*Miridae*	*Hemiptera*	-	0.08	0.29	0.25	0.62	0.08	0.29
Pantilius.tunicatus	*Miridae*	*Hemiptera*	oligo	0.00	0.00	0.08	0.29	0.00	0.00
Phylus.melanocephalus	*Miridae*	*Hemiptera*	omni	0.17	0.58	0.00	0.00	0.00	0.00

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	SD	Mean	SD	Mean	SD
Phytocoris.longipennis	*Miridae*	*Hemiptera*	omni	0.08	0.29	0.17	0.58	0.08	0.29
Phytocoris.tiliae	*Miridae*	*Hemiptera*	omni	0.92	1.73	0.58	0.79	0.67	1.07
Rhabdomiris.striatellus	*Miridae*	*Hemiptera*	omni	0.00	0.00	0.08	0.29	0.00	0.00
Oxycarenus.modestus	*Oxycarenidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Dolycoris.baccarum	*Pentatomidae*	*Hemiptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Palomena.prasina	*Pentatomidae*	*Hemiptera*	poly	0.17	0.39	0.08	0.29	0.00	0.00
Pentatoma.rufipes	*Pentatomidae*	*Hemiptera*	omni	1.33	2.10	0.42	0.79	0.75	2.30
Cacopsylla.melanoneura	*Psyllidae*	*Hemiptera*	oligo	0.00	0.00	0.17	0.39	0.00	0.00
Arytainilla.spartiophila	*Psyllidae*	*Hemiptera*	mono	0.17	0.58	0.00	0.00	0.00	0.00
Cacopsylla.peregrina	*Psyllidae*	*Hemiptera*	mono	0.75	2.30	0.25	0.45	0.00	0.00
Psyllopsis.fraxinicola	*Psyllidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Rhinocola.aceris	*Psyllidae*	*Hemiptera*	mono	0.33	1.15	0.25	0.62	0.08	0.29
Physatocheila.dumetorum	*Tingidae*	*Hemiptera*	omni	0.00	0.00	0.08	0.29	0.00	0.00
Trioza.remota	*Triozidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Symphyta.sp.1	*Pamphiliidae*	*Hymenoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Symphyta.sp.2	*Pamphiliidae*	*Hymenoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Symphyta.sp.3	*Pamphiliidae*	*Hymenoptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Symphyta.sp.4	*Pamphiliidae*	*Hymenoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Lepidoptera.sp.2	-	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Lepidoptera.sp.1	-	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Lepidoptera.sp.5	-	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Coleophora.sp.1	*Coleophoridae*	*Lepidoptera*	-	0.17	0.39	0.00	0.00	0.00	0.00
Coleophora.sp.2	*Coleophoridae*	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Biston.strataria	*Geometridae*	*Lepidoptera*	poly	0.00	0.00	0.00	0.00	0.08	0.29
Ennomos.quercinaria	*Geometridae*	*Lepidoptera*	poly	0.00	0.00	0.17	0.58	0.17	0.39
Erannis.defolaria	*Geometridae*	*Lepidoptera*	poly	0.33	0.89	0.08	0.29	0.00	0.00
Geometridae.sp.2	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	SD	Mean	SD	Mean	SD
Geometridae.sp.3	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Geometridae.sp.4	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Geometridae.sp.5	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Geometridae.sp.6	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Geometridae.sp.7	*Geometridae*	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Geometridae.sp.8	*Geometridae*	*Lepidoptera*	-	0.25	0.87	0.00	0.00	0.00	0.00
Hypomecis.punctinalis	*Geometridae*	*Lepidoptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Operophtera.brumata	*Geometridae*	*Lepidoptera*	poly	1.00	2.66	0.00	0.00	0.17	0.39
Paradarisa.consonaria	*Geometridae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Parectropis.similaria	*Geometridae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Plagodis.dolabraria	*Geometridae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Hesperidae.sp.1	*Hesperidae*	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Incurvariidae.sp.1	*Incurvariidae*	*Lepidoptera*	-	0.00	0.00	0.25	0.62	0.00	0.00
Calliteara.pudibunda	*Lymantriidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Euproctis.chrysorrhoea	*Lymantriidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Lymantria.monarcha	*Lymantriidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Lymantriidae.sp.2	*Lymantriidae*	*Lepidoptera*	-	0.00	0.00	0.17	0.58	0.00	0.00
Amphipyra.pyramidea	*Noctuidae*	*Lepidoptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Cosmia.trapezina	*Noctuidae*	*Lepidoptera*	poly	0.33	0.78	0.25	0.87	0.17	0.39
Eupsilia.transversa	*Noctuidae*	*Lepidoptera*	poly	0.17	0.58	0.25	0.62	0.00	0.00
Noctuidae.sp.1	*Noctuidae*	*Lepidoptera*	-	0.33	1.15	0.00	0.00	0.08	0.29
Noctuidae.sp.2	*Noctuidae*	*Lepidoptera*	-	0.25	0.87	0.00	0.00	0.00	0.00
Noctuidae.sp.3	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Noctuidae.sp.4	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.17	0.58
Noctuidae.sp.5	*Noctuidae*	*Lepidoptera*	-	0.08	0.29	0.17	0.58	0.00	0.00
Noctuidae.sp.6	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Noctuidae.sp.7	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	SD	Mean	SD	Mean	SD
Noctuidae.sp.8	*Noctuidae*	*Lepidoptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Orthosia.cerasi	*Noctuidae*	*Lepidoptera*	poly	0.50	1.24	0.25	0.87	0.58	1.08
Orthosia.gothica	*Noctuidae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Orthosia.incerta	*Noctuidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Orthosia.munda	*Noctuidae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Archips.xylosteana	*Tortricidae*	*Lepidoptera*	poly	0.08	0.29	0.08	0.29	0.08	0.29
Pandemis.ribeana	*Tortricidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Tortricodes.alternella	*Tortricidae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Tortrix.viridana	*Tortricidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Ypsolopha.parentesella	*Ypsolophidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00

Taxonomic Experts

Peter Sprick: *Coleoptera*
Thomas Thieme: *Aphidoidea*
Sabine Walter: *Auchenorrhyncha*
Jürgen Deckert: *Heteroptera*
Daniel Burckhardt: *Psylloidea*
Erwin Rennwald: *Lepidoptera*
Heidrun Melzer: *Lepidoptera*
Rolf Mörtter: *Lepidoptera*

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Chapter 4

Biodiversity, edge response, and conservation value of arboricolous insects in beech canopies of the Northern Palatinate highlands

Tranquility and serenity experienced during sunrise at the Königsberg/Wolfstein after getting up at 2 am to search for suitable beech trees to apply fogging. Worth it.

INTRODUCTION

Home to the majority of arthropod abundance and diversity within forests, are the tree canopies naturally, due to their sheer volume, ressource abundance, and habitat complexity (Lowman 1995, Ozanne et al. 2003, Horchler & Morawetz 2008). For example, they are thought to house about 40% of extant global species (Ozanne et al. 2003). Yet, most research in forest ecology was focused on the understory, just out of better accessibility (Horchler & Morawetz 2008). Therefore, forest canopies were and still mostly are '*white spots*' on the '*map of biodiversity*' and have been called '*the last biological frontier*' (Erwin 1983, Lowman & Wittman 1995). First indications for the immense biodiversity waiting to be unveiled stem from Erwin's pioneering study in 1982, reporting over 900 beetle species from the insecticidal treatment (back then a rarely used methodology) of only 19 tree individuals (*Luehea seemannii*, *Malvaceae*) (Erwin 1982, Floren & Schmidl 2008). Ever since, tropical forest canopies have been the '*frontline of biodiversity research*' (Floren & Schmidl 2008), leading to frequent corrections in the estimation of global species richness (Ødegaard 2000, Novotny et al. 2002). Although we are still far from a comprehensive picture, even less research has been conducted in temperate forest canopies (Lowman & Wittman 1995, Floren & Schmidl 2008). It has not been until the last few decades that European forests came under scientific focus (Floren & Schmidl 2008). There are plentiful indications that temperate canopies are similar centers of arthropod abundance and biodiversity. For instance Floren estimated the minimum abundance of arboricolous arthropods to be 1,000,000 per hectare of mixed forests (Floren 2008). This would correspond to 1.5 trillion canopy arthropods for the entire forested area of Germany (Floren & Schmidl 2008). Nevertheless, empirical results are still sketchy.

Furthermore, we lack in knowledge on how human forest modification affects arboricolous insect communities (Foggo et al. 2001, Bail & Schmidl 2008). There has been done initial work on the effect of silvicultural management on canopy communities (Floren et al. 2008, Horstmann & Floren 2008), but studies on forest fragmentation effects are practically nonexistent (Ozanne et al. 2000, Foggo et al. 2001, Sutton 2001). This is all the more surprising, as tree crowns, by their very nature, form a dorsal forest edge (Sutton 2001), and hence are interfaces between the forest interior and the microclimatic much harsher atmosphere (Madigosky 2004, Horchler & Morawetz 2008). It hence follows to ask whether arboricolous insect communities react to the increased influence of the *two forest edges* at forest margins (one vertical and one horizontal edge). Furthermore, there is evidence for higher plant diversity in edges of temperate forest understories (Krüsi et al. 1996, Honnay et al. 2002, Bartsch & Röhrig 2016). Insect communities are well known to change along plant diversity gradients (Haddad et al. 2001, 2011). Hence, vertically mobile insects might benefit from higher understory plant diversity, as temperate forests (including their canopies) are comparably poor in tree species (Rüther & Walentwoski 2008, Ulyshen 2011, Schulze et al. 2015). Therefore, canopy communities might respond in diversity and community composition to edge effects.

In addition, a further description of arboricolous insect communities in beech crowns is valuable, as their ecological importance is not solely defined by diversity measures, but also by identity and natural history of the species they consist of. Although insect communities of beech canopies have been assessed sporadically (Floren 2008, Sprick & Floren 2008), we are still far from a solid empirical basis. This is probably partly because beech (*Fagus sylvatica*) is, by comparison, a poor host for arthropods (Goßner 2008, Sprick & Floren 2008). Nevertheless, *F. sylvatica* naturally is the dominant tree species over large areas of Europe, and continuous monodominant beech stands are the reality of many forest tracts (Ellenberg & Leuschner 1996, Schulze et al. 2015). Stands with a legacy of silvicultural management have been reported to form closed, poorly structured canopies (Ellenberg & Leuschner 1996), and the continuity of ceased management must be pronounced for beech stands to display complex, multi-layered crown habitats (Ellenberg & Leuschner 1996, Commarmot et al. 2005). It is hence pivotal to assess whether beech canopies are valuable habitats for arboricolous insects, particularly for habitat specialists with high vulnerability, and whether there are indicator species for particular forest habitats.

Taken together, this study aims to (i) contribute in unraveling the hidden insect diversity of beech canopies, (ii) assess, whether arboricolous insect communities in beech crowns react to edge effects, and to (iii) evaluate the conservation value of beech canopies for arboricolous insects by considering their natural history. For this, I sampled 24 beech canopies with insecticidal knockdown in mixed forests of the Northern Palatinate highlands, SW Germany.

METHODS

Study landscape – The study landscape was located in the Northern Palatinate highlands, a low, undulating mountain range (250 – 687 m asl) of Permian origin covering an area of 1,556.4 km^2 in SW Germany. It is characterized by temperate Central European climate under oceanic influence (MAP: 800 mm; MAT: 9.4°C, 1970-2010, Deutscher Wetterdienst 2013). Studied forests are deciduous, broad-leaved woodlands, phytosociologically classified as *Carpino-Fagetalia* mixed forests with varying transitional degrees of *Fagion* and *Carpinion betuli* stands. Extensive deforestation in the Middle Ages occurred mainly in sand and siltstone-dominated valleys, while the agriculturally less valuable igneous hilltops were mostly forested. This has led to a landscape of hyper-fragmented forests, embedded in a matrix of cultivated fields, pastures and meadow orchards. Forest cover of the selected portion (32%) of this landscape (1,010 km^2, 49° 36' N and 7° 44' E) is representative for Germany (31%, MUF 2002). Despite its high fragmentation degree with over 1,300 forest fragments ranging from 0.1 to 5616 ha (ca. 80% of them < 10 ha) and a total edge length of over 5,700 km, the region still harbors seven large forest tracts exceeding 1,000 ha.

Tree Selection – Across the study landscape, 24 beech trees were selected for insecticidal knockdown sampling, 12 in edges and 12 in the interior of large continuous forest tracts (median = 7866.35 ha). Beech trees in forest edges were positioned close to the physical forest margin (maximal distance 69 m). Those in the forest interior (> 100 m edge distance) were either located in natural forest reserves (n = 8) or in small and remote privately owned forest parcels (n = 4). Tree individuals were selected according to the following categories: (i) tree physiognomy: trees had to form a distinctive upper crown, with as few intercepting branches between canopy and forest floor as possible. (ii) Stand continuity: it was ensured that no alien tree branches penetrated the target beech canopy in order to avoid contamination by insects not originating from the target tree. Simultaneously, large canopy gaps seaming the target canopy were avoided as well, to ensure representative conditions of a continuous canopy cover. (iii) Tree age: similar and maximal age class of sampled trees was achieved by selecting beeches with maximal diameter at breast height (*DBH*) within a stand (42.4 ± 7.6 cm; mean ± sd). All trees were sampled between 2013-06-25 and 2013-07-25.

Insecticidal Knockdown (*Fogging*) – Insecticidal knockdown is a holistic, yet selective methodology for sampling of canopy arthropods. The used insecticide, natural pyrethrum (*NP*, extracted from tansies, *Tanacetum cinerariifolium*, *Asteraceae*), inhibits the closure of sodium-dependent transporters in the postsynaptic membrane of arthropods, hence inhibiting movement coordination (Katz et al. 2008, Floren 2010). In endotherms, enzymes missing in arthropods quickly break up NP, rendering it relatively harmless (Bradberry et al. 2005, Floren 2010). Although much more expensive than synthetically produced pyrethroids, NP is the ecologically superior choice as it quickly denaturates under natural UV light (ca. 10 min, Floren 2010). For application, NP is mixed with a carrier oil (white oil, medicinal quality) and dispersed into droplets < 10 µm in the resonating air coloumn produced within the fogging machine (Swingtec SN-50, Swingtec GmbH, Germany) by the combustion engine (**Color Plate 1**). The hot aerosol column emitted by the machine is carried into the canopy under proper weather conditions (**Color Plate 1, 2**, also see the following link for coverage by the SWR short news on the study and the sampling process: https://goo.gl/snhNNE). Ideal are times before dawn and after dusk, when there are no thermal winds. Hence, fogging was performed between ca. 5:00 and 9:30 a.m. (penetration time of 5 - 10 min) (Floren 2010). Arthropods were collected in two tarpaulins (4 x 5 m) placed beneath the fogged target trees. Tarpaulin margins were lifted by sticks to prevent contamination by walking forest floor fauna (**Color Plate 3**). During fogging, arthropods immediately start dropping into the sheets and are collected after a drop time of 2 h with fine brushes and stored in 70% ethanol (**Color Plate 3**).

Arthropod Sample Processing – All arthropods are stored at the department of Plant Ecology and Systematics at the University of Kaiserslautern, except psyllids (*Psylloidea*, stored at the Natural Museum of Basel). Sampled arthropods (> 46,000 individuals) were classified and separated into meaningful groups, considering their systematic position, life stage, and consistency in life strategy, where available. Completeness of these groups and of identified species (see below) was assessed by evaluating the saturation level of calculated accumulation curves, assuming asymptotic curve behavior (Moreno & Halffter 2000) with the *specaccum* function in the R package *vegan* (Oksanen et al. 2015). Due to this immense arthropod collection, only particular groups could be further separated and identified to species level. Those groups were chosen, where many herbivore species were expected (roaches, *Blattodea*; beetles, *Coleoptera*; earwigs, *Dermaptera*; true bugs, *Hemiptera* excluding *Auchenorrhyncha*; sawflies, *Symphyta*; and *Orthoptera*). Auchenorrhyncha were excluded due to limited identification capacities. Caterpillars were left out, as identification after preservation in

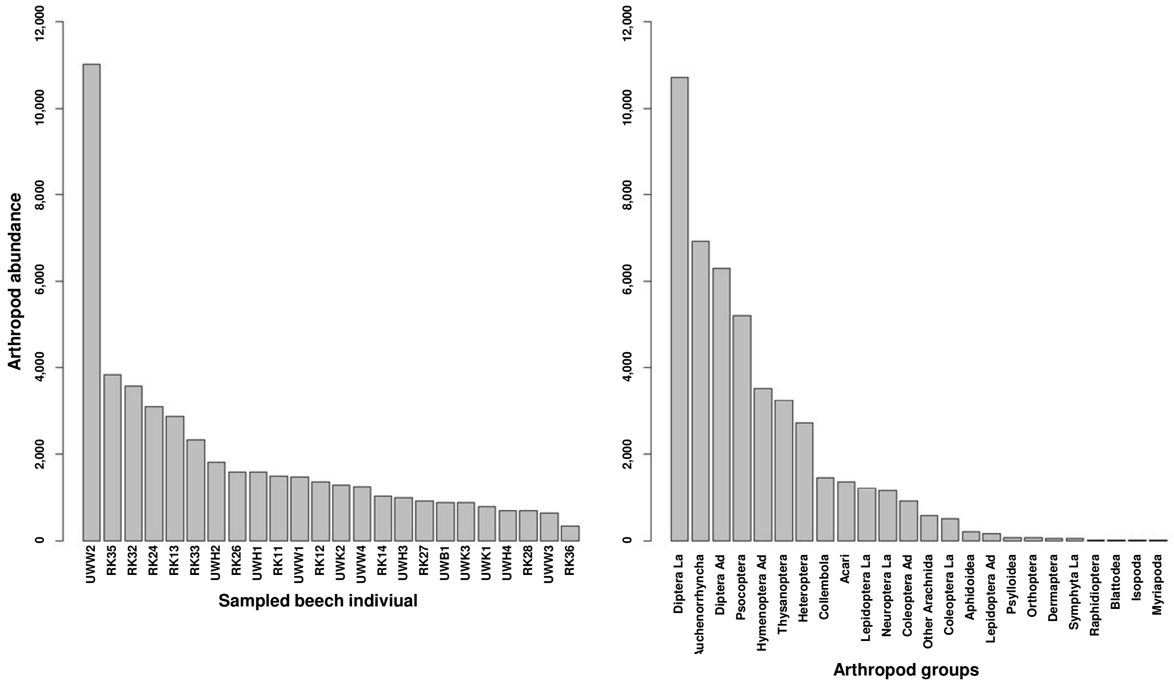

Figure 1: Abundance distribution of arboricolous arthropods in beech canopies (Fagus sylvatica) of the Northern Palatinate highlands. Left: Abundances across 24 sampled beech individuals from forest edges and the forest interior. Beech canopy faunas originating from edge trees are coded beginning with *R*, faunas from interior trees begin with *U*. **Right:** Abundances across identified arthropod groups. Holometabolous insects were divided into adults (*Ad*) and larvae (*La*), if both life stages were encountered.

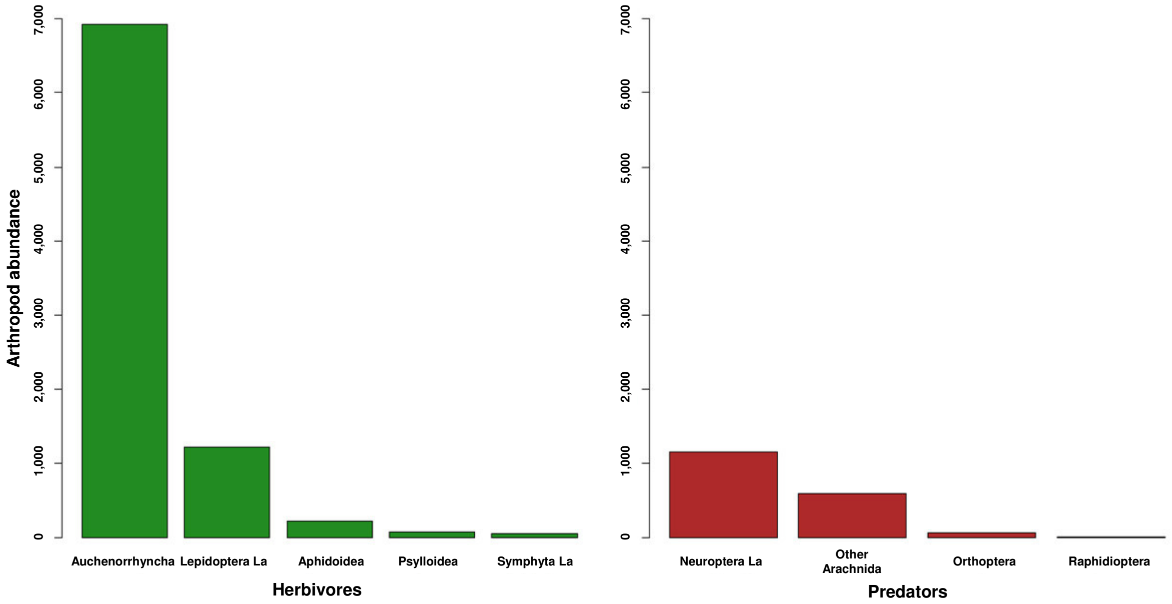

Figure 2: Abundances of obligatory herbivorous (green, left) and predatory (red, right) arthropod groups in 24 beech canopies in the Northern palatinate highlands. The y-axis was kept constant for both figures for illustrative purposes.

ethanol is close to impossible, and as separation before conservation was similarly unfeasible. Identification was performed by Kevin Bähner, as well as by pertinent experts for respective taxonomic groups (compare acknowledgements).

Community Analysis – Community segregation across forest habitats (edge vs. interior) was analyzed using similarity values in a non-metric multidimensional scaling (NMDS, Bray-Curtis dissimilarity of square-root transformed abundance data, function *metaMDS*, *vegan* package) and performing an ADONIS permutation test (999 permutations) with forest habitat as a grouping variable. Habitat-wise comparison of beta dispersion was achieved similarly to Anderson et al. (2006) by measuring the distances of sites spanning the convex hull of a habitat in the NMDS ordination to their centroid (one-way ANOVA). I chose to use the convex hull because I wanted to compare the maximum spread in community dissimilarity amongst habitats. Identification of indicator species for forest habitats was performed using a Dufrêne-Legrende indicator species analysis in the *labdsv* package (Roberts 2015). Indicator values range from 0 (no habitat association) to 1 (perfect habitat association). For all identified insect species data was collected on their natural history regarding their trophic mode, habitat specificity, microhabitat preferences, relationship to beech as host tree, dead wood requirements, Red List status, and identity as indicator species (Schmidl & Bußler 2004) (**Table S1**).

Data analysis was entirely performed in the programming language *R* (R Core Team 2013).

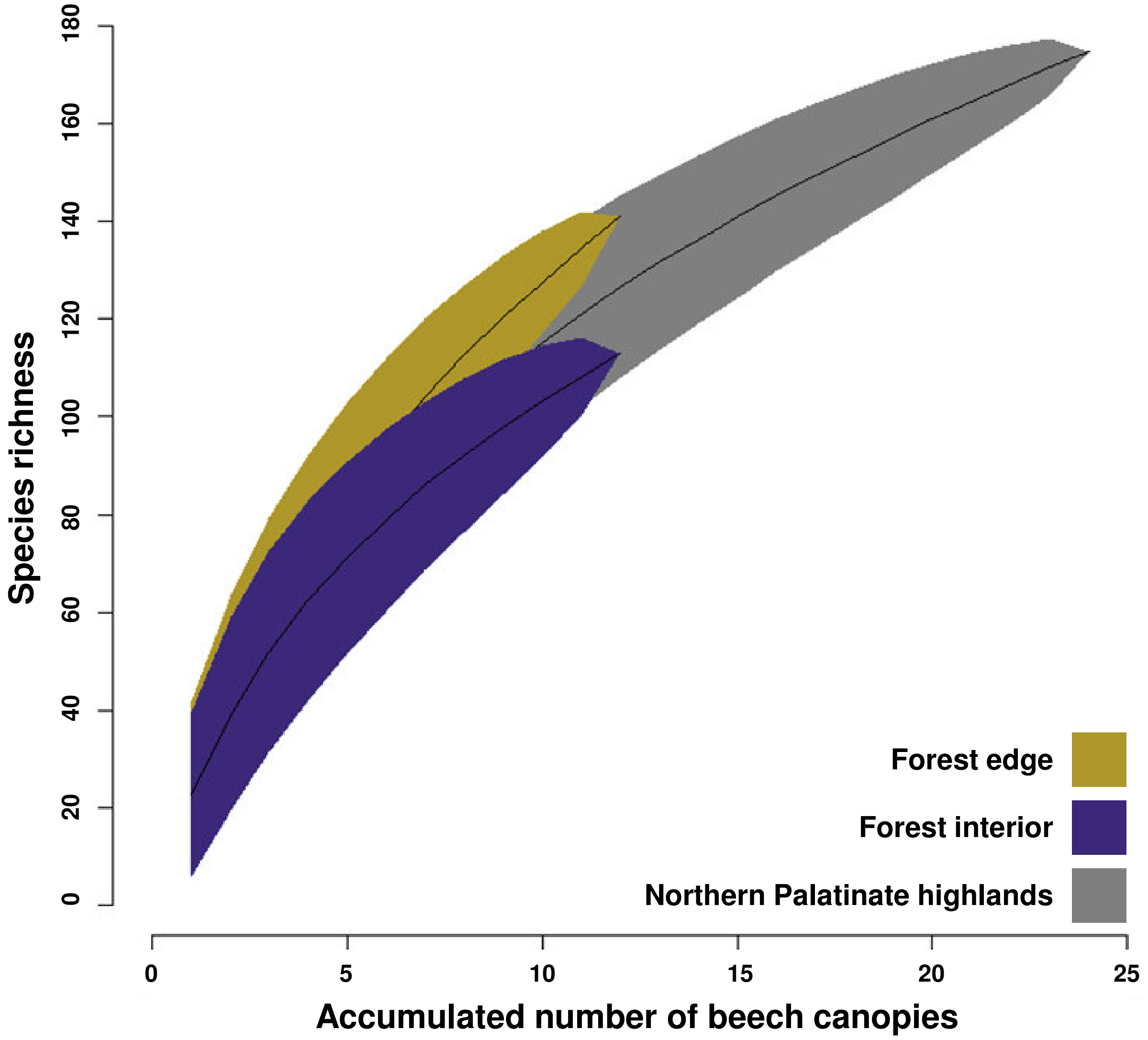

Figure 3: Accumulated species richness of arboricolous insects in beech canopies situated in forest edges (yellow, 12 trees) and the forest interior (blue, 12 trees) across the Northern Palatinate highlands (grey, all 24 trees). Polygons represent the 95th percentile.

RESULTS

Fogging of the 24 sampled beech trees resulted in an immense arthropod collection, totaling 46,504 individuals (1,937.7 ± 2,153.6, mean ± sd). Across sampled trees, abundances were fairly uneven (median = 1,330.5), the most abundant sample contributing nearly a quarter of all arthropods to the collection (11,026, 23.7%) (**Figure 1**). In total 24 major groups of arthropods were identified, with highly uneven abundances (median = 759.5), roughly resembling a geometric distribution (**Figure 1**). The three most abundant groups (*Diptera* larvae, *Auchenorrhyncha*, and *Diptera* adults) constitute 51.5% (23,932) of all arthropods. For major arthropod groups sampling was complete, as accumulation curves indicated 99.5% saturation. Several of those groups could be categorized into obligatory

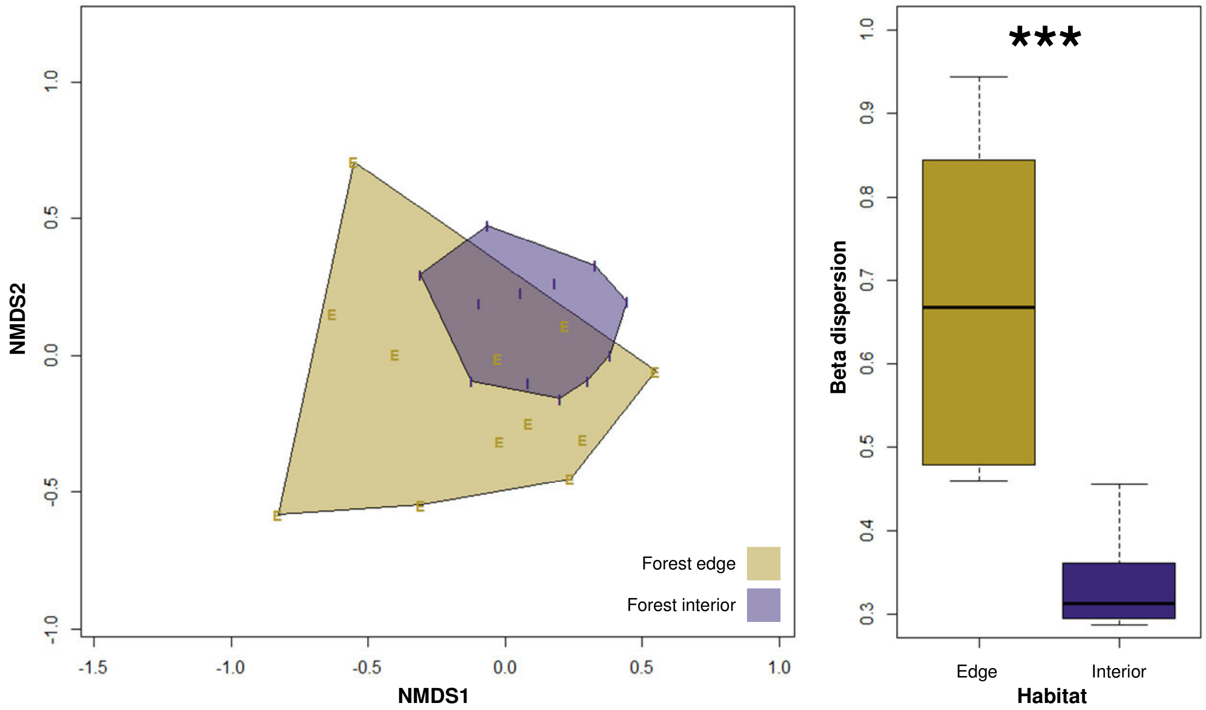

Figure 4: Edge effects on segregation and homogenization of arboricolous insect communities in the Northern Palatinate highlands. Left: NMDS ordination based on square-root transformed Bray-Curtis similarities of insect communities (stress = 0.24). Letters and polygons represent and encompass the insect communities of fogged *Fagus sylvatica* individuals (E: forest edges, yellow; I: forest interior, blue). Community separation was tested with a permutational multivariate analysis of variance (ADONIS-test, 999 permutations, square-root transformed Bray-Curtis similarities, $p < 0.05^*$, $R^2 = 0.08$). **Right:** Beta-dispersion of the insect communities, measured as the distance of the hull plots in the NMDS space to the polygon centroid (log-transformation; linear regression with F-test, $F_{(11,1)} = 25.44$, $p < 0.001^{***}$, $R^2 = 0.70$; untransformed data is shown).

herbivores (5) or predators (4). Again, abundances were distributed highly unevenly, with the most abundant herbivore and predator groups contributing 81.6% and 63.7%, respectively (**Figure 2**). Across the mentioned groups (*Blattodea*, *Coleoptera*, *Dermaptera*, *Hemiptera* excluding *Auchenorrhyncha*, *Symphyta*, and *Orthoptera*) all 3,101 associated individuals were identified into 175 species, 52 families and 6 orders, with largest portions belonging to beetles (*Coleoptera*, 127 species, 73%) and true bugs (*Hemiptera*, 42 species, 24%) (see **Color Plate 4** for assorted highlighted species). Despite the immense sampling intensity, I only managed to capture a fraction of the insect community, as accumulation curves gave 68.9% (estimated 254 species) of saturation for the whole community (175 species), and 54.9% (estimated 257 species) and 61.7% (estimated 183 species) for forest edges (141 species) and the interior (113 species), respectively (**Figure 3**). Non-overlapping 95th percentiles of species richness of forest edges and interior indicate significantly higher species richness in edge canopies (26%, **Figure 3**), but this did not translate into differences in Shannon diversity

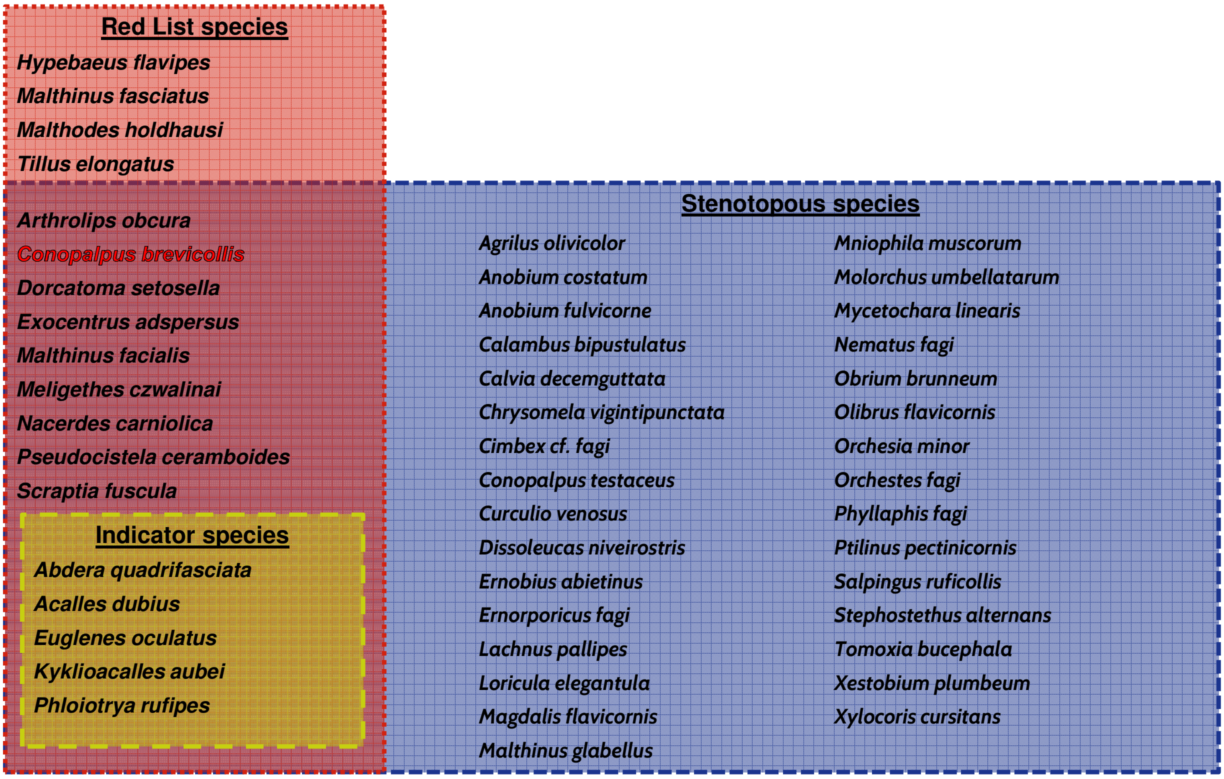

Figure 5: Distribution of conservational important arboricolous insects (all beetles, *Coleoptera*) from beech canopies in the Northern Palatinate highlands across three categories of protective relevance (Venn diagram). Stenotopous insects are dependent on very closely defined habitats (blue rectangle). Red List (red rectangle) species are either vulnerable or endangered according to the German Red List (BfN 1998). Indicator species (yellow rectangle) demark *Urwald* relict species, as well as ecologically particularly important species sensu Schmidl & Bußler (2004). Rectangle areas and their overlap are proportional to their respective set of insect species. *Conopalpus brevicollis* is highlighted separately, as this melandryid was one of the two empirically attested indicator species in the analysis of this study (compare text).

(ANOVA, $F_{1,22} = 0.3446$, $p > 0.05$). Insect communities of both habitats significantly segregated from each other, although there was noticeable remaining overlap (**Figure 4**). On the other hand, edge communities displayed distinctive higher beta diversity, as interior communities were highly homogeneous and significantly more constrained in their beta dispersion (**Figure 4**).

Dufrêne-Legendre analysis returned two indicator species with respective preference for edge and interior habitats: *Cortinicara gibbosa* (*Latriidae*, indicator value = 0.42, $p < 0.05$*) and *Conopalpus brevicollis* (*Melandryidae*, indicator value = 0.53 $p < 0.05$*). The first is listed as an ubiquist with broad trophic spectrum (pollenophagous, mycophagous), whereas the latter is a threatened arboricolous forest dweller, with close affinity to dead wood (xylodetritiphagous, **Table S1**). Further on, a total of 49 insect species were found which were either categorized as stenotopous (45 species), recorded in the German Red List (18 species, **Color Plate 5**, BfN 1998), or classified as ecologically important *Urwald* relict species by Schmidl & Bußler (5 species, Schmidl & Bußler 2004). Many of them fell into several of these three categories, including the empirically verified indicator species, *Conopalpus brevicollis*, (**Figure 5**). Five species are particularly noteworthy, as they were stenotopous, red-listed, as well as indicator species.

DISCUSSION

As typical for studies using insectidal knockdown, one of the most defining properties of the obtained collection of canopy arthropods is its immense abundance (total of 46,504) and diversity. Yet, mean numbers of arthropods per tree (1,937.7 ± 2,153.6, mean ± sd) were lower than mean abundances reported from other foggings of German beech individuals (two studies, means = 6,709 and 6,218, respectively, Floren 2008). Differences could be explained by comparatively late sampling in this study (end of June to end of July), as many arthropods tend to decrease in abundance in high summer (Southwood et al. 2004, Goßner 2008). On the other hand, data exploration did not show any signs of time related decreases in abundance or diversity (not shown), and the data set was considered to be very diverse, considering the lower abundance (Peter Sprick, personal communication, 2015). Furthermore, unbalanced individual numbers across trees, like the larval hyperabundance of one dipteran species (7,883 specimens in one canopy, **Figure 1**), are a well known phenomenon and are often local outbreaks of small arthropods (Floren 2008).

All relevant groups of arthropods were present, as revealed by accumulation curves. Interestingly enough, groups often addressed in the literature (e.g. *Coleopera*, *Heteroptera*, *Hymenoptera*) were strikingly less abundant than more cryptic groups (e.g. *Psocoptera*, *Auchenorrhyncha*). Differences in scientific attention might hence be less caused by fewer occurrences, but rather greater difficulties in taxonomy and identification (Nickel 2008), which is further supported by similar group abundances in oaks (*Quercus* spp., Floren 2008). Furthermore, considering only exclusively herbivorous groups of insects, *Auchenorrhyncha* distinctively dominated the arboricolous herbivore communities, being even five times more abundant than caterpillars (**Figure 2**). This highlights the importance of the *Auchenorrhyncha* for future herbivory studies in forest systems, as there is hardly any literature on the matter (Nickel 2008). Considering the proportion of herbivore to predator abundances (more than five times higher), the well known pattern of higher abundances/biomasses in lower trophic level was confirmed (Bartsch & Röhrig 2016). *Neuroptera* larvae were the most important group of predators, even surpassing spiders (**Figure 2**), which is surprising, as this group was found to be rather rare on oaks and hornbeams (*Carpinus betulus*, Floren 2008).

One's best way to contextualize the immense diversity found within the identified species is to consult the corresponding species accumulation curves, showing no saturation whatsoever, despite the comprehensive sampling regime (**Figure 3**).

Extrapolations estimated nearly double as many species to be found within the beech canopies, irrespective of habitat. This pattern is well documented in the literature, e.g. for phytophagous beetles (Sprick & Floren 2008), but also for other insect taxa and on other tree species (Bail & Schmidl 2008, Horstmann & Floren 2008). Hence, my findings further underline the importance of forest canopies as hotspots of temperate biodiversity, particularly in the case of beech forests. Concerning structuring mechanisms of insect diversity and community composition, I found similar, yet differently strong edge effects, compared to studies from the understory of the same study region (**Chapter 3**). While there was no difference in Shannon diversity, edge canopies were slightly richer in insect species, and communities showed weak separation from and much higher heterogeneity than interior communities. Minor edge effects on species richness can be interpreted as facilitative effects of rich edge floras in the understory on insect diversity transmitting into the canopy (Haddad et al. 2001, Honnay et al. 2002, **Chapters 2**, **3**). One might hence say that understory patterns in the edge dilute into the canopy. This might be due to spatial effects, as the described high floral/faunal diversity relationship is located substantially below the canopy. There are several insect species known to migrate vertically in forest systems, which could benefit from rich understory floras (Asshoff et al. 2008, Ulyshen 2011). Yet, many more insect species are strictly arboricolous, ever-living in the green sea above the ground (Asshoff et al. 2008, Nickel 2008). Another reason might lie in the different reference systems in the mentioned Chapter: There insects were sampled across the entire woody vegetation (**Chapter 3**), not only on *Fagus sylvatica*, as it was done here. Similarly, in this study, insects of all trophic guilds were assessed, not only herbivores with by nature much higher host specifity. This might explain why high plant diversity in the understory only marginally translates into higher insect diversity in the canopy. Distinctively higher beta dispersion in insect communities of forest edge crowns is likely a result of edge induced differences in canopy microclimates. As mentioned earlier, tree crowns in proximity to forest margins are confronted with two edges: the *dorsal* edge, which separates the crown from the atmosphere, and the *lateral* edge, which severs forest and matrix (Ozanne et al. 2000, Sutton 2001). Naturally, interior crowns are similarly exposed to more extreme microclimates in the top canopy than in the sub canopy (Horchler & Morawetz 2008). For illustration, the canopy accounts for two thirds of the temperature difference between the top canopy and the forest floor (Tal et al. 2008). This gradient should be even stronger in beech stands, as beech exhibits a pronounced horizontal leaf architecture for maximal light interception, with only 1-2% of PAR (*photosynthetically active radiation*) reaching the ground (Ellenberg & Leuschner 1996, Hagemeier 2002). On the contrary, light might hence penetrate deeper into edge canopies, particularly under skewed angles of entry. This should lead to higher variability in microclimates within the canopy and hence microhabitats for insects, in turn increasing insect community variability (Tal et al. 2008). Further variability in edge canopy microclimates could be explained by differences in exposition, slope inclination, canopy contextualization within adjacent tree canopies (and species), and cardinal direction. The pattern of high insect community heterogeneity in edge crowns has also been shown by Foggo et al. (2001), where they clearly stated that "*the more light and open the forest canopy…, the more variability there was in the faunal composition*" (Foggo et al. 2001).

Foggo et al. further held microclimatic sensitivity of specific arthropod groups responsible for separating edge and interior communities (2001). This might have been of lesser importance in this study, as among the identified 175 species, only two showed significant habitat preferences as indicator species. Fittingly, one of them, *Conopalpus brevicollis* (indicator for the relatively unmanaged interior), is stenotopous to beech forests, classified as threatened, and has a high affinity for dead wood. Such species worth of notice and protection (being either red-listed, stenotopous, or indicator species of pristine forests) constituted a significant portion of arboricolous insects with 49 species (28%). Many of them fitted more than one category, and it is logical to assume that protective value of a species rises with the number of categories it fits into. Hence, the following five species meeting all three '*requirements*' (**Figure 5**), together with *Conopalpus brevicollis*, may be considered as priority species for the Northern Palatinate highlands, in reference to the Habitats Directive of the EU (Rat der Europäischen Gemeinschaften 2013): *Abdera quadrifaciata* (*Melandryidae*), *Acalles dubius* (*Curculionidae*), *Euglenes oculatus* (*Aderidae*), *Kyklioacalles aubei* (*Curculionidae*), and *Phloiotrya rufipes* (*Melandryidae*). All of them are strongly dependent on dead wood and three exhibit rather restricted distributions in Germany. *Kyklioacalles aubei*, for instance, has its main area of distribution in southern Germany. Similarly, *Abdera quadrifasciata* can exclusively be found in Baden-Württemberg and Rhineland-Palatinate. But the smallest (yet protracted) range can probably be attributed to *Acalles dubius*, between Basel in the South and only sporadically extending beyond Bonn to the North, roughly following the course of the Rhine (Bleich et al. 2016). *Phloiotrya rufipes* is further noteworthy, as it is obligatory bound to the occurrence of lung oyster (*Pleurotus pulmonarius*, *Basidiomycota*) (Möller 2005). With the increasing retention of dead wood by foresters, *P. rufipes* is noticeably spreading in the Rhineland (Möller 2005). Summarizing, regardless of habitat, beech canopies of the Northern Palatinate highlands are valuable habitats for many species worth of protection, including several species with priority protection needs.

In synthesis, I can deduce several take-home messages from the analysis and description of the arboricolous insect fauna of the Northern Palatinate highlands. First, even when using a very comprehensive sampling method, it may be possible to collect all relevant arthropod groups, however enormous effort is needed to capture the majority of species, due to the tremendous insect diversity found in the canopies. Second, edge effects on arboricolous insects are noticeable, mainly via direct abiotic effects, but act differently strong on insect diversity and community composition. Third, although there are hardly any species with preferences for relatively unmanaged forests, there is a distinct number of ecologically relevant insect species with pronounced need of protection. This includes six species, which should receive priority attention in conservation and management considerations. Hence, beech canopies in the Northern Palatinate highlands are home to a tremendously abundant and diverse arthropod fauna, worthy of protection.

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SUPPLEMENTARY

Table S1: List of identified arboricolous insects from beech canopies in the Northern Platinate highlands and their corresponding natural history characteristics. Insect orders are abbreviated: *Blatto*(*dea*), *Coleo*(*ptera*), *Hemi*(*ptera*), *Hymeno*(*ptera*), *Ortho*(*ptera*). Microhabitats are abbreviated, missing the ending *'colous'* e.g. *arboricolous*. Trophy is abbreviated missing the ending 'phagous', e.g. *panthophagous*. If trophy differs across life stages, (*L*)arvae are separated from (*I*)magi. Relation to beech is classified into (*S*)pecialists, (*T*)ransient species, and (*O*)portunists. Affinity for dead wood is classified into preferences for old dead wood (*a*), duff-filled cavities (*m*), dead wood associated fungi (*p*), and fresh dead wood (*f*), following Schmdil & Bußler (2004). Insects were classified into habitat specifity as either being (*s*)tenotopous, (*e*)urytopous, and (*u*)biquitous. Insects were further classified according to Red List status into threatened (*2*), vulnerable (*3*), not threatened (*ng*), being *invasive*, or data source being *deficient*.

Species Number	Species	Familia	Ordo	Size (mm)	Microhabitat	Trophy	Relation to beech	CWD affinity	Habitat specifity	Red List status
1	Ectobius sylvestris	Ectobiidae	Blatto	6-14		pantho	O		eur	ng
2	Euglenes oculatus	Aderidae	Coleo	2.1-2.6	arbori, herbi	NA	O	m	ste	2
3	Mycetochara linearis	Alleculidae	Coleo	4-6	xylo	kopro, necro	O	a	ste	ng
4	Pseudocistela ceramboides	Alleculidae	Coleo	10-12	flori, arbori	xylodetriti	O	m	ste	2
5	Anobium costatum	Anobiidae	Coleo	3-5	arbori, xylo	xylodetriti	O	a	ste	ng
6	Anobium fulvicorne	Anobiidae	Coleo	2.2-3.5	arbori, xylo	xylodetriti	O	a	ste	ng
7	Dorcatoma setosella	Anobiidae	Coleo	2.2-2.5	myco	myco	O	p	ste	2
8	Ernobius abietinus	Anobiidae	Coleo	2-3	arbori, xylo	xylodetriti	O	a	ste	ng
9	Hedobia imperialis	Anobiidae	Coleo	3.1-5.2	arbori, xylo	nectaro	T	a	eur	ng
10	Ptilinus pectinicornis	Anobiidae	Coleo	3.5-5.5	xylo	xylodetriti	O	a	ste	ng
11	Xestobium plumbeum	Anobiidae	Coleo	3-5.7	arbori, xylo	nectaro	S	a	ste	ng
12	Dissoleucas niveirostris	Anthribidae	Coleo	2-4	xylo	myco	O	a	ste	ng
13	Protapion fulvipes	Apionidae	Coleo	1.8-2.2	herbi	mono	T		ubi	ng
14	Agrilus olivicolor	Buprestidae	Coleo	4-4.5	arbori	poly	O	f	ste	ng
15	Cantharis livida	Cantharidae	Coleo	9-13.5	herbi, flori	zoo	O		eur	ng
16	Malthinus facialis	Cantharidae	Coleo	3-4.5	arbori	zoo	O	a	ste	3
17	Malthinus fasciatus	Cantharidae	Coleo	4-5	arbori	zoo	O	a	eur	3
18	Malthinus flaveolus	Cantharidae	Coleo	5-6.5	arbori	zoo	O		eur	ng
19	Malthinus glabellus	Cantharidae	Coleo	4.5	arbori	zoo	O	a	ste	ng
20	Malthinus seriepunctatus	Cantharidae	Coleo	4-5	arbori	zoo	O	a	eur	ng
21	Malthodes cf. brevicollis	Cantharidae	Coleo	2.3	arbori	zoo	O	a	eur	ng
22	Malthodes guttifer	Cantharidae	Coleo	4-5	arbori	zoo	O	a	eur	ng
23	Malthodes hexacanthus	Cantharidae	Coleo	2	arbori, herbi	zoo	O	a	eur	ng
24	Malthodes holdhausi	Cantharidae	Coleo	3	arbori	zoo	O	a		3
25	Malthodes marginatus	Cantharidae	Coleo	4.8	arbori	zoo	O	a	eur	ng

(continued)

Species Number	Species	Familia	Ordo	Size (mm)	Microhabitat	Trophy	Relation to beech	CWD affinity	Habitat specifity	Red List status
26	Malthodes minimus	Cantharidae	Coleo	3.3-4	arbori	zoo	O	a	eur	ng
27	Malthodes pumilus	Cantharidae	Coleo	1.3-1.5	arbori, flori	zoo	O	a	eur	ng
28	Malthodes spathifer	Cantharidae	Coleo	2.6-3.2	arbori, herbi	zoo	O	a	eur	ng
29	Dromius agilis	Carabidae	Coleo	5-6.6	corti	zoo	O		eur	ng
30	Dromius quadrimaculatus	Carabidae	Coleo	4-6	arbori	zoo	O		eur	ng
31	Exocentrus adspersus	Cerambycidae	Coleo	5-8	arbori	xylo	O	f	ste	3
32	Leiopus linnei	Cerambycidae	Coleo	6-10	arbori, xylo, corti	xylo	O	f	eur	ng
33	Leiopus nebulosus	Cerambycidae	Coleo	6-10	arbori, xylo, corti	xylo	O	f	eur	ng
34	Molorchus umbellatarum	Cerambycidae	Coleo	5-8	flori, xylo	xylo, polleno	O	f	ste	ng
35	Obrium brunneum	Cerambycidae	Coleo	4-7	xylo, flori	xylo, polleno	O	f	ste	ng
36	Rutpela maculata	Cerambycidae	Coleo	14-20	flori, xylo	L: xylo, I: polleno	O		eur	ng
37	Aphthona venustula	Chrysomelidae	Coleo	1.8-2.4	herbi	mono	T		eur	ng
38	Chaetocnema concinna	Chrysomelidae	Coleo	1.8-2.4	herbi	poly	O		ubi	ng
39	Chaetocnema hortensis	Chrysomelidae	Coleo	1.5-2.3	graminei	oligo	T		eur	ng
40	Chrysomela vigintipunctata	Chrysomelidae	Coleo	6.5-8.5	arbori	mono	T		ste	ng
41	Cryptocephalus pusillus	Chrysomelidae	Coleo	2.5-3	arbori	poly	O		eur	ng
42	Mniophila muscorum	Chrysomelidae	Coleo	1.2-1.7	musci	poly	T		ste	ng
43	Phyllotreta cruciferae	Chrysomelidae	Coleo	1.8-2.5	herbi	oligo	T		eur	ng
44	Phyllotreta vittula	Chrysomelidae	Coleo	1.5-1.8	graminei	oligo	T		eur	ng
45	Orthocis alni	Cisidae	Coleo	1.8-2.9	myco	myco	O	a	eur	ng
46	Clambus simsoni	Clambidae	Coleo	1	fungi	myco	O		eur	invasive
47	Tillus elongatus	Cleridae	Coleo	6-10	xylo	zoo	O	a	eur	3
48	Adalia decempunctata	Coccindellidae	Coleo	3.5-5	arbori	zoo	O		eur	ng
49	Aphidecta obliterata	Coccindellidae	Coleo	3.3-5	arbori	zoo	O		eur	ng
50	Calvia decemguttata	Coccindellidae	Coleo	5-7	arbori	zoo	O		ste	ng

(continued)

Species Number	Species	Familia	Ordo	Size (mm)	Microhabitat	Trophy	Relation to beech	CWD affinity	Habitat specifity	Red List status
51	Arthrolips obcura	Corylophidae	Coleo	1.16-1.58	xylo	myco	O	p	ste	2
52	Orthoperus atomus	Corylophidae	Coleo	0.86-1.1	corti, phytodetriti	myco	O	p	eur	ng
53	Sericoderus lateralis	Corylophidae	Coleo	0.9-1.1	phytodetriti	myco	O		eur	ng
54	Atomaria fuscata	Cryptophagidae	Coleo	1.4-1.9	humi, phytodetriti	myco	O		ubi	ng
55	Atomaria linearis	Cryptophagidae	Coleo	1.2-1.6	phytodetriti, herbi	oligo	O		eur	ng
56	Cryptophagus dentatus	Cryptophagidae	Coleo	1.9-2.9	xylo, corti	myco	O		eur	ng
57	Acalles dubius	Curculionidae	Coleo	2.5	arbori, xylo	xylo	O	a	ste	3
58	Curculio glandium	Curculionidae	Coleo	4-7.5	arbori	poly	O		eur	ng
59	Curculio venosus	Curculionidae	Coleo	7-9	arbori	mono	T		ste	ng
60	Kyklioacalles aubei	Curculionidae	Coleo	3.5-5.5	phytodetriti, xylo	xylo	O	a	ste	2
61	Magdalis flavicornis	Curculionidae	Coleo	2.7	arbori	mono	T	f	ste	ng
62	Orchestes fagi	Curculionidae	Coleo	2-2.5	arbori	mono	S		ste	ng
63	Phyllobius argentatus	Curculionidae	Coleo	3.5-6	arbori	poly	O		eur	ng
64	Polydrusus cervinus	Curculionidae	Coleo	3.9-5.7	arbori	poly	O		ubi	ng
65	Polydrusus marginatus	Curculionidae	Coleo	4-5	arbori	poly	O		eur	ng
66	Polydrusus pilosus	Curculionidae	Coleo	5-6.5	arbori	poly	O		eur	ng
67	Polydrusus pterygomalis	Curculionidae	Coleo	4-5.5	arbori	poly	O		eur	ng
68	Polydrusus sericeus	Curculionidae	Coleo	5.5-7	arbori	poly	O		eur	ng
69	Rhinoncus perpendicularis	Curculionidae	Coleo	2.1-2.9	herbi	mono	T		eur	ng
70	Strophosoma melanogrammum	Curculionidae	Coleo	4-5.5	arbori	poly	O		eur	ng
71	Trachodes hispidus	Curculionidae	Coleo	2.8-3.6	xylo	xylo	O	a	eur	ng
72	Agriotes pallidulus	Elateridae	Coleo	3.5-5.7	arbori, herbivol	polleno	T		eur	ng
73	Ampedus pomorum	Elateridae	Coleo	9-12	arbori, xylo	zoo	O	a	eur	ng
74	Ampedus sanguinolentus	Elateridae	Coleo	9-11.5	arbori, xylo, corti	zoo	O	a	eur	ng
75	Athous haemorrhoidalis	Elateridae	Coleo	9.5-15	arbori, flori, herbi	poly, polleno	O		ubi	ng

(continued)

Species Number	Species	Familia	Ordo	Size (mm)	Microhabitat	Trophy	Relation to beech	CWD affinity	Habitat specifity	Red List status
76	Athous subfuscus	Elateridae	Coleo	7.8-10.5	arbori, flori	poly, polleno	O		eur	ng
77	Athous vittatus	Elateridae	Coleo	9-11.5	arbori, flori	poly	O		eur	ng
78	Calambus bipustulatus	Elateridae	Coleo	6.3-8.5	arbori, flori	zoo, polleno	O	a	ste	ng
79	Helophorus brevipalpis	Hydrophilidae	Coleo	2.2-3.2	limni	detriti	T		eur	ng
80	Lagria hirta	Lagriidae	Coleo	7-10	herbi. arbori	poly	O		eur	ng
81	Cartodere nodifer	Latridiidae	Coleo	1.5-2	phytodetriti	myco	O		ubi	ng
82	Corticaria elongata	Latridiidae	Coleo	1.3-1.6	phytodetriti und humi	myco	O		eur	ng
83	Corticarina fuscula	Latridiidae	Coleo	1.5-1.8	herbi, phytodetriti	myco	O		eur	ng
84	Corticarina similata	Latridiidae	Coleo	1-1.7	herbi, phytodetriti	myco	O		eur	ng
85	Cortinicara gibbosa	Latridiidae	Coleo	1-1.6	flori, phytodetriti	polleno, myco	O		ubi	ng
86	Dienerella spec. 1	Latridiidae	Coleo	1-1.8	fungi	myco	O			ng
87	Enicmus spec. 1	Latridiidae	Coleo	1-2.4		myco	O			ng
88	Enicmus transversus	Latridiidae	Coleo	1.8-2.2	phytodetriti	myco	O		ubi	ng
89	Stephostethus alternans	Latridiidae	Coleo	2.5	arbori, xylo	myco	O	p	ste	ng
90	Agathidium varians	Leiodidae	Coleo	2.5-3	fungi	myco	O		eur	ng
91	Hypebaeus flavipes	Malachiidae	Coleo	2	arbori	zoo, polleno	O	a	eur	3
92	Abdera quadrifasciata	Melandryidae	Coleo	2.5-4	xylo	myco	O	p	ste	3
93	Conopalpus brevicollis	Melandryidae	Coleo	3.5-4	xylo, arbori	xylodetriti	O	a	ste	2
94	Conopalpus testaceus	Melandryidae	Coleo	5-7	xylo, arbori	xylodetriti	O	a	ste	ng
95	Orchesia minor	Melandryidae	Coleo	3-4	xylo, arbori	xylodetriti	O	p	ste	ng
96	Phloiotrya rufipes	Melandryidae	Coleo	5-9	xylo, arbori	xylodetriti	O	a	ste	3
97	Aplocnemus impressus	Melyridae	Coleo	4-5	arbori	L: zoo, I: polleno	O	a	eur	ng
98	Dasytes plumbeus	Melyridae	Coleo	3.5-4.6	arbori, herbi, flori	L: zoo, I: polleno	T	a	ubi	ng
99	Tomoxia bucephala	Mordellidae	Coleo	5.5-8.5	xylo, flori	L: xylodetriti, I: polleno	T	a	ste	ng
100	Litargus connexus	Mycetophagidae	Coleo	2.3-3.8	corti, xylo	myco	O	p	eur	ng

(continued)

Species Number	Species	Familia	Ordo	Size (mm)	Microhabitat	Trophy	Relation to beech	CWD affinity	Habitat specifity	Red List status
101	Epuraea melanocephala	Nitidulidae	Coleo	2-3	flori, arbori	polleno	T		eur	ng
102	Meligethes aeneus	Nitidulidae	Coleo	1.5-2.7	flori, herbi	L: phytophag, I: polleno	T		ubi	ng
103	Meligethes czwalinai	Nitidulidae	Coleo	2.3-3.1	flori, herbi	L: mono, I: polleno	T		ste	2
104	Nacerdes carniolica	Oedemeridae	Coleo	9-15	xylo, flori	L: xylodetriti, I: polleno	T	a	ste	3
105	Omalisus fontisbellaquaei	Omalisidae	Coleo	5-7	herbi, flori		O		eur	ng
106	Olibrus flavicornis	Phalacridae	Coleo	2.3-3	flori, herbi	oligo	T		ste	ng
107	Acrotrichis intermedia	Ptiliidae	Coleo	1-1.1	detriti	myco	O		eur	ng
108	Ptinus rufipes	Ptinidae	Coleo	3-4.5	arbori	xylodetriti	O	a	eur	ng
109	Lasiorhynchites olivaceus	Rhynchitidae	Coleo	3.3-5.5	arbori	mono	T		eur	ng
110	Lissodema denticolle	Salpingidae	Coleo	2.5-3.3	arbori	zoo	O	f	eur	ng
111	Salpingus planirostris	Salpingidae	Coleo	3-3.5	corti, xylo	zoo	O	f	eur	ng
112	Salpingus ruficollis	Salpingidae	Coleo	3.3-4.5	corti, xylo	zoo	O	f	ste	ng
113	Ernorporicus fagi	Scolytidae	Coleo	1.5-2	arbori, corti	xylo	O	f	ste	ng
114	Scolytus intricatus	Scolytidae	Coleo	2.5-3.5	arbori, corti	xylo	O	f	eur	ng
115	Anaspis flava	Scraptiidae	Coleo	2.8-4	herbi, arbori	L: xylodetriti, I: polleno	T	a	eur	ng
116	Anaspis maculata	Scraptiidae	Coleo	2.5-3	flori, arbori, herbi	L: xylodetriti, I: polleno	T	a	eur	ng
117	Anaspis thoracica	Scraptiidae	Coleo	2.5-3	flori, arbori, herbi	L: xylodetriti, I: polleno	T	a	eur	ng
118	Scraptia fuscula	Scraptiidae	Coleo	2.3-2.8	xylo, arbori	xylodetriti	O	a	ste	3
119	Atheta fungi	Staphylinidae	Coleo	2.4-2.8	humi, phytodetriti	zoo	O		ubi	ng
120	Atheta palustris	Staphylinidae	Coleo	2.6	phytodetriti	zoo	O		eur	ng
121	Cypha longicornis	Staphylinidae	Coleo	1-1.4	phytodetriti	zoo	O		ubi	ng
122	Eusphalerum rectangulum	Staphylinidae	Coleo	1.5-2.2	flori	polleno	T		eur	ng
123	Holobus flavicornis	Staphylinidae	Coleo	1.5	arbori	zoo	O		eur	ng
124	Leptusa ruficollis	Staphylinidae	Coleo	2-2.3	arbori, corti	zoo	O		eur	ng
125	Phloeocharis subtilissima	Staphylinidae	Coleo	1.5-2	arbori, corti	zoo	O	a	eur	ng

(continued)

Species Number	Species	Familia	Ordo	Size (mm)	Microhabitat	Trophy	Relation to beech	CWD affinity	Habitat specifity	Red List status
126	Tachinus fimetarius	Staphylinidae	Coleo	4-5	phytodetriti, flori, stercori	zoo	O		eur	ng
127	Nalassus laevioctostriatus	Tenebrionidae	Coleo	7-11	arbori, corti	L: detriti, I: algo	O	a	eur	ng
128	Trixagus dermestoides	Throscidae	Coleo	2.1-3.2	arbori, herbi	L: detriti, I: algo	O		eur	ng
129	Apterygida media	Forficulidae	Derma	9-15		pantho	O		eur	ng
130	Acanthosoma haemorrhoidale	Acanthosomatidae	Hemi	14-17	arbori	poly	O		eur	ng
131	Anthocoris confusus	Anthocoridae	Hemi	3.2-3.9	arbori	zoo	O			ng
132	Anthocoris nemoralis	Anthocoridae	Hemi	3.3-4.1	arbori	zoo	O			ng
133	Anthocoris nemorum	Anthocoridae	Hemi	3.5-4.4	arbori, herbi	pantho	O			ng
134	Orius minutus	Anthocoridae	Hemi	2.1-2.5	herbi, arbori	zoo	O		eur	ng
135	Temnostethus gracilis	Anthocoridae	Hemi	2.3-2.6	arbori, corti	zoo	O			ng
136	Temnostethus pusillus	Anthocoridae	Hemi	2.5-3.1	arbori, corti	zoo	O		eur	ng
137	Xylocoris cursitans	Anthocoridae	Hemi	1.8-2.5	xylodentriti	zoo	S	a	ste	ng
138	Aphididae sp. 1	Aphididae	Hemi	1.5			O			ng
139	Aphis fabae	Aphididae	Hemi	1.5-3.1	herbi	poly	T		eur	ng
140	Aphis farinosa	Aphididae	Hemi	1.6-2.5	arbori	mono	T		eur	ng
141	Aphis spec. 1	Aphididae	Hemi	1.5			T			ng
142	Chaitophorus sp. 1	Aphididae	Hemi	1.5	arbori	mono	T			ng
143	Drepanosiphum platanoidis	Aphididae	Hemi	3.2-4.3	arbori	mono	T		eur	ng
144	Drepanosiphum sp. 1	Aphididae	Hemi	1.5	arbori	mono	T			ng
145	Dysaphis anthrisci	Aphididae	Hemi	1.9-2.3	arbori, herbi	mono	T		eur	ng
146	Lachnus pallipes	Aphididae	Hemi	2.8-5	arbori	oligo	S		ste	ng
147	Macrosiphum euphorbiae	Aphididae	Hemi	1.7-3.6	herbi	poly	T		eur	ng
148	Macrosiphum sp. 1	Aphididae	Hemi	1.5		mono	T			ng
149	Myzocallis coryli	Aphididae	Hemi	1.3-2.2	arbori	mono	T		eur	ng
150	Myzocallis spec. 1	Aphididae	Hemi	0.9-3	arbori	mono	T			ng

(continued)

Species Number	Species	Familia	Ordo	Size (mm)	Microhabitat	Trophy	Relation to beech	CWD affinity	Habitat specifity	Red List status
151	Periphyllus sp. 1	Aphididae	Hemi	1.5	arbori	mono	T			ng
152	Phyllaphis fagi	Aphididae	Hemi	1.1-3.2	arbori	mono	S		ste	ng
153	Pterocallis sp. 1	Aphididae	Hemi	1.5	arbori	mono	T			ng
154	Thelaxes dryophila	Aphididae	Hemi	1.1-2.3	arbori	mono	T		eur	ng
155	Therioaphis riehmi	Aphididae	Hemi	2-2.7	herbi	oligo	T		eur	ng
156	Tuberculatus annulatus	Aphididae	Hemi	1.7-2.2	arbori	mono	T		eur	ng
157	Tuberculatus borealis	Aphididae	Hemi	1.9-2.3	arbori	mono	T		eur	ng
158	Tuberculatus sp. 1	Aphididae	Hemi	1.5	arbori	mono	T			ng
159	Loricula elegantula	Microphysidae	Hemi	1.4-2.3	arbori, licheni	zoo	O		ste	ng
160	Campyloneura virgula	Miridae	Hemi	3.9-4.7	arbori	zoo	O		eur	ng
161	Orthotylus tenellus	Miridae	Hemi	4.2-4.7	arbori	pantho	O			ng
162	Phylus melanocephalus	Miridae	Hemi	4.6-6	arbori	pantho	O		eur	ng
163	Phytocoris pini	Miridae	Hemi	5.5-6.6	arbori	zoo	O			ng
164	Phytocoris tiliae	Miridae	Hemi	6-6.9	arbori, corti	pantho	O		eur	ng
165	Psallus mollis	Miridae	Hemi	3.2-3.8	arbori	pantho	O		eur	ng
166	Psallus variabilis	Miridae	Hemi	3.5-4.3	arbori	pantho	O			ng
167	Psallus varians	Miridae	Hemi	3.8-4.7	arbori	pantho	O		eur	ng
168	Rhabdomiris striatellus	Miridae	Hemi	7-8.5	arbori	pantho	O		eur	ng
169	Pentatoma rufipes	Pentatomidae	Hemi	12-15	arbori	pantho	O		eur	ng
170	Psyllopsis distinguenda	Psyllidae	Hemi	3-4	arbori	mono	T		eur	ng
171	Rhinocola aceris	Psyllidae	Hemi	1.5-2.5	arbori	mono	T		eur	ng
172	Cimbex cf. fagi	Cimbicidae	Hymeno	45	arbori	mono	S		ste	deficient
173	Nematus fagi	Tenthredinidae	Hymeno	45	arbori	mono	S		ste	deficient
174	Meconema thalassinum	Tettigoniidae	Ortho	11-15	arbori	zoo	O		eur	ng
175	Pholidoptera griseoaptera	Tettigoniidae	Ortho	13-20		pantho	O		eur	ng

Color Plates

Color Plate 1: Insecticidal knockdown ('*fogging*') of arboricolous arthropods in beech canopies of the Northern Palatinate highlands. The cannon-like barrel resonates at high frequencies in order to disperse the oil-insecticide solution. A cumulative duration of 5-10 min is sufficient for an exhaustive sampling. © Rainer Wirth. Also see coverage by SWR short news on the study and the sampling methodology: https://goo.gl/snhNNE.

Color Plate 2: Rising column of insecticide used in fogging of arboricolous arthropods. Note that insecticidal knockdown can only be sensibly applied at dusk or early dawn (seen here), when thermal dynamics are minimal and the column rises by its own inherent heat. © Tatjana Koch. Also see coverage by SWR short news on the study and the sampling methodology: https://goo.gl/snhNNE.

Color Plate 3: Arthropod collection after fogging. Top: Two tarpaulins (4 x 5 m) are placed beneath the fogged target tree and margins lifted by sticks to prevent contamination by walking forest floor fauna. © Tatjana Koch. Bottom: After a drop time of 2 h, arthropods are collected with fine brushes and stored in 70% ethanol. Large arthropods are visible by eye (see picture), together with inevitable debris particles. © Kevin Bähner.

Color Plate 4 (next page): Taxonomic and morphological variety of arboricolous insect collections in beech canopies in the Northern Palatinate highlands. Species were chosen either for their dominance, attractivity, or peculiarity of their ecological role.

A *Cimbex* cf. *fagi*, *Cimbicidae*
45 mm, monophagous. This caterpillar-like herbivore is one of the few sawflies exclusively feeding on beech. They are therefore preferably found in beech vegetation, particularly the crown. Sawfly larvae are easily confused with *Lepidoptera* caterpillars, but the formation of prolegs on all abdominal segments identifies them as *Symphyta* (*Hymenoptera*). © Miroslav Fiala.

B *Campyloneura virgula*, *Miridae*
3.9-4.1 mm, zoophagous. This mirid was strikingly dominant in the collection of arboricolous arthropods, with 1,378 specimen. Males are hardly found, strengthening the impression that this species reproduces parthenogenetically (hence the name *virgula*). They indiscriminately suck on smaller invertebrates, such as aphids, psyllids, and mites. Adults, and even more nymphs (small picture), are easily recognized by the red stripes on their pronotum, head, and antennae. © Brian Valentine (adult), User *Sarefo*, Wikimedia (nymph).

C *Pentatoma rufipes*, *Pentatomidae*
12-15 mm, panthophagous. This comparatively large shield bug is widespread and common across European forests, including the Northern Palatinate highlands (Bähner et al. 2016a, b). It opportunistically sucks on leaves, fruits, and captured invertebrates. © Dirk Vorbusch.

D *Dromius quadrimaculatus*, *Carabidae*
4-6 mm, zoophagous. This comparatively small carabid with the striking four dorsal yellow patches on the abdomen is one of the few ground beetles exclusively found in the canopy. It roams the bark of deciduous trees hunting for invertebrates. © Waldentomologie WSL.

E *Leiopus nebulosus*, *Cerambycidae*
6-10 mm, xylophagous. This longhorn beetle with rather thick built can be found on bark, small twigs, and in brushwood, feeding on dry dead wood. It is easily recognized by its black speckles on gold/ocher colored back. © Frank Köhler.

F *Curculio glandium*, *Curculionidae*
4-7.5 mm, polyphagous. Females of the acorn weevil, as its name suggests, bore holes into acorns for oviposition, where the larvae develop. Adults feed on a wide range of deciduous trees. This genus is eponymous for the weevil family. © Ingrid Altmann.

G *Orchestes fagi* (= *Rhynchaenus fagi*), *Curculionidae*
2-2.5 mm, monophagous. This rather small weevil feeds exclusively on beech. Although it can cause calamities in mass outbreaks, it was found in rather small numbers in this study (38). As the German common name (Buchenspringrüssler) suggests, these insects are capable of escaping by jumping, as further indicated by their thick hind legs. © Andreas Haselböck.

H *Phyllaphis fagi*, *Aphididae*
1.1-3.2 mm, monophagous. This herbivore is exclusively found on *Fagus sylvatica* and is unmistakable by its wax wool, which is most probably used to irritate predators. Colonies are typically found under beech leaves (often whitish leaf surface due to wax wool) and can cause curling of the leaves. They are common and widespread in Europe and the Northern Palatinate highlands (Petry 2013). © Ondřej Zicha.

I *Ectobius sylvestris*, *Ectobiidae*
6-14 mm, panthophagous. This is one of the six free living cockroach species found in Germany, none of them being household pests. They can be easily confused with the German cockroach (*Blattella germanica*, *Blattelidae*), but does not exhibit two brown longitudinal stripes on the pronotum and is entirely harmless. © Marion Friedrich.

J *Loricula elegantula*, *Microphysidae*
1.5-2.3 mm, zoophagous. This predator is one of the smallest bugs found in Germany. They roam the bark of various trees within epiphytic lichens, particularly *Parmelia* spp. and *Cladonia* spp. © Joe Botting.

K *Xylocoris cursitans*, *Anthocoridae*
1.8-2.5 mm, zoophagous. This flower bug is one of the few true bugs with a pronounced affinity for dead wood. Nymphs and adults hunt for smaller arthropods under the bark of woody debris. They are widespread and common. © Gernot Kunz.

L *Cryptocephalus pusillus*, *Chrysomelidae*
2.5-3 mm, polyphagous. This leaf beetle can be considered an opportunist on beech, as it feeds on various deciduous trees, but has a natural affinity for *Salix* spp., *Alnus* spp. and *Populus* spp. It is therefore often found in riparian forests and is considered hygrophilous. © Marek Roman Swadzba.

M *Rhabdomiris striatellus*, *Miridae*
7-8.5 mm, panthophagous. Nymphs of this comparatively large plant bug feed preferably on flowers and fruits of host trees, whereas adults are predators, particularly of aphids. The striking, attractive striation of black and gold is variable and might hence increase risk of confusion with the taller, more slender *Miris striatus* (*Miridae*). A distinguishing feature is the cuneus, which is never black-tipped in *M. striatus*. © Ekkehard Wachmann.

N *Lagria hirta*, *Lagriidae*
7-10 mm, polyphagous. This species received its name (*hirta*) by the dense, fine hair, by which it is covered. It is an unselective herbivore on herbs and trees, widespread and common, with a preference for warm, dry habitats (xerophilous). © Holger Gröschl.

O *Meconema thalassinum*, *Tettigoniidae*
11-15 mm, zoophagous. This rather large predator is strictly arboricolous, preferring light crowns of deciduous trees. This lifestyle is reflected in its mode of communication: *M. thalassinum* lost its ability for stridulation, instead drumming its hind legs on thick leaves and small twigs. While it is widespread across Germany, the similar congeneric *M. meridionale* has had a more southern, Mediterranean distribution. Yet, it is now increasingly found Germany, shifting it northern distribution border year by year. © Christian Roesti.

P *Athous vittatus*, *Elateridae*
9-11.5 mm, polyphagous. Although this click beetle feeds on various deciduous trees, it is indicative of beech forests. Eponymous for the family is the ability to snap their prothorax forward, producing the typical click-sound and catapulting the beetle into the air as an evasive strategy. © Andrea Haselböck.

Q *Tomoxia bucephala*, *Mordellidae*
5.5-8.5 mm, xylophagous/pollenophagous. This species of pintail beetles changes its lifestyle during development. Larvae feed on dead wood of deciduous trees, while adults eat pollen of various understory flowers. They are hence dependent on the occurrence of dead wood. © User Siga, Wikimedia.

R *Lachnus pallipes*, *Aphididae*
2.8-5 mm, monophagous. This aphid is substantially larger than P. fagi and rather conspicuous through its dark coloration. It forms a mutualistic bond with ants, mostly wood ants (*Formica* spp.), which provide protection in exchange for nutritious honeydew. Adaptions include dense setae at the aphid's back, forming a basket (trophobiotic organ) to hold honeydew droplets, as well as lifting of hind legs to imitate antennae movement of worker ants. © Bob Dransfield.


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Color Plate 5 (next page): Red listed insects (all beetles, *Coleoptera*) in beech canopies in the Northern Palatinate highlands. Numbers indicate threat level. RL2: endangered; RL3: vulnerable (see below).

A *Conopalpus brevicollis, Melandryidae*
3.5-4.0 mm, xylophagous, RL2. This arboricolous species from the family of false darkling beetles is not only stenotopous and endangered, but also one of the two significant indicator species in this study. It showed a preference for relatively unmanaged interior forests, which is in line with its natural dependence on old, standing dead wood. As it is simultaneously thermophilous, one might speculate that it inhabits the upper parts of the canopy and exposed snags. © Frank Köhler.

B *Pseudocistela ceramboides, Alleculidae*
10-12 mm, xylophagous, RL2. Larvae of this species of comb-clawed beetles develop in arboreal duff and woody debris of advanced decomposition. Similarly, the relatively large adults inhabit decaying wood, but are also occasionally found on flowers, possibly complementing their nutrition with pollen or nectar. © Christoph Benisch.

C *Dorcatoma setosella, Anobiidae*
2.2-2.5 mm, mycetophagous, RL2. Among the few things known about this minute beetle is its strong dependence on polypores, being polyporicolous and mycetophagous. Hence, by extension, it is also reliant on the occurrence of dead wood in late decompositional stages with strong fungal infestation. © Frank Köhler.

D *Arthrolips obscura, Corylophidae*
1.2-1.6 mm, mycetophagous, RL2. This small species of minute fungus beetles feeds on wood decaying fungi, dwells in small twigs, rotting foliage, and rotting wood and prefers warm and moist forest habitats. © Arved Lompe.

E *Kyklioacalles aubei* (= *Acalles aubei*), *Curculonidae*
3.5-5.5 mm, xylophagous, RL2. While most weevil species are phytophagous, this species prefers feeding on old decaying twigs of deciduous trees. It is pholeophilous, preferring shady microhabitats in old, close-to-nature forests, particularly beech forests. © Josef Dvořák.

F *Exocentrus adspersus, Cerambycidae*
50-80 mm, xylophagous, RL3. Although it is a comparatively large species of longhorn beetles with a rather sturdy built, *E. adspersus* is excellently camouflaged by its mottled coloration of brown and white. It is xylophagous on recently died deciduous trees, with a preference for oak, and inhabits light and warm forest stands. © Frank Köhler.

G *Euglenes oculatus, Aderidae*
2.1-2.6 mm, RL2. This species of ant-like leaf beetles with unknown feeding mode has a preference for shady forest habitats (pholeophilous), possibly inhabiting arboreal duff. © Christoph Benisch.

H *Nacerdes carniolica, Oedemeridae*
9-15 mm, pollenophagous, RL3. *N. carniolica* can be considered a transient species in beech canopies. Larvae of this species of false blister beetles develops in rotting wood of *Pinus sylvestris*, whereas adults feed on pollen of scented flowers including *Rosa* spp. (*Rosaceae*), *Aesuclus* spp. (*Sapindaceae*), or *Tilia* spp. (*Malvaceae*). © Frank Köhler.

I *Acalles dubius, Curculionidae*
2.5 mm, xylophagous, RL3. A small weevil, which prefers warm, yet dark habitats, feeding on dead wood of various deciduous trees. © Friedhelm Bahr.

J *Hypebaeus flavipes, Malachiidae*
2 mm, zoophagous, RL3. This species of soft-winged flower beetles predates other arthropods in warm, light forests, hence a suitable species to be found in beech crowns. Adults occasionally complement their nutrition with pollen. © Christoph Benisch.

K *Meligethes czwalinai, Nitidulidae*
2.3-3.1 mm, pollenophagous, RL2. This species of sap beetles can be considered to be transient in beech canopies, as its natural history is centered on *Fraxino-Aceretum* forests. It is hygrophilous, its larvae are monophagous on perennial honesty (*Lunaria rediviva*, *Brassicaceae*), and adults are flower visitors. © Lech Borowiec.

L *Scraptia fuscula, Scraptiidae*
2.3-2.8 mm, xylophagous, RL3. A wood-foraging species of false flower beetles, preferring light deciduous forests, forest edges, and occasionally gardens. © Frank Köhler.

M *Abdera quadrifasciata, Melandryidae*
2.5-4.0 mm, mycophagous, RL3. Photophilous and thermophilous, this species of false darkling beetles inhabits dead trunks and branches of deciduous trees (preferably oak), feeding on bracket fungi. © Frank Köhler.

N *Phloiotrya rufipes, Melandryidae*
5-9 mm, xylophagous, RL3. A false darkling beetle with a preference for dark, moist forests, feeding on dead wood of deciduous trees, particularly beech, hornbeam, willow, and alder. © Hubert Polacek.

O *Tillus elongatus, Cleridae*
6-10 mm, zoophagous, RL3. Although it is indicative of beech forests, this species of checkered beetles prefers light, warm patches. Females oviposit eggs in holes and crevices of dead wood (particularly beech). Larvae hunt for larvae of other insects (especially *Ptilinus* spp., *Anobiidae*) within their own galleries. © User Siga, Wikimedia.

P, Q, and R *Malthinus facialis*, *Malthinus fasciatus*, and *Malthodes holdhausi*, *Cantharidae*
3-4.5 mm, all zoophagous and RL3. From the thirteen species of *Malthinus* and *Malthodes* in this study, these three are under protection. The high species richness of these two genera in the Northern Palatinate highlands is quite striking. Like the majority of soldier beetles, they are predatory, with occasional visits on flowers. *M. facialis* is further indicative of *Fagetalia* forests. © Christoph Benisch, Udo Schmidt, Johannes Reibnitz.


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Chapter 5

Robustness of plant-herbivore interaction networks to climate change in a fragmented temperate forest landscape

Elephant hawk-moth (*Deilephila elpenor*, *Sphingidae*) a polyphagous herbivore, encountered on loosestrife (*Lythrum* spp.) on the way to a study site. Note the eye-like patches. When startled, the head is retracted (compare picture), and the thorax is swayed sideways, imitating a snake's head.

INTRODUCTION

No doubt, forest fragmentation and climate change, alone or in combination, are among the greatest threats to biodiversity persistence and ecosystem functioning (Thomas et al. 2004, Traill et al. 2010, Morris 2010). It is well known that tropical forest fragmentation, via habitat loss and isolation (habitat fragmentation *per se*), and edge effects (Fahrig 2003), is likely to cause population collapse, species extirpation, and reorganization of native communities towards simplified and more similar communities in taxonomic and functional terms (Laurance & Lovejoy 2002, Wirth et al. 2008, Santos et al. 2008, Leal et al. 2012). Relatively little is known, however, about fragmentation effects on temperate forest ecosystems (Honnay et al. 2002), most probably because of the traditional focus on forest management, although deforestation is often extensive (e.g. 31% in Germany, MUF 2002) and many centuries old (Frey & Lösch 2010). Our understanding how climate change impacts on the reorganization of tropical or temperate native communities is even more rudimentary, despite increasing attention given to plant-animal interactions in this context (Tylianakis et al. 2008, Morris 2010). In Europe, climate change is expected to profoundly affect the composition of plant communities (Pompe et al. 2010) through distributional shifts, altered competition dynamics (Klanderud 2005), such as proliferation of thermophiles (Reid 2006), and local extinction (Pompe et al. 2010). Forests are particularly threatened (predicted cover reduction of 11.7% – 19.9%, (Pompe et al. 2010), because of their long life cycle (Lindner et al. 2010). Consequently, re-organization of plant communities may cascade to higher trophic levels and disrupt trophic interaction (Kaneryd et al. 2012), e.g., through phenological (Traill et al. 2010) and distributional mismatch (Schweiger et al. 2008), while thermotolerant species will benefit (Filz et al. 2013).

Trophic webs represent a key component of ecosystems, with substantial importance for ecosystem level properties such as functioning (Morris 2010, Rzanny & Voigt 2012, Miranda et al. 2013), service provision (Memmott et al. 2004), biodiversity persistence (Morris 2010) and stability (Emmerson et al. 2005, Rzanny & Voigt 2012). Amongst them, plant-herbivore interaction networks (PHNs) harbour the bulk of terrestrial biodiversity (Price 2002) and play a significant functional role, e.g., for the distribution of energy and biomass to other trophic levels (Haddad et al. 2011, Rzanny & Voigt 2012). By integrating over multiple taxa across trophic levels, PHNs go far beyond what could be addressed in previous studies on plant-herbivore interactions. Therefore, and because they are closely linked to the global loss of species and ecosystem functioning (Morris 2010, Rzanny & Voigt 2012, Miranda et al. 2013), ecological networks have received increasing awareness as indicators of trophic disruptions (Heleno et al. 2012, Rzanny & Voigt 2012) and progressive simplification of ecosystems in the face of anthropogenic disturbance (Tylianakis et al. 2007, Laliberté & Tylianakis 2010, Valladares et al. 2012).

In the case of temperate forests, more research on fragmentation effects on PHNs is needed, as the scarce evidence suggests contrasting patterns to the far better researched tropics. For example, fragmented forests in temperate regions harbour higher plant diversity than continuous forests (Honnay et al. 2002). This may lead to greater herbivore diversity (van Halder et al. 2010) and more potential feeding links for polyphagous herbivores in forest edges, thus leading to increased complexity of trophic interactions and hence food web stability (Haddad et al. 2011). On the other hand, PHNs in managed continuous forests can be expected to be composed of generalist herbivores with narrow realized niches, as silviculturally important tree species (e.g., beech, *Fagus sylvatica*) with a low natural set of specialists (Sprick & Floren 2008) are predominant and therefore offer little resource diversity. In relation to climate change, some inferences may be drawn from previous research on single trophic levels and their interactions, such as the intensifications of particular trophic links via higher plant productivity (Emmerson et al. 2005, Traill et al. 2010) or temperature-driven increase in the abundance/performance of insect herbivores (reviewed in Bale et al. 2002). Differential responses of generalist and specialist herbivores to climate change may alter competition dynamics towards more uneven and simplified PHNs. Bottom-up extinction cascades are likely because of proportionally higher extinction-probabilities for primary producers, compared to other trophic levels (Kaneryd et al. 2012), and increasing variability of overall population densities and temperatures (Emmerson et al. 2005).

The implications for food web functioning and stability resulting from anthropogenic disturbance can be evaluated via structural network components such as complexity (Rzanny & Voigt 2012), niche redundancy (Blüthgen et al. 2006, Blüthgen & Klein 2011) and cohesiveness (Tylianakis et al. 2010), as well as by modelling extinction cascades (Dunne et al. 2002, Memmott et al. 2004). After several studies highlighting the sensitivity of ecological networks to extinction cascades based on structured (e.g. random) extinction scenarios (Dunne et al. 2002, Memmott et al. 2004), species-oriented approaches allowing biologically more meaningful predictions are now increasingly adopted (Ives & Cardinale 2004, Kaiser-Bunbury et al. 2010, Bellingeri & Bodini 2012). In this context, linking structural network topology to network robustness against biologically plausible extinction cascades (Fortuna & Bascompte 2006, Morris 2010, Miranda et al. 2013) may serve as a tool for identifying fragile (parts of) food webs, with potential relevance for conservation principles (Heleno et al. 2012).

The present study investigates for the first time the conjoined impacts of temperate forest fragmentation and climate change on the structure of PHNs and relates network topology to network robustness under realistic extinction sequences. For this I adopted an extensive sampling regime of insect herbivores on more than 1300 individual trees across 36 plots in forest edges, small fragments, and the interior of continuous control forests in a highly fragmented and managed temperate forest landscape in SW-Germany. Following previous evidence indicating a fragmentation-induced rise in species numbers of both plant and insect herbivores (Honnay et al. 2002, van Halder et al. 2010), I expected that PHNs in edges and small fragments have (i) higher complexity, cohesiveness and trophic redundancy as well as (ii) increased robustness against secondary extinctions in climate change-based extinction scenarios, as opposed to networks from the forest interior. I assume this decline in climate change susceptibility to be caused by a combination of higher thermotolerance across the plant communities (Reid 2006) and higher network complexity, cohesiveness and redundancy, which can be demonstrated by linking network topology to PHN robustness. Furthermore, this paper aims at discussing management implications arising from the potential anthropogenic changes in PHN integrity, with particular emphasis on the conservation value of European beech forests.

METHODS

The study landscape is located in the Northern Palatinate highlands, a low, undulating mountain range (250 – 687 m asl) of Permian origin covering an area of 1,556.4 km² in SW Germany (**Figure 1**). It is characterized by temperate Central European climate under oceanic influence (mean annual precipitation: 800 mm; mean annual temperature: 9.4°C, 1970-2010, Deutscher Wetterdienst 2013). Forests are deciduous, broad-leaved woodlands, phytosociologically classified as *Carpino-Fagetalia* mixed forests with varying transitional degrees of *Fagion* and *Carpinion betuli* stands. Extensive deforestation in the Middle Ages occurred mainly in sand and siltstone-dominated valleys, while the agriculturally less valuable igneous hilltops were mostly forested. This has led to a landscape of hyper-fragmented forests, embedded in a matrix of cultivated fields, pastures and meadow orchards. The length of all forest edges of the federal state totals 45,170 km (exceeding even earth's circumference, (MUF 2002). Forest cover of the selected portion (32%) of this landscape (1,010 km², 49° 36' N and 7° 44' E) is representative for rest of Germany (31%, MUF 2002). Despite its high fragmentation degree with over 1,300 forest fragments ranging from 0.1 to 5616 ha (ca. 80% of them < 10 ha) the region still harbours large forest tracts exceeding 1,000 ha.

Study sites were established in 2008 as 36 permanent plots (20 x 50 m; 0.1 ha) in three habitat types reflecting fragmentation-induced and continuous forest conditions: (i) forest edges: peripheral areas within 50 m of the border of large forest tracts (continuous control forests, the three largest forest tracts in the study region, 1,049, 3,512 and 5,616 ha) to address edge effects; (ii) center of 12 small forest fragments (ranging between 2.2 and 145.1 ha) entirely surrounded by matrix, reflecting habitat loss, isolation and fragmentation effects *per se*; (iii) forest interior: core areas of control forests beyond 100 m of the border and without detectable edge influence. This design reflects the landscape configuration available to us, that is, a severely fragmented region typical for Germany (Forest Europe 2011) including three large forest stands that could be adopted as control areas

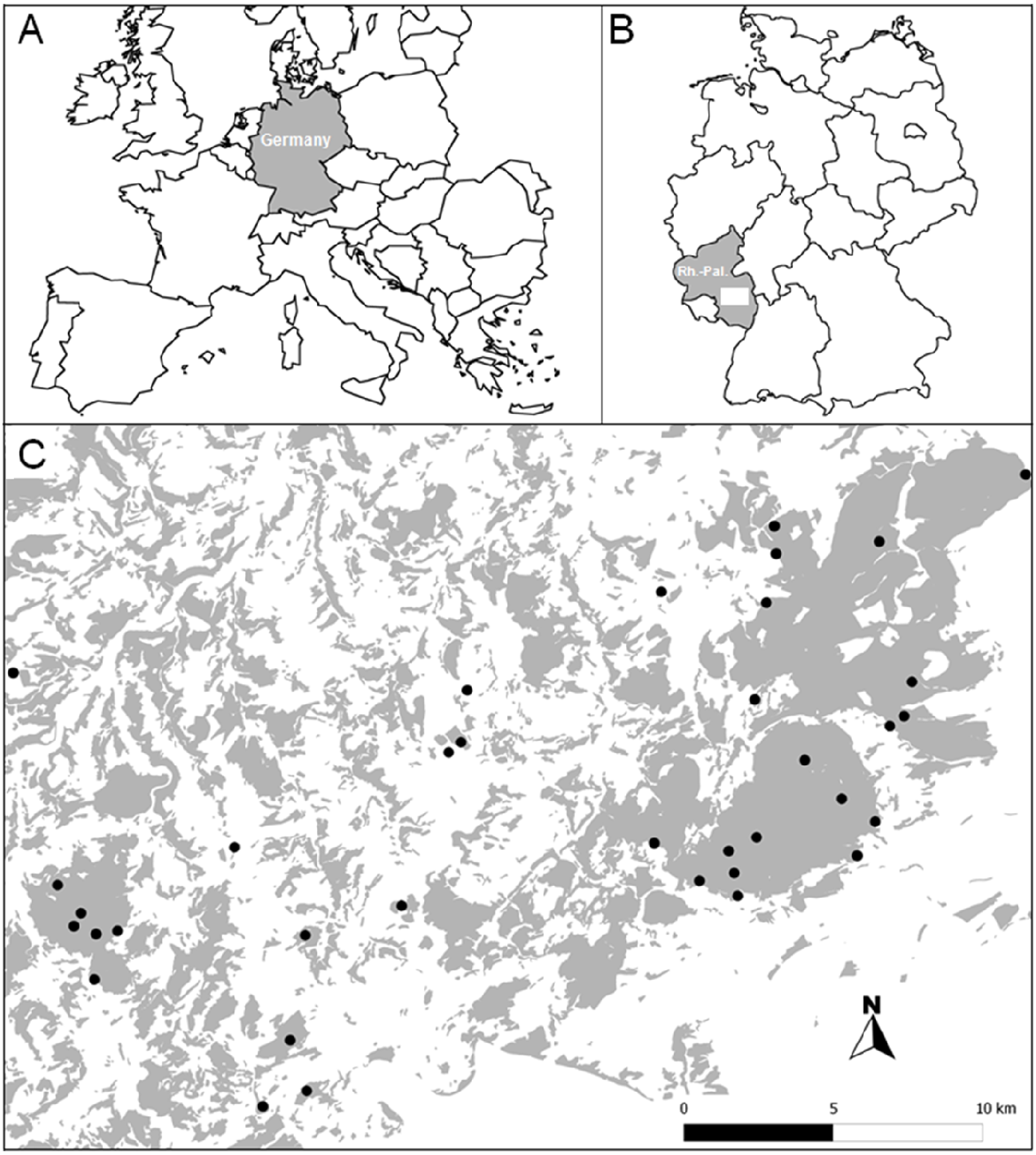

Figure 1: Maps showing the location of the study landscape, the Northern Palatinate highlands, with respect to Central Europe (A) and SW Germany (B), indicated as white rectangle in the state of Rhineland-Palatinate (Rh.-Pal.). The study landscape (C) shows forest fragments (grey polygons) embedded in a matrix of agricultural land uses (white) and 36 randomly established sampling sites (black dots) in the centre of small forest fragments (< 1,000 ha), along forest edges, and in forest interiors within continuous control forests (> 1,000 ha).

following similar studies (Girão et al. 2007, Valladares et al. 2012). Inter-plot distance ranged from 0.3 to 35.4 km with 13.9 ± 7.6 km (mean ± SD). All woody plant species > 1.3 m height were identified. Plant diversity (Shannon-index) declined more than threefold from forest edges over forest fragments to interior control forests, with the three most dominant tree species being *Fagus sylvatica* (44.27%), *Carpinus betulus* (29.86%) and *Quercus petraea* (5.17%, supplementary, **Figure S2**, **Table S1**).

Insect herbivores were sampled alive in the understory stratum (1.3 – 2 m) of the plots during two field campaigns (May to August 2010 and August to September 2010) by beating the foliage of each woody plant individual regardless of age class over a funnel-shaped trap (**Figure S1**). Sampling intensity totaled 207 h of beating and 1,353 woody plant individuals. PHNs may be confounded by false positive interactions (tourists), because herbivores are often highly mobile and found on non-host trees. Separation of such transients from true herbivores was achieved by using no-choice feeding-assays and analyzing published host plant records of identified species (supplementary, **Table S3**). Insects were assigned to morphospecies and later identified to species level whenever possible (56%) using standard keys or experts (see acknowledgements and supplementary). Caterpillars were reared to adults, if possible, and then identified. Voucher specimens were deposited at the Natural Museum of Basel (*Psylloidea*) and at the department of Plant Ecology and Systematics at the University of Kaiserslautern (all other taxa).

For network-related definitions and terminology I followed Dormann et al. (2009). To quantify topological network properties related to network robustness (complexity, cohesiveness and trophic niche redundancy) I measured Shannon diversity of interactions (H_2, Rzanny & Voigt 2012), nestedness (Bascompte et al. 2003) and the complementary specialization at network level (H_2’, Blüthgen et al. 2008). Shannon diversity of interactions simply is the two-dimensional equivalent of the Shannon index (Rzanny & Voigt 2012) and is positively affected by the number of links and their evenness (Blüthgen et al. 2008). In nested bipartite networks few species from both trophic levels form a core or hub of many strong links that also connects to all other species as succeeding subsets. Nestedness therefore also is a measure for trophic redundancy (Bascompte & Jordano 2007). Consequently, nested PHNs are highly resistant to extinctions, in which least abundant species die off first, because a large core of interactions remains relatively unchanged until the very end of an extinction series (Bascompte & Jordano 2007), yet they are highly fragile if strongly connected species are eliminated first (Memmott et al. 2004). Nestedness is affected by, and must hence be controlled for, sampling effort, since nested interaction patterns can be the result of abundance-based interactions (Blüthgen 2010) under interaction neutrality (Vázquez et al. 2009). From the various available metrics that measure nestedness, I chose the *BINMATNEST* algorithm (Rodríguez-Gironés & Santamaría 2006) that gives values between 0 (perfect nestedness) and 100 (maximal matrix entropy). The complementary specialization on network level (H_2’, (Blüthgen et al. 2006) measures niche-based trophic complementarity in a network. It is a normalized derivative from the Shannon diversity of interactions (H_2, see above) based on constant matrix row- and column sums. An H_2' score of 0 represents maximal redundancy, i.e. each trophic niche is nested within another (Blüthgen & Klein 2011), while values close to 1 indicate high niche complementarity (Blüthgen et al. 2006), i.e. the full range of host plants is needed to sustain the herbivore community. Note that the metric measures the topology of realized, rather than fundamental niches (Blüthgen & Klein 2011), as it is applied to empirical data under field conditions.

Concerning network analysis, it is noteworthy that managed European forests are inherently poor in woody plant species, which further induces low herbivore richness. Hence, PHNs often remain poor in interactions, resulting in networks of low dimensionality, especially on a local scale. Given that ecological networks are prone to sampling bias (Blüthgen 2010), tools are therefore needed to home in on the 'true' structure of a network and in order to make PHNs in temperate forests researchable (Vázquez et al. 2009). To maximize standardization and comparability of my data, I adopted three approaches proposed by Blüthgen (2010): (i) Sampling of equal areas (12,000 m^2 in each of the two sampling campaigns) in each habitat, (ii) rarefaction (Blüthgen et al. 2006) of PHNs to the size of the smallest network (forest interior, m = 217) with 100 rarefaction cycles per habitat (**Figures S3**, **S4**) and (iii) comparison of PHNs with null models (Patefield algorithm, Blüthgen et al. 2008, 10 per step in each rarefaction cycle). Habitat-wise comparisons of network metrics were made between the large networks (comprising all interactions minus one randomly deleted interaction in the rarefaction procedure, hereafter "full networks") and between the small networks (rarefied to the size of m = 216 interactions, hereafter "rarefied networks") (Kruskal–Wallis one-way analysis of variance with a Nemenyi-Damico-Wolfe-Dunn post-hoc test). Empirical network metrics (n = 100) and their counterparts received from null models (n = 1,000) were statistically compared using Mann–Whitney/Wilcoxon tests.

I simulated co-extinction scenarios to explore the effects of climate change on PHNs in edge/fragmentation-affected versus continuous forest habitats by consecutively deleting individual plant species from the networks according to sequences obtained from four proxies for susceptibility to climate change. For each proxy and forest habitat the relative proportion of consecutive primary extinctions (plant level) was plotted against the relative proportion of remaining herbivore species (i.e., herbivores that did not lose all trophic links), resulting in extinction curves. Robustness of interaction networks towards primary extinction was measured by calculating the integral under these curves (Burgos et al. 2007, Menke et al. 2012). The first two proxies for susceptibility to climate change, Ellenberg's indicators values (Ellenberg & Leuschner 1996, Pompe et al. 2011) for temperature and plant moisture availability, were used to create extinction sequences ordered by increasing temperature and decreasing moisture requirements. Plants classified as indifferent were removed last; extinction order among plant species with identical Ellenberg values was randomized. As a third proxy for extinction sequences I used modified risk classes (R1 – R5) for plant species based on predicted relative changes in species range from the GRAS (*GRowth Applied Strategy*, Pompe et al. 2010) climate change scenario (Pompe et al. 2011): R1 > 0%, 0% ≤ R2< 25%, 25% ≤ R3 < 50%, 50% ≤ R4 < 75% and R5 ≥ 75% range change. The GRAS scenario is based on an average rise in temperature from 1961-1990 (reference time period) to 2051-2080 (future time period) of 3.8°C (Pompe et al. 2010). I were able to gain risk group data for 18 out of 28 plant species. Unclassified plants contributed 7% (fragments), 16% (edges) and 13% (forest interior) of interactions to the networks and were set to die out randomly. A more conservative analysis, in which those plants were left out completely, did not change results qualitatively. A fourth proxy used continuous percentage data of range gain or loss from the GRAS scenario (Pompe et al. 2011). To account for biases in the extinction order induced by identical (Ellenberg) or missing (GRAS scenario) proxy values, I calculated extinction curves and their respective integrals 100 times for each habitat and susceptibility proxy. Habitat-wise comparisons of the integrals were examined using Kruskal–Wallis one-way analysis of variance with a Nemenyi-Damico-Wolfe-Dunn post-hoc test. Integrals for each proxy and habitat were compared with null-models (random extinction sequence, 100 cycles, Kaiser-Bunbury et al. 2010) using Mann-Whitney/Wilcoxon tests.

To evaluate the predictive capacity of network topology regarding the robustness of plant-herbivore interaction networks against climate change, I related network metrics to integrals of extinction curves (climate change-based and random). For this I split my data: Analysis of network topology and extinction robustness for the three habitats was repeated twice during the vegetation period (early to midsummer, campaign 1 and mid to late summer, campaign 2), thereby generating six networks. As these season-specific networks were not independent from each other, I employed linear mixed models with network robustness as response variable, network topology as fixed factor and season as random intercept (package nlme, version 3.1-122, Pinheiro et al. 2015). (Marginal) R^2 values for the fixed effects were calculated following Nakagawa & Schielzeth (2013).

Analyses were carried out with the statistical computing software R version 3.0.2 (R Core Team 2013). All network representations and network analyses were performed with the package “bipartite” version 2.3-1 (Dormann et al. 2008).

RESULTS

In the understory of the studied forest landscape 24 woody plant species and 134 insect herbivore taxa were involved in PHNs, with a total of 696 recorded

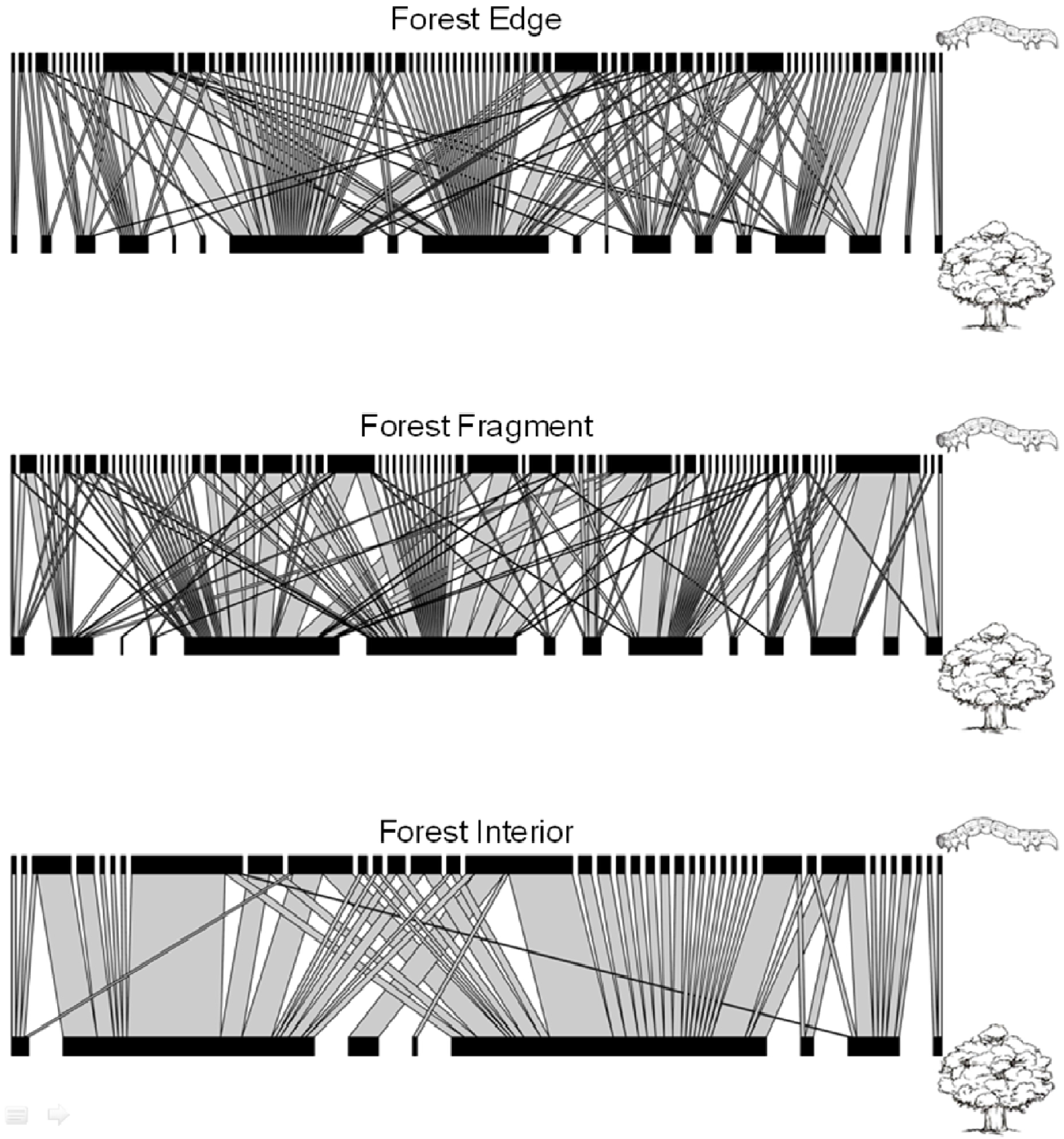

Figure 2: Quantitative bipartite graphs of plant-herbivore interaction networks for temperate forest edges, forest fragments and interior of continuous control forests in the Northern Palatinate highlands, SW-Germany. Upper (lower) bars depict individual herbivore (plant) species according to their relative interaction strength (bar width). Grey bars represent links between species respective to their relative link weight.

interactions. Forest fragmentation profoundly affected PHNs, which can be inferred at different levels of analytical scrutiny, from visual inspection, basic network attributes, and topological network metrics associated with robustness. Interaction networks declined in species richness, link

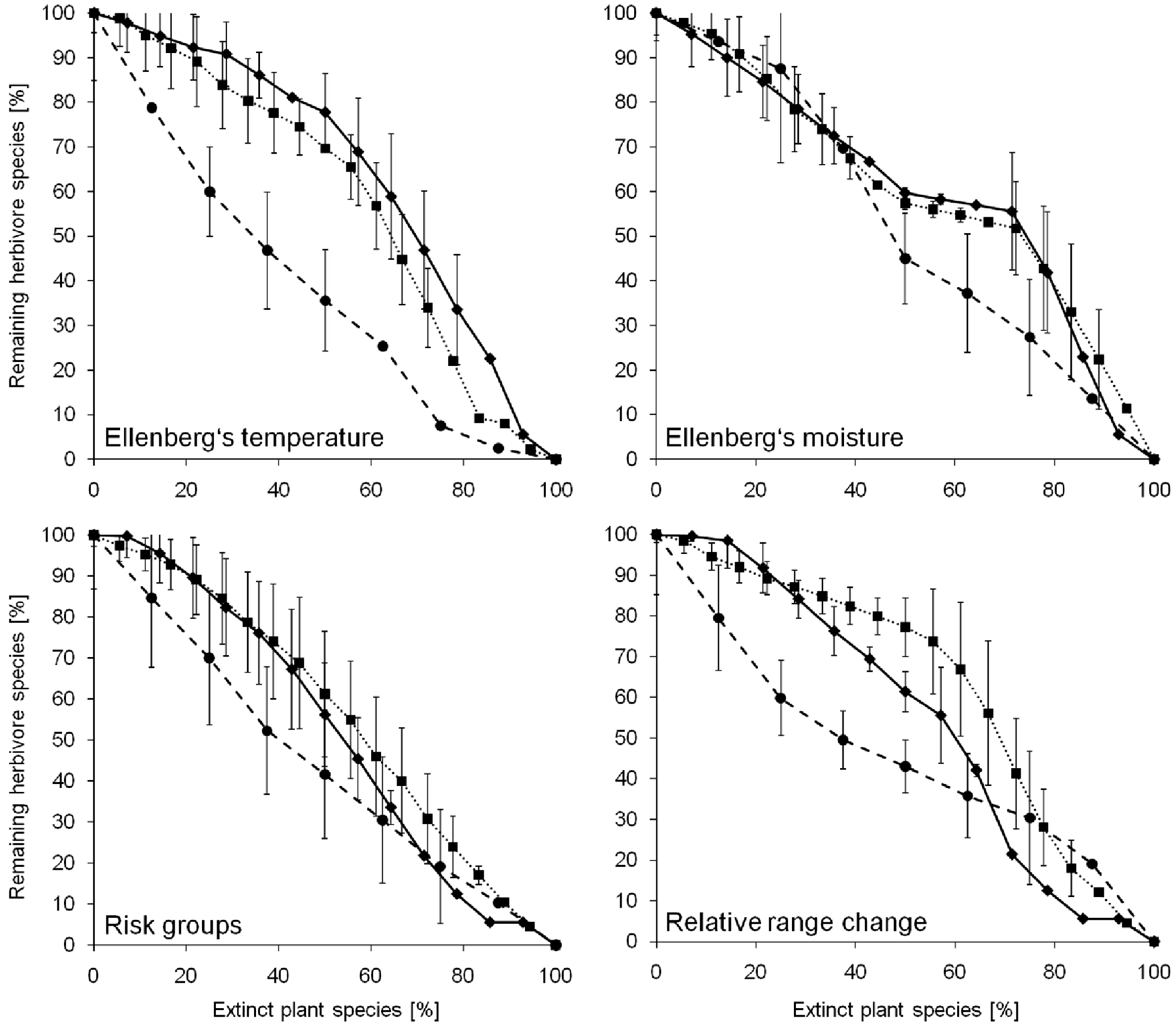

Figure 3: Effects of forest fragmentation on climate change-driven extinction scenarios of plant-herbivore interaction networks. Extinction curves depict secondary extinctions of herbivores upon loss of their host plants (primary extinction) for three forest habitats: forest edges (squares, dotted lines), forest fragments (diamonds, continuous lines), and interior of continuous control forests (circles, dashed lines). Sequence of plant extinction followed predicted sensitivity to climate change, based on four proxies (Ellenberg's temperature, Ellenberg's moisture, risk-groups and relative range change). Mean and standard deviation (error-bars) are obtained from 100 iterations of extinction sequences. SDs equalling zero stem from constant co-extinction proportions at particular steps, regardless of the iteration.

abundance (L) and complexity at both trophic levels with declining influence of edge effects (**Figure 2**, **Table 1**), while the highest amount of individual interactions (m) amongst forest habitats was found in forest fragments (m = 318). Interaction evenness of plant species (evenness of lower black bar width, **Figure 2**) was similar in fragmentation-related habitats (0.77 in forest edges and 0.78 in fragments) and lowest in the forest interior (0.63), with increasing dominance of *F. sylvatica* and *C. betulus* (51.4%, 53.8%, and 82.1% of

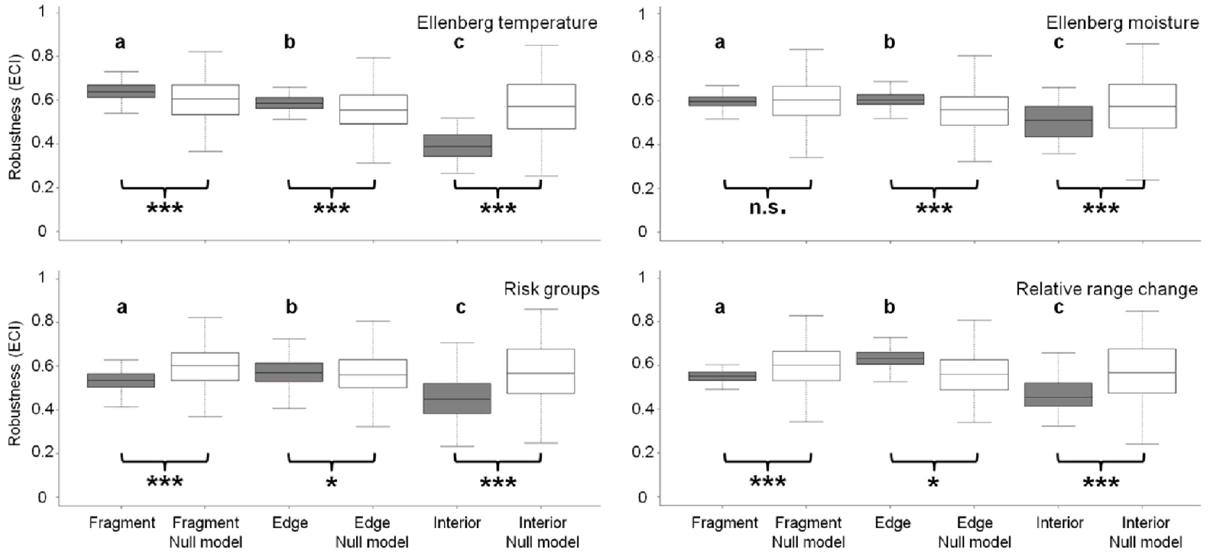

Figure 4: Effects of forest fragmentation on robustness of plant-herbivore interaction networks against simulated extinction cascades under climate change. Robustness (integrals of extinction curves in **Figure 3**, ECI) is depicted for forest fragments, edges and interior of continuous control forests (grey boxes) and corresponding null models (random extinction, white boxes) for four models of extinction sequences (Ellenberg's temperature, Ellenberg's moisture, risk groups and relative range change). Box-plots show the median (line), interquartile range (box) and range (whiskers). Habitat-wise comparisons yielded significant differences for all models (Kruskal-Wallis, results in **Table S2**) indicated by different letters (Nemenyi-Damico-Wolfe-Dunn post-hoc test). Network robustness in climate change-based models significantly differed from null models in most cases, as denoted by asterisks (*, $p < 0.05$; ***, $p < 0.001$; Mann-Whitney/Wilcoxon, results in **Table S2**.

interactions of both tree species for edges, fragments and interior forests, respectively, **Figure S2**). While topological network metrics showed clear positive responses to forest fragmentation (increased complexity, nestedness and redundancy), the adopted standardization procedures underline their ecological validity, as the metrics of full and rarefied PHNs were similarly affected (**Table 2**) and empirical values always significantly differed from null model values (Mann-Whitney/Wilcoxon tests, all $p < 0.001$). For the full networks PHNs declined in complexity, nestedness and niche redundancy from forest edges over fragments to the forest interior (**Table 2**). Network complexity, as measured by Shannon diversity of interactions, significantly decreased by 24% from forest edges to the interior, suggesting a drop in link abundance and evenness. Generally high nestedness across all habitats, with values never exceeding 18 for any network, implies the existence of hub-sections (i.e., cores of many strong links) in PHNs. Nevertheless, nestedness significantly declined by more than half from forest edges to the forest interior (**Table 2**). Trophic niche complementarity (H_2') was 26% lower in forest edges than in forest interior habitats, indicating that PHNs along forest edges had the highest overall degree

Table 1: Descriptive network measures for herbivore-plant interaction networks in forest edges, fragments and forest interior. L: Sum of trophic links; m: Sum of Interactions.

Habitat	Species richness		L	m
	Herbivores	Plants		
Edge	87	18	136	216
Fragment	72	14	127	318
Interior	40	8	58	162

of overlap of realized niches. In a nutshell, forest fragmentation and particularly edge creation significantly increased the complexity, cohesiveness and trophic niche redundancy of interaction networks between trees and insect herbivores. Network robustness, as depicted by the area under extinction curves (**Figure 3**), was positively affected by forest fragmentation, revealed similar patterns across all extinction scenarios (Kruskal-Wallis-tests, **Table S2**), and consistently differed from null models (random extinctions, Mann-Whitney/Wilcoxon tests, **Table S2**). Forest interior networks experienced a more pronounced collapse (**Figures 3**, **4**), while highest robustness was found either in forest fragments (Ellenberg's temperature) or edges, depending on the underlying proxy reflecting the extinction sequence (**Figure 4**). To give an example, removing 50% of woody plants using Ellenberg's temperature values as a proxy resulted in 78% and 70% of herbivore species remaining in forest fragments and edges respectively, while PHNs in the forest interior suffered nearly two thirds of co-extinction (36% remaining herbivore species).

While topological network metrics were entirely unrelated to network robustness against random extinctions (**Table 3**), they revealed several strong relationships and trends with ecologically realistic extinction scenarios. Among the tested metrics, the most important factor was complementary specialization on network level (H_2'), which showed significant negative relations with Ellenberg's moisture (marginal R^2 = 0.71), risk groups (marginal R^2 = 0.78) and predicted range change (marginal R^2 = 0.79). In addition, there was a trend between the Shannon diversity of interactions (H_2) and Ellenberg's temperature (marginal R^2 = 0.56), whereas network cohesiveness (as measured via nestedness) showed no relation to any extinction scenarios. Thus, the higher the degree of complexity and realized niche redundancy in the network, the more stable it performs against climate change-based extinction scenarios.

DISCUSSION

To my knowledge, this is the first study to address the impacts of temperate forest fragmentation on PHNs, while accounting for their susceptibility to climate change. my results indicate that fragmentation, particularly edge proliferation, positively affects the complexity and climate change-related robustness of PHNs, thereby reducing their proneness to simulated climate-

Table 2: Effects of forest fragmentation on topological network-metrics of full and rarefied plant-herbivore interaction networks. Full networks consist of all interactions of the respective habitat minus one randomly deleted interaction, while rarefied networks were rarefied by random deletion of interactions to the size of the smallest PHN minus one interaction (forest interior, m = 161) for standardization purposes. H_2: Shannon diversity of interactions; Nestedness: ranges from 0 (perfectly nested) to 100 (maximal entropy); H_2': Trophic niche complementarity on network level, ranges from 0 (maximal redundancy) to 1 (maximal complementarity).

		Habitat						Kruskal-Wallis-		
Network	Network	Edge		Fragment		Interior		X^2	Df	p
Full Networks	H_2	4.68	±	4.36	±	3.57	±	2745.	2	<
	Nestedne	7.39	±	12.73	±	17.55	±	2665.	2	<
	H_2'	0.374	±	0.429	±	0.507	±	2672.	2	<
Rarefied Networks	H_2	4.33	±	3.37	±	3.57	±	2674.	2	<
	Nestedne	8.21	±	13.79	±	17.58	±	2491.	2	<
	H_2'	0.410	±	0.513	±	0.507	±	1998.	2	<

H_2: Shannon diversity of interactions. H_2': Trophic niche complementarity on network

driven extinction. These findings provide insight into how network-inherent attributes drive the susceptibility of trophic web members to climate change in fragmented forest landscapes and allow the inference of silvicultural and conservation implications.

Contrary to numerous published reports that describe disruption and simplification of ecological networks by human disturbance across many ecosystems and trophic levels (Fortuna & Bascompte 2006, Tylianakis et al. 2007, Weiner et al. 2011) including PHNs (Valladares et al. 2012), my findings show positive effects of forest fragmentation (notably edge effects) on robustness-related network parameters of PHNs. This may result from two sometimes overlooked features of temperate forest in human-dominated landscapes. First, the flora of forest edges is relatively more species-rich than the forest interior (Gehlhausen et al. 2000). This is due to a generally high proportion of light-adapted, thermotolerant species that received century-long anthropogenic facilitation in the cultural landscape (Hermy et al. 1999). Second, greater tree diversity along edge zones and small fragments may also be caused by their partly release from intensive silvicultural regimes, for practical and forest edge management reasons (Coch 1995). As a plausible consequence, this may have enhanced herbivore species richness, link abundance and average width of realized trophic niches via a wider range of food sources to polyphagous herbivores. This in turn increased complexity of interactions and niche redundancy (as broader niches were more likely to overlap) – network features that have previously been reported to be affected by different components of forest fragmentation (Valladares et al. 2012, Menke et al. 2012, Albrecht et al. 2013). On the other hand, the vast majority of Germany's forest interior receives extensive management (Forest Europe 2011) and is often shaped by mono- or oligocultures of few tree species of high economic value arranged in block-wise stands (Gärtner & Reif 2004). For

Table 3: Relationships between network robustness against random and climate change-driven extinction sequences (response variable) and topological network metrics (fixed effects), modulated by seasonality (random intercept) using linear mixed models (all n = 6). H_2: Shannon diversity of interactions; H_2': Trophic niche complementarity on network level. Est: Estimated slope value of the network metric. R^2: R^2 of the fixed effect; p: p-value of the fixed effect. Bold letters indicate statistically significant values ($p < 0.05$); statistical trends ($0.05 < p < 0.1$) are denoted by a cross †.

	H_2			Nestedness			H_2'		
Extinction	Est	R^2	p	Est	R^2	p	Est	R^2	p
Random	-	0.17	0.388	-	0.07	0.588	-	0.16	0.406
Ellenberg's	0.155	0.56	0.098†	-	0.06	0.615	-	0.53	0.125
Ellenberg's	0.134	0.46	0.192	-	0.22	0.316	**-**	**0.71**	**0.048***
Risk groups	0.077	0.48	0.202	-	0.18	0.376	**-**	**0.78**	**0.026***
Relative range	0.158	0.43	0.224	-	0.10	0.511	**-**	**0.79**	**0.022***

example, in my study overall dominance of *F. sylvatica* and *C. betulus* in the forest interior was high (**Figure S2**), reaching up to 100% in individual plots. According to the natural tendency of these species to host mainly generalist herbivores (Sprick & Floren 2008), generalists constituted at least 65% of all interactions in the forest interior (classification described in the supplementary). This should have led to higher complexity and redundancy in PHNs, but my results showed quite the opposite. The restricted offer of potential feeding links forced generalist herbivores to establish narrow realized niches, resulting in low redundancy on network level. Consequently, links in PHNs were less abundant and highly uneven, resulting in lower network complexity. This is in line with recent findings about the importance of species abundances on the architecture of antagonistic networks (Hagen et al. 2012). Taken together with the findings from previous studies indicating both beneficial and adverse consequences for the structure of plant-animal networks (Valladares et al. 2012, Menke et al. 2012), my study suggests that the response of ecological networks to forest fragmentation (particularly edge effects and small fragment size) is highly dependent on network type and the particularities of the studied biome.

My results provide insights into the interaction of two major human impacts on food-webs by showing that PHNs in forest edges and, to a lesser extent, in small forest fragments were relatively more robust to climate change-based extinction scenarios (**Figures 3, 4**). This occurred because tree assemblages of forest edges and small fragments were characterized by plant species with varying degrees of thermotolerance (including thermophiles such as common hawthorn, *Crataegus monogyna*, **Table S1**), whereas interior habitats supported mainly shade- or cold-adapted trees (e.g., *Acer pseudoplatanus*, **Table S1**), with sometimes decisive importance for PHNs (e.g., *F. sylvatica* with 14 exclusive herbivores and 43% of all interactions in the forest interior). Hence, in fragmented/edge habitats larger proportions of interactions and herbivore species were found on warm-adapted plants than in the forest interior.

Because in all extinction models these thermotolerants were more likely to die out later in the extinction sequence than shade-tolerant ones, the corresponding links were conserved longer in the network, making fragmented habitats more robust against climate change-induced coextinctions. While less frequently observed, such positive effects of land use on the redundancy of functional traits have been previously documented for specific combinations of ecosystem type and disturbance regimes (Laliberté et al. 2010). Further, my results corroborate earlier findings that extinction risk can be influenced by network structure (Melian & Bascompte 2002). Among the different metrics used to assess PHN structure, trophic niche redundancy has proved particularly suitable as an indicator of network susceptibility against climate change. Network redundancy was lowest in the forest interior and highest in forest edges, indicating higher niche overlap in edge-influenced forests. Therefore, a higher proportion of insect herbivores persisted longer during extinction series due to the delayed loss of all available host plants. Robust relations with several outcomes of ecologically realistic extinction scenarios (**Table 3**) confirmed the recently proposed value of trophic niche redundancy as an evaluation metric for network robustness (Blüthgen & Klein 2011) in the context of climate change. By emphasizing how network architecture modulates responses to local and global disturbances, the present research has important potential implications for the improvement of silvicultural and conservation practices. While conventional approaches prioritize species richness at single trophic levels or even single charismatic flagship species (Segura et al. 2014), network studies allow us to identify and specifically target critical key parts of the food webs (Traill et al. 2010), for example those that are relevant for ecosystem robustness and functioning. Another aspect of high relevance for conservation practices is the identification of hub species (Olesen et al. 2007), like European beech (*F. sylvatica*) in my PHNs. This suggests that *F. sylvatica* should receive priority attention with regard to susceptibility against climate change, as all extinction models were largely dependent on its high extinction scores, as well as its high dominance and association with many exclusive herbivores (e.g., 35% of all herbivore species in the forest interior). In addition, such high scores are justified by a projected distributional decline of beech at its southern border following climatic warming (Kramer et al. 2010). This is consistent with strong climate change-driven shifts in plant species distributions predicted for Southwest Germany, where my study was situated (Pompe et al. 2010). Different, but nonetheless far-reaching conservation implications arise from the apparent impression that fragmented, edge-dominated forest habitats seemed pre-adapted to climate change and (provocatively suggested) should therefore be promoted as reservoirs for insect diversity and PHN integrity. In fact, this would be a misleading conclusion, considering that higher PHN complexity/robustness rather reflects the intrinsic floristic richness of temperate forest margins, which, in addition, are partially released from intensive silvicultural regimes, as explained above. Instead, conservation measures should aim at strengthening PHNs in the continuous forest interior at the local and the landscape scale (e.g. via close-to-nature practices, such as single-tree harvesting, site-specific tree species matching, or mimicking natural gap dynamics as suggested by Brunet et al. (2010). While management issues were beyond the scope of this study, future research efforts should more closely examine whether such diversity-oriented silviculture translates into higher PHN complexity and ecosystem resilience via increasing functional redundancy.

In synthesis, this paper reinforces the notion that trophic interactions are highly sensitive to human impacts and sheds some light on the interrelations between two key disturbance agents in forest ecosystems. Using biologically realistic models of plant species extinction risk, my study provided strong evidence that fragmentation of temperate forests positively affects the structural integrity/complexity of plant-herbivore food webs under climate change, while forest interior networks rapidly decline following simulated loss of their plant components. These findings contrast with previous studies in the fragmentation context, e.g., fragment size related simplifications of PHNs (Valladares et al. 2012) and thereby point to the potential importance of floristic and management-related peculiarities of European timber forests. The documented impoverishment of PHNs in managed forest interiors and their vulnerability to climate change highlights the need for further research efforts focusing on the promotion of PHN complexity and implications for ecosystem functioning by adequate silvicultural and conservation approaches.

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SUPPLEMENTARY

Insect Sampling And Verification Of Trophic Interactions – Knocked off insects were collected in a sample-jar attached to the bottom of a plastic-funnel attached to a metal ring of 50 cm in diameter and a slope of about 30° via a tube of PE-foil of 15 cm (**Figure S1**). Sampled vegetation per plant individual varied between half and full cover of the funnel.

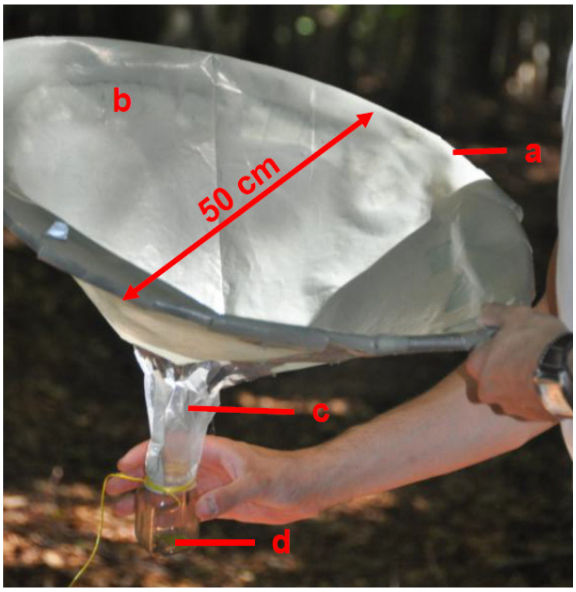

Figure S1: Design/dimensions of the sampling funnel used to collect insect *via* the foliage beating method. a Outer metal ring of 50 cm in diameter, covered with **b** a robust plastic foil. **c** Attached PE foil that leads to **d** the sampling jar.

Individually collected insects with chewing mouth parts were tested in no-choice feeding-assays to verify active herbivory. Insects were kept in an arena (50 ml PP tubes) with 10 – 20 mm^2 pieces of leaf material conspecific to the sampled host plant on the bottom and 2 cm^2 of moistened paper clips on the top to provide humidity. Leaf pieces were screened for chewing traces (positive interaction) 24 – 48 h after start. Insects with negative no-choice assays were excluded. As insects with sucking mouth parts (e.g. cicadas) usually don’t show clear feeding traces in plant material, they were identified to species level and checked if their published records of host plants included the sampled plant species (**Table S1**). Wingless insects that belonged to exclusively herbivorous taxa (e.g. cicada nymphs) were not submitted to no-choice feeding-assays but instead assigned to morphospecies levels and kept in the analysis, as they were most probably no tourists on the particular host plant. Caterpillars were reared to adults (in 50 ml PP tubes with moisture paper clips and plenty of source plant material), if possible, and then identified. Where final identification was impossible, morphosecies were assigned. Voucher specimens of all herbivores were deposited at the Natural Museum of Basel (*Psylloidea*) and at the department of Plant Ecology and Systematics at the University of Kaiserslautern (all other taxa). Reared butterflies were conserved by pinning, about half of the caterpillars frozen, all other insects stored in 70% Ethanol. Using published host plant ranges, herbivores were classified into two levels of trophic specialization: Specialists (not feeding on more than one plant family) and generalists (feeding on several plant families or being zoophytophagous) (**Table S3**). Voucher specimens were deposited at the Natural Museum of Basel (Psylloidea) and at the department of Plant Ecology and Systematics at the University of Kaiserslautern (all other taxa).

Sampled Plant Community – Herbivorous insects were obtained from 24 woody plant species from seven different families across all habitats (**Table S1**). Plant diversity, as measured by Shannon diversity, was highest in forest edges (1.11 ± 0.20) and lowest in the forest interior (0.36 ± 0.51) with intermediate forest fragments (0.79 ± 0.60) (Kruskal-Wallis test; n = 12, X^2 = 12.15, df = 2, p = 0.002**). Differences among groups were only significant between the forest interior and forest edges (Nemenyi-Damico-Wolfe-Dunn post-hoc Test). Evenness of the plant community was highest in forest edges (0.37 ± 0.07) and lowest in the forest interior (0.16 ± 0.23) with forest fragments in between (0.30 ± 0.23) (Kruskal-Wallis test; each n = 12, X^2 = 8.50, df = 2, p = 0.014*). Differences among groups were only significant between the forest interior and forest edges (Nemenyi-Damico-Wolfe-Dunn post-hoc Test). Correspondingly, while the dominance structure of the plant community showed high overall dominance of beech (*Fagus sylvatica* L.) and hornbeam (*Carpinus betulus* L.) across all habitats, forest edges and fragments revealed a more even distribution of plant abundances (**Figure S2**).

Sampled Herbivore Community – Overall I found 134 herbivore taxa (including morphospecies) from at least 28 families in 5 orders. Species richness declined from forest edges (87 taxa) over forest fragments (72 taxa) to the forest interior (40 taxa). Herbivore diversity, as measured by Shannon diversity, did not statistically differ across habitats (edges 2.16 ± 0.33, fragments 1.87 ± 0.39, interior 1.41 ± 0.59), although a trend was evident (one-way ANOVA; each n = 12, F = 2.503, df = 2, p = 0.097). Detailed information about sampled herbivore taxa (e.g. herbivore identity) can be found in **Table S3**.

Analysis Of Effects Of Forest Fragmentation On Plant-Herbivore Interaction Networks (PHNs) Via Rarefaction Curves – I rarefied my networks to the size of the smallest network (forest interior, m = 217) minus one interaction by randomly deleting one consecutive interaction at a time (Blüthgen et al. 2006, Vázquez et al. 2009). Each individual rarefaction per habitat was performed 100 times (see **Figures S3** and **S4** for a set of example curves).

Effects Of Forest Fragmentation On Robustness Of PHNs Against Extinction Cascades Based On Predicted Plant Susceptibility To Climate Change – For a detailed description on the calculation of extinction curves and resulting robustness values, please refer to the method section of the main text.

Table S1: Sampled plant taxa and their mean abundance in 0.1-ha plots in forest fragments, edges and interior habitats. Means and standard deviations (SD) are given for 12 plots per habitat.

		Fragment		Edge		Interior	
Species		Mean	SD	Mean	SD	Mean	SD
Acer campestre	*Sapindaceae*	0.75	2.60	1.42	2.11	0.08	0.29
Acer platanoides	*Sapindaceae*	0.00	0.00	0.00	0.00	0.42	1.00
Acer pseudoplatanus	*Sapindaceae*	0.00	0.00	0.58	1.44	0.42	1.16
Alnus glutinosa	*Betulaceae*	0.00	0.00	0.42	1.44	0.00	0.00
Betula pendula	*Betulaceae*	0.00	0.00	0.00	0.00	0.08	0.29
Carpinus betulus	*Betulaceae*	16.25	18.33	10.67	11.27	6.75	13.88
Corylus avellana	*Betulaceae*	1.75	5.75	1.08	2.31	0.00	0.00
Crataegus laevigata	*Rosaceae*	3.33	6.96	2.08	2.02	0.00	0.00
Crataegus monogyna	*Rosaceae*	0.50	1.17	0.17	0.39	0.00	0.00
Cytisus scoparius	*Fabaceae*	0.17	0.58	0.17	0.39	0.00	0.00
Fagus sylvatica	*Fagaceae*	12.75	15.86	19.67	16.60	17.50	21.38
Fraxinus excelsior	*Oleaceae*	0.00	0.00	0.92	1.98	0.25	0.87
Prunus avium	*Rosaceae*	1.17	2.33	0.17	0.39	0.00	0.00
Prunus spinosa	*Rosaceae*	0.00	0.00	1.00	1.71	0.00	0.00
Pyrus sp. 1	*Rosaceae*	0.17	0.58	0.08	0.29	0.00	0.00
Quercus petraea	*Fagaceae*	2.92	5.90	1.67	3.68	1.25	4.33
Quercus robur	*Fagaceae*	0.33	0.78	1.42	3.48	0.00	0.00
Rosa sp. 1	*Rosaceae*	0.08	0.29	0.00	0.00	0.00	0.00
Sambucus nigra	*Adoxaceae*	0.67	1.37	0.25	0.62	0.00	0.00
Sambucus racemosa	*Adoxaceae*	0.00	0.00	0.75	2.60	0.00	0.00
Sorbus aucuparia	*Rosaceae*	0.00	0.00	0.33	1.15	0.00	0.00
Sorbus torminalis	*Rosaceae*	0.08	0.29	0.08	0.29	0.00	0.00
Tilia cordata	*Malvaceae*	0.00	0.00	0.33	1.15	0.08	0.29
Tilia platyphyllos	*Malvaceae*	0.00	0.00	0.00	0.00	1.17	4.04

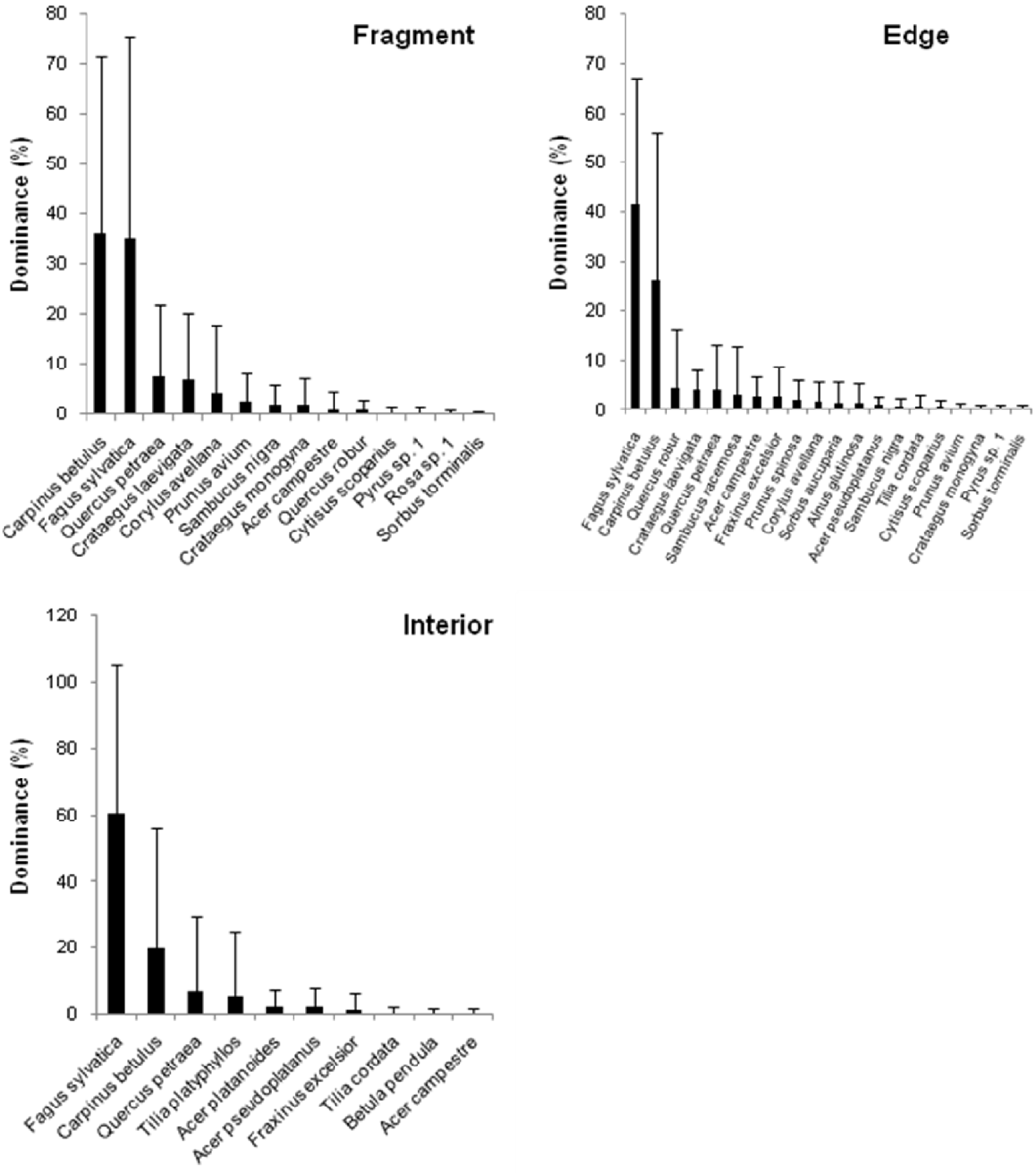

Figure S2: Dominance structure of tree communities in forest fragments, edges and the interior of continuous forest. The dominance of each species refers to the mean ± SD across 12 plots per habitat.

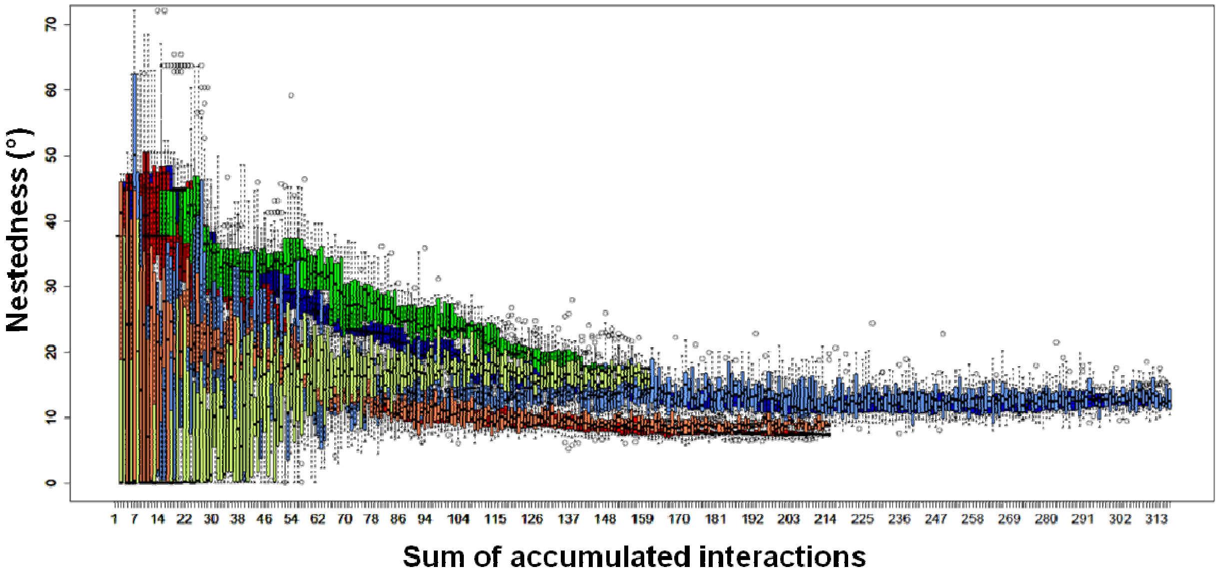

Figure S3: Rarefaction curves of nestedness in forest fragments (deep blue), edges (deep red) and forest interior (deep green). The curves are based on n = 10 rarefaction cycles per habitat owing to limited computational capacities. For each cycle and step, n = 10 null models (Patefield algorithm) were calculated and plotted (fragments light blue, edges light red and forest interior light green).

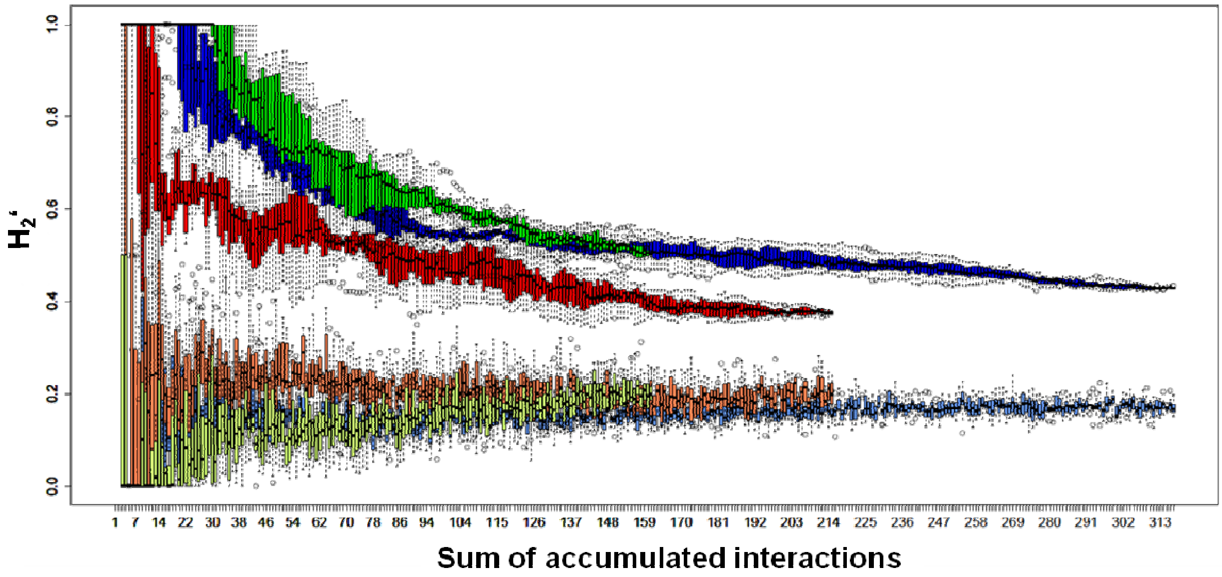

Figure S4: Rarefaction curves of trophic niche complementarity (H_2') in forest fragments (deep blue), edges (deep red) and forest interior (deep green). The curves are based on n = 10 rarefaction cycles per habitat, owing to limited computational capacities. For each cycle and step, n = 10 null models (Patefield algorithm) were calculated and plotted (fragments light blue, edges light red and forest interior light green).

Table S2: Habitat-wise comparison of robustness (integrals of extinction curves, ECI) of plant herbivore interaction networks from forest fragments, edges and continuous control forests to climate change-based extinction sequences (Kruskal-Wallis tests). Mean robustness values (± SD) were further compared to null models (i.e., random extinctions) via Mann-Whitney/Wilcoxon tests. ECI: Integral under extinction curve. SD: Standard deviation.

			Mann-Whitney/ Wilcoxon		Kruskal Wallis		
Proxy for susceptibility to climate change	Habitat	ECI Mean + SD	W	p	X^2	df	p
Ellenberg's temperature	Fragment	0.64 ± 0.04	636568	< 0.001	2319.29	2	< 0.001
	Edge	0.59 ± 0.03	616404	< 0.001			
	Interior	0.39 ± 0.07	131272	< 0.001			
Ellenberg's moisture	Fragment	0.60 ± 0.03	484438	0.228	912.17	2	< 0.001
	Edge	0.60 ± 0.03	642823	< 0.001			
	Interior	0.51 ± 0.08	348062	< 0.001			
Risk groups	Fragment	0.53 ± 0.04	272447	< 0.001	848.41	2	< 0.001
	Edge	0.57 ± 0.06	527101	0.036			
	Interior	0.46 ± 0.09	251635	< 0.001			
Relative range change	Fragment	0.55 ± 0.03	317770	< 0.001	2071.44	2	< 0.001
	Edge	0.63 ± 0.04	759002	0.036			
	Interior	0.46 ± 0.07	256030	< 0.001			

Table S3: List of insect herbivores participating in plant-herbivore interaction networks in forest fragments, edges and forest interior. Degree of host plant specialization was categorized as follows: Monophagous (mono): Feeding on not more than one plant genus; oligophagous (oligo): Feeding on not more than one plant family; polyphagous (poly): Feeding on several plant families; omnivorous (omni): Feeding on plants as well as animals.

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
Pogonocherus.hispidus	*Cerambycidae*	*Coleoptera*	poly	0.17	0.39	0.00	0.00	0.00	0.00
Andrion.regensteiniensis	*Curculionidae*	*Coleoptera*	mono	0.00	0.00	0.17	0.58	0.00	0.00
Barypeithes.sp.1	*Curculionidae*	*Coleoptera*	-	0.00	0.00	0.17	0.39	0.00	0.00
Coeliodes.transversealbofasciatus	*Curculionidae*	*Coleoptera*	mono	0.08	0.00	0.00	0.00	0.00	0.00
Curculio.glandium	*Curculionidae*	*Coleoptera*	oligo	0.25	0.62	0.00	0.00	0.00	0.00
Otiorhynchus.veterator	*Curculionidae*	*Coleoptera*	poly	0.00	0.00	0.17	0.58	0.00	0.00
Phyllobius.argentatus	*Curculionidae*	*Coleoptera*	poly	0.17	0.58	0.17	0.58	0.25	0.62
Phyllobius.pyri	*Curculionidae*	*Coleoptera*	poly	0.00	0.00	0.42	1.44	0.00	0.00
Polydrusus.cervinus	*Curculionidae*	*Coleoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Polydrusus.marginatus	*Curculionidae*	*Coleoptera*	poly	3.92	13.57	0.08	0.29	0.00	0.00
Polydrusus.mollis	*Curculionidae*	*Coleoptera*	poly	0.08	0.29	0.08	0.29	0.08	0.29
Strophosoma.melanogrammum	*Curculionidae*	*Coleoptera*	poly	0.17	0.39	0.58	1.00	0.25	0.45
Athous.haemorrhoidalis	*Elateridae*	*Coleoptera*	omni	0.00	0.00	0.08	0.29	0.00	0.00
Lagria.hirta	*Lagriidae*	*Coleoptera*	poly	0.83	1.64	0.33	0.65	0.33	1.15
Apterygida.media	*Forficulidae*	*Dermaptera*	omni	0.33	0.89	1.50	2.54	0.83	1.80
Chelidurella.guentheri	*Forficulidae*	*Dermaptera*	omni	3.00	5.56	2.50	3.12	1.25	2.26

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	SD	Mean	SD	Mean	SD
Forficula.auricularia	*Forficulidae*	*Dermaptera*	omni	0.00	0.00	0.33	0.65	0.08	0.29
Hemiptera.sp.1	-	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Heteroptera.sp.1	-	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Psylloidea.sp.2	-	*Hemiptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Acanthosoma.haemorrhoidale	*Acanthosomatidae*	*Hemiptera*	poly	0.00	0.00	0.17	0.39	0.17	0.39
Aphidina.sp.2	*Aphididae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Aphidinae.sp.6	*Aphididae*	*Hemiptera*	-	0.50	1.17	0.08	0.29	0.75	2.05
Drepanosiphum.aceris	*Aphididae*	*Hemiptera*	mono	0.00	0.00	0.33	0.89	0.00	0.00
Drepanosiphum.sp.1	*Aphididae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Dysaphis.crataegi	*Aphididae*	*Hemiptera*	mono	0.08	0.29	0.00	0.00	0.00	0.00
Lachnus.roboris	*Aphididae*	*Hemiptera*	oligo	0.00	0.00	0.08	0.29	0.00	0.00
Myzocallis.carpini	*Aphididae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Periphyllus.testudinaceus	*Aphididae*	*Hemiptera*	mono	0.17	0.58	0.17	0.39	0.00	0.00
Aphrophora.alni	*Aphrophoridae*	*Hemiptera*	poly	0.00	0.00	0.25	0.87	0.00	0.00
Phyllaphis.fagi	*Callaphididae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.17	0.39
Tuberculatus.sp.1	*Callaphididae*	*Hemiptera*	oligo	0.00	0.00	0.08	0.29	0.00	0.00
Acericerus.sp.1	*Cicadellidae*	*Hemiptera*	mono	0.08	0.29	0.00	0.00	0.00	0.00
Alebra.sp.1	*Cicadellidae*	*Hemiptera*	poly	0.00	0.00	0.08	0.29	0.08	0.29
Arboridia.sp.1	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.17	0.58	0.00	0.00
Cicadellidae.sp.1	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.25	0.87	0.00	0.00
Cicadellidae.sp.10	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Cicadellidae.sp.11	*Cicadellidae*	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Cicadellidae.sp.13	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Cicadellidae.sp.14	*Cicadellidae*	*Hemiptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Cicadellidae.sp.2	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.17	0.58
Cicadellidae.sp.5	*Cicadellidae*	*Hemiptera*	-	0.58	0.79	0.42	1.44	2.17	6.89
Cicadellidae.sp.7	*Cicadellidae*	*Hemiptera*	-	0.00	0.00	0.00	0.00	0.17	0.58

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
Cicadellidae.sp.9	*Cicadellidae*	*Hemiptera*	-	0.33	0.78	0.00	0.00	0.00	0.00
Eurhadina.sp.1	*Cicadellidae*	*Hemiptera*	mono	0.08	0.29	0.00	0.00	0.00	0.00
Iassus.lanio	*Cicadellidae*	*Hemiptera*	mono	0.50	0.90	0.17	0.39	0.00	0.00
Ledra.aurita	*Cicadellidae*	*Hemiptera*	poly	0.25	0.62	0.08	0.29	0.25	0.45
Oncopsis.carpini	*Cicadellidae*	*Hemiptera*	mono	0.00	0.00	0.17	0.58	0.00	0.00
Ribautiana.sp.1	*Cicadellidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Typhlocyba.bifasciata	*Cicadellidae*	*Hemiptera*	poly	0.00	0.00	0.00	0.00	0.08	0.29
Zygina.angusta	*Cicadellidae*	*Hemiptera*	poly	0.33	1.15	0.00	0.00	0.00	0.00
Zygina.flammigera	*Cicadellidae*	*Hemiptera*	poly	2.17	3.74	0.33	0.89	0.17	0.58
Zygina.griseombra	*Cicadellidae*	*Hemiptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Cicadidae.sp.1	*Cicadidae*	*Hemiptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Tachycixius.pilosus	*Cixiidae*	*Hemiptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Issus.coleoptratus	*Issidae*	*Hemiptera*	poly	2.33	3.52	1.25	1.48	2.08	3.40
Lygus.pratensis	*Miridae*	*Hemiptera*	poly	0.17	0.39	0.00	0.00	0.00	0.00
Lygus.rugulipennis	*Miridae*	*Hemiptera*	omni	0.00	0.00	0.00	0.00	0.08	0.29
Megacoelum.infusum	*Miridae*	*Hemiptera*	omni	0.00	0.00	0.17	0.39	0.00	0.00
Miridae.sp.1	*Miridae*	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.33	0.89
Miridae.sp.10	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.08	0.29
Miridae.sp.2	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Miridae.sp.3	*Miridae*	*Hemiptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Miridae.sp.5	*Miridae*	*Hemiptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Miridae.sp.6	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Miridae.sp.7	*Miridae*	*Hemiptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Miridae.sp.8	*Miridae*	*Hemiptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Miridae.sp.9	*Miridae*	*Hemiptera*	-	0.08	0.29	0.25	0.62	0.08	0.29
Pantilius.tunicatus	*Miridae*	*Hemiptera*	oligo	0.00	0.00	0.08	0.29	0.00	0.00
Phylus.melanocephalus	*Miridae*	*Hemiptera*	omni	0.17	0.58	0.00	0.00	0.00	0.00

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
Phytocoris.longipennis	*Miridae*	*Hemiptera*	omni	0.08	0.29	0.17	0.58	0.08	0.29
Phytocoris.tiliae	*Miridae*	*Hemiptera*	omni	0.92	1.73	0.58	0.79	0.67	1.07
Rhabdomiris.striatellus	*Miridae*	*Hemiptera*	omni	0.00	0.00	0.08	0.29	0.00	0.00
Oxycarenus.modestus	*Oxycarenidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Dolycoris.baccarum	*Pentatomidae*	*Hemiptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Palomena.prasina	*Pentatomidae*	*Hemiptera*	poly	0.17	0.39	0.08	0.29	0.00	0.00
Pentatoma.rufipes	*Pentatomidae*	*Hemiptera*	omni	1.33	2.10	0.42	0.79	0.75	2.30
Cacopsylla.melanoneura	*Psyllidae*	*Hemiptera*	oligo	0.00	0.00	0.17	0.39	0.00	0.00
Arytainilla.spartiophila	*Psyllidae*	*Hemiptera*	mono	0.17	0.58	0.00	0.00	0.00	0.00
Cacopsylla.peregrina	*Psyllidae*	*Hemiptera*	mono	0.75	2.30	0.25	0.45	0.00	0.00
Psyllopsis.fraxinicola	*Psyllidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Rhinocola.aceris	*Psyllidae*	*Hemiptera*	mono	0.33	1.15	0.25	0.62	0.08	0.29
Physatocheila.dumetorum	*Tingidae*	*Hemiptera*	omni	0.00	0.00	0.08	0.29	0.00	0.00
Trioza.remota	*Triozidae*	*Hemiptera*	mono	0.00	0.00	0.08	0.29	0.00	0.00
Symphyta.sp.1	*Pamphiliidae*	*Hymenoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Symphyta.sp.2	*Pamphiliidae*	*Hymenoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Symphyta.sp.3	*Pamphiliidae*	*Hymenoptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Symphyta.sp.4	*Pamphiliidae*	*Hymenoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Lepidoptera.sp.2	-	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Lepidoptera.sp.1	-	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Lepidoptera.sp.5	-	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Coleophora.sp.1	*Coleophoridae*	*Lepidoptera*	-	0.17	0.39	0.00	0.00	0.00	0.00
Coleophora.sp.2	*Coleophoridae*	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Biston.strataria	*Geometridae*	*Lepidoptera*	poly	0.00	0.00	0.00	0.00	0.08	0.29
Ennomos.quercinaria	*Geometridae*	*Lepidoptera*	poly	0.00	0.00	0.17	0.58	0.17	0.39
Erannis.defolaria	*Geometridae*	*Lepidoptera*	poly	0.33	0.89	0.08	0.29	0.00	0.00
Geometridae.sp.2	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
Geometridae.sp.3	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Geometridae.sp.4	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Geometridae.sp.5	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Geometridae.sp.6	*Geometridae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Geometridae.sp.7	*Geometridae*	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Geometridae.sp.8	*Geometridae*	*Lepidoptera*	-	0.25	0.87	0.00	0.00	0.00	0.00
Hypomecis.punctinalis	*Geometridae*	*Lepidoptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Operophtera.brumata	*Geometridae*	*Lepidoptera*	poly	1.00	2.66	0.00	0.00	0.17	0.39
Paradarisa.consonaria	*Geometridae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Parectropis.similaria	*Geometridae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Plagodis.dolabraria	*Geometridae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Hesperidae.sp.1	*Hesperidae*	*Lepidoptera*	-	0.08	0.29	0.00	0.00	0.00	0.00
Incurvariidae.sp.1	*Incurvariidae*	*Lepidoptera*	-	0.00	0.00	0.25	0.62	0.00	0.00
Calliteara.pudibunda	*Lymantriidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Euproctis.chrysorrhoea	*Lymantriidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Lymantria.monarcha	*Lymantriidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Lymantriidae.sp.2	*Lymantriidae*	*Lepidoptera*	-	0.00	0.00	0.17	0.58	0.00	0.00
Amphipyra.pyramidea	*Noctuidae*	*Lepidoptera*	poly	0.08	0.29	0.08	0.29	0.00	0.00
Cosmia.trapezina	*Noctuidae*	*Lepidoptera*	poly	0.33	0.78	0.25	0.87	0.17	0.39
Eupsilia.transversa	*Noctuidae*	*Lepidoptera*	poly	0.17	0.58	0.25	0.62	0.00	0.00
Noctuidae.sp.1	*Noctuidae*	*Lepidoptera*	-	0.33	1.15	0.00	0.00	0.08	0.29
Noctuidae.sp.2	*Noctuidae*	*Lepidoptera*	-	0.25	0.87	0.00	0.00	0.00	0.00
Noctuidae.sp.3	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.00	0.00
Noctuidae.sp.4	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.08	0.29	0.17	0.58
Noctuidae.sp.5	*Noctuidae*	*Lepidoptera*	-	0.08	0.29	0.17	0.58	0.00	0.00
Noctuidae.sp.6	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29
Noctuidae.sp.7	*Noctuidae*	*Lepidoptera*	-	0.00	0.00	0.00	0.00	0.08	0.29

(continued)

Table S3: (continued)

Taxon	Family	Order	Degree of host-plant specialization	Abundance Fragment		Abundance Edge		Abundance Interior	
				Mean	SD	Mean	SD	Mean	SD
Noctuidae.sp.8	*Noctuidae*	*Lepidoptera*	-	0.08	0.29	0.08	0.29	0.00	0.00
Orthosia.cerasi	*Noctuidae*	*Lepidoptera*	poly	0.50	1.24	0.25	0.87	0.58	1.08
Orthosia.gothica	*Noctuidae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Orthosia.incerta	*Noctuidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Orthosia.munda	*Noctuidae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Archips.xylosteana	*Tortricidae*	*Lepidoptera*	poly	0.08	0.29	0.08	0.29	0.08	0.29
Pandemis.ribeana	*Tortricidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Tortricodes.alternella	*Tortricidae*	*Lepidoptera*	poly	0.00	0.00	0.08	0.29	0.00	0.00
Tortrix.viridana	*Tortricidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00
Ypsolopha.parentesella	*Ypsolophidae*	*Lepidoptera*	poly	0.08	0.29	0.00	0.00	0.00	0.00

Taxonomic Experts

Peter Sprick: *Coleoptera*
Thomas Thieme: *Aphidoidea*
Sabine Walter: *Auchenorrhyncha*
Jürgen Deckert: *Heteroptera*
Daniel Burckhardt: *Psylloidea*
Erwin Rennwald: *Lepidoptera*
Heidrun Melzer: *Lepidoptera*
Rolf Mörtter: *Lepidoptera*

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Chapter 6

Synthesis

Putting it all together. Top left: pale tussock moth (*Calliteara pudibunda*, *Lymantriidae*), a polyphagous herbivore on various deciduous trees. Left center: talking business in the field. Top center: Sunrinse atop the ridges of the forest reserve *Hohfelshalde*. Top right: a supervisor not shying away from lending a hand. Bottom: forest fragments within the undulating Northern Palatinate highlands.

CENTRAL RESULTS

Evidently, the anthropogenic modification of natural landscapes is a global driver of biotic impoverishment and homogenization across species and inter-species interactions. Alterations of forest ecosystems are of particular concern, as around the globe forests are persistently deforested and comprehensively and heavily used, with often grave consequences for basal ecosystem components. The aim of this thesis was therefore to disentangle the main contributing factors and interdependencies shaping species and interaction diversity of plants and their herbivores in an old, fragmented, and managed cultural forest landscape. And sure enough, when I synthesize the central results of this thesis' core chapters into a comprehensive picture, we observe a complex network of (inter)dependencies across and between anthropogenic and biotic factors (**Figure 1**), which I will elucidate in this subsection and discuss in the following further subsections.

The Northern Palatinate Highlands Are A Hyperfragmented Landscape Under Extensive Silviculture – Indeed, the Northern Palatinate highland proved to be a well suited cultural landscape to study the implications of both forest fragmentation and silvicultural forest use. No less than 2,900 individual fragments are scattered across the landscape, with a total edge length of over 5,700 km and with about 85% of fragments being smaller than 10 ha and contributing 8.5% to the total forest area (**Chapter 1**). Only seven forest tracts exceed 1,000 ha, making them ideal choices to address forest continuity and extensive management. The selected plots investigated in this thesis exhibited strikingly noticeable fragmentation, edge, and management effects (**Chapter 2**). Using comprehensive indices, which integrate several individual proxies of the respective anthropogenic factors, (un)fragmented and (un)managed forest habitats differed strongly and highly significantly. Small forest fragments showed a nearly four times higher fragmentation index and two times higher edge index than continuous managed forests. Similarly, edge plots were affected by over twofold higher edge intensity (vs. interior forests) and managed forests displayed more than a threefold higher management intensity than their preserved counterparts (**Chapter 2**).

Human Landscape Modification And Woody Plant Communities – This interplay of human forest alterations strongly impacted the woody plant community across multiple ecological attributes, including species richness, diversity, community variability, taxonomic composition, and functional traits. From 57 plots (0.1 ha) across the landscape, 4,139 woody plant individuals were censused, comprising 34 species and 15 families. Forest edges were between 77% and 103% more species rich than any other habitat and edge intensity significantly correlated with plant diversity. Furthermore, edge communities were characterized by large variability in taxonomic composition, in contrast to striking biotic

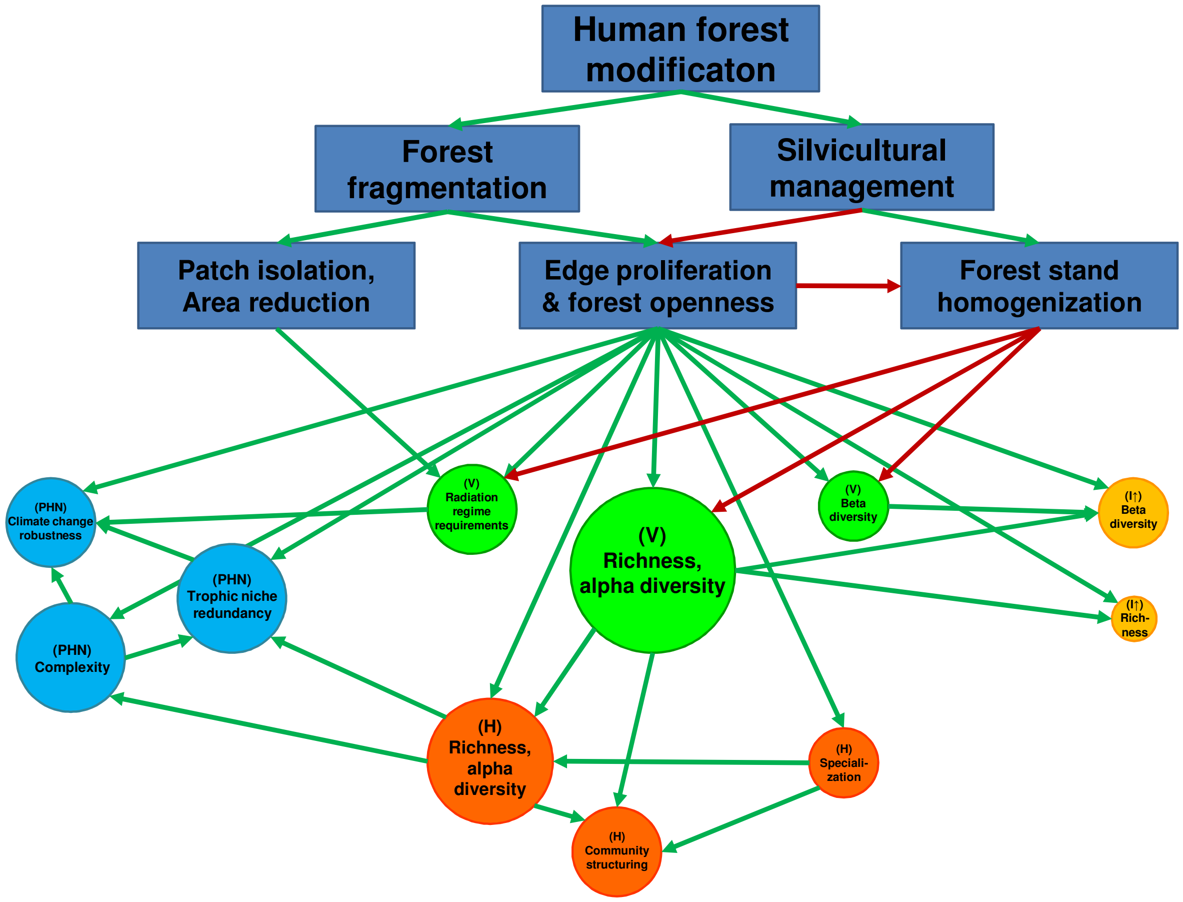

Figure 1: Conceptual network of relationships and interdependencies driving the reactions of plants, herbivores, and their interactions to human modification of forest habitats in the Northern Palatinate highlands. Rectangles represent anthropogenic disturbances, circles represent biotic reactions/drivers. Arrow colors indicate the nature of relationships: green: "the higher (arrow source), the higher (arrow target)"; red: "the higher (arrow source), the lower (arrow target)". Circles and corresponding font sizes are proportional to the amount of incoming and outgoing arrows (degree) to highlight ecologically important biotic factors. For results and discussions supporting shown relationships, refer to the chapters corresponding to the arrow targets: **Chapter 1** (dark blue rectangles), **Chapter 2** (green circles), **Chapter 3** (dark orange circles), **Chapter 4** (light orange circles), **Chapter 5** (light blue circles). Constructed with Gephi (version 0.9.1, *Force Atlas* algorithm) and modified in Powerpoint.

homogenization in managed interior forests. In unmanaged forests, cessation of management was less noticeable in alpha diversity, but rather in 35% higher community heterogeneity and significant compositional segregation from plant communities under silviculture. These extensively used forests were further characterized by shade/cold-tolerant tree assemblages, as demonstrated by the revelation of *Fagus sylvatica* and *Larix decidua* as indicator species (Dufrêne-Legendre analysis) and the pronounced low radiation regime requirements. This further underlined the impression of floristically poor, commercially oriented forests. On the other hand, unmanaged forests displayed higher (variability of) microclimatic demands. Moreover, edge and particularly fragmentation intensity were strongly related to high radiation regime requirements within the plant communities, demonstrating the inherently open habitat structure of fragmentation affected forests. Consequently, the natural history of the found indicator species adequately reflect these environmental attributes (edges: *Prunus avium*, *Prunus spinosa*, and *Sorbus aucuparia*; small fragments: *Sambucus nigra*). Taken together, these patterns proved that plant assemblages responded to habitat modifications via changes in diversity, community composition, and functional traits (**Chapter 2**).

Understory Herbivores Under Forest Fragmentation – Insect herbivores evolved an antagonistic, yet intimate relationship to their plant hosts as means to cope with plant defenses and interspecific competitive forces. This is visible in their often pronounced trophic specialization and the resulting relationship between plant and herbivore diversity. Consequently, anthropogenic forest modification had significant influence on diversity, composition, and trophic traits of the herbivore community in the understory, particularly via bottom-up forces of the associated plant community. Although the collection of empirically proven herbivores in the understory comprised over 1,000 specimens, less than half of the expected herbivore species were captured. Edge effects more than doubled species richness and increased herbivore diversity by 71%. Furthermore, trophic specialization was higher in forest margins, compared to the forest interior. Additionally, edge intensity, as well as trophic specialization highly significantly increased herbivore diversity, explaining 31% of variation. Moreover, bottom-up effects contributed in shaping herbivore assemblages, as there was evidence for a positive relationship between plant and herbivore diversity, and as plant diversity was a significant structuring factor of herbivore community composition. Further structuring forces consisted of the herbivore community itself, herbivore diversity and trophic specialization. Interestingly enough, forest fragmentation did not directly affect community composition or beta diversity, as demonstrated by the pronounced congruence of community composition in habitat-wise comparison. Hence, herbivore assemblages noticeably reacted to forest fragmentation directly via environmental and indirectly via biotic effects (**Chapter 3**).

Significance Of Arboricolous Insects And Their Relation To Forest Edges – Although most studies in forest ecology focus on the understory, most biotic activity can be found within the *last biological frontier*, the canopies. Hence, a study analyzing ecological changes in a forest landscape cannot be complete without addressing the treetops. In order to complement the grand picture, I sampled arboricolous arthropods via insecticidal fogging from 24 beech canopies across forest edges and interior forests. The resulting collection comprised over 46,000 specimens and all relevant taxonomic/functional groups. Nevertheless, after identification of selected groups, estimates based on the returned 175 species indicated that I found 55 - 69% of expected species. While diversity was homogeneous across all trees, species richness in edge canopies was significantly higher (26%) than in the interior. Edge effects were less pronounced in community segregation, but much more pronounced in differences in beta diversity, as interior communities displayed striking homogenization and compositional constraint. Beech canopies of both habitats contributed about equally in harboring insects of conservational importance, with 49 species either being stenotopous, red-listed, or indicator species of near-natural forests. Among these, six species were identified as priority species of the Northern Palatinate highlands, including the empirically proven indicator species *Conopalpus brevicollis* (Dufrêne-Legendre analysis). Hence, beech canopies of the Northern Palatinate highlands are centers of biodiversity, modulated by edge effects, and are important habitats to a wide range of insect species, including many vulnerable ones (**Chapter 4**).

Stability Of Plant-Herbivore Networks Under Forest Fragmentation And Climate Change – So far I saw noticeable effects of anthropogenic forest modification on plant and herbivore assemblages. However, as already mentioned, the two are deeply connected. Hence, only an analysis paying respect to this interdependence can be judged complete. An ideal conceptual framework to present, describe, and (more importantly) quantitatively analyze this is the network approach. This way, the complexity and trophic niche redundancy of plant-herbivore networks (PHNs) can be evaluated in the context of forest fragmentation. Furthermore, ecosystems are dynamic, displaying specific variability, resilience, and persistence in the face of disturbances. This is highly relevant in the context of human impacts changing ecosystems globally, at present and in the future. A prime example for this is climate change. Hence, the evaluation of how ecosystems under different anthropogenic influences (such as forest fragmentation) might respond to future changes is of essential importance for conservation concerns. To illuminate this matter, I constructed PHNs from live-sampled, empirically proven herbivores, compared their network topology across habitats, and tested their robustness against simulated extinction cascades under climate change. Finally, I related network topology to stability to evaluate whether specific topology indices are appropriate indicators of climate change robustness. Integrating over the total landscape, I identified 696 individual interactions between 134 herbivore and 24 plant species. There was a striking, significant, and consistent pattern of increasing network complexity (32%), cohesiveness (> 100%), and trophic niche redundancy (35%) with increasing edge influence. This could be inferred at different levels of analytical scrutiny, from visual inspection, basic network attributes, and topological network metrics associated with robustness. To assess network robustness against climate change, four different predictive models of plant susceptibility to climate change were employed. Using these, plant species were progressively removed from the networks, according to the order of their respective climate change susceptibility, and the remaining herbivore species recorded. These simulated extinction cascades consistently showed higher PHN robustness in fragmentation affected forests, particularly edges. Networks in the interior, on the other hand, quickly and profoundly collapsed with progressive loss of plant species. Among the used topological indices, trophic niche redundancy was the most reliable indicator of climate change susceptibility, explaining between 71% and 79% of network robustness in three out of four climate change models. Finally, network structure allowed the identification of *Fagus sylvatica* as a pivotal hub species for the integrity of PHNs. In conclusion, PHNs in forest edges were more complex, cohesive, redundant, and stable against climate change, compared to interior forests. Furthermore, I could demonstrate the suitability of PHN topology for the evaluation of ecosystem stability, particularly in the case of future threats, which might turn out to be invaluable in conservation considerations (**Chapter 5**).

In Synthesis – Human modification of the forests in the Northern Palatinate highlands comprehensively and noticeably shaped plant and herbivore assemblages, their interactions, as well as arboricolous insect communities. The primary underlying factor was the edge/interior contrast caused by the proliferation of forest edges during fragmentation. By comparison, patch isolation and forest management were of secondary relevance. The causes and interrelations of these patterns, the deduced implications for other ecosystems, and the ensuing consequences for conservationists, foresters, and decision makers will be discussed in the following subsection.

GENERAL DISCUSSION

For the general discussion, I deem four partly interrelated topics pivotal, which can be derived from the previously presented research. Firstly, it is essential to pinpoint the central patterns and processes shaping plant and herbivore communities and their interactions in the Northern Palatinate highlands and discuss the underlying mechanisms. For this I will rely on the conceptual framework, which was illustrated as a network of anthropogenic and biotic factors introduced in the previous subsection (**Figure 1**). Secondly, I will give particular consideration to the exceptional position Central European forests hold (old deforestation and extensive management) by assessing whether the presented results in these forest systems are suitable future projections for biomes under recent deforestation, with special regard to tropical forests. Thirdly, such a thesis on the human impacts on essential components of forest biodiversity would be incomplete without deriving recommendations for practical application, particularly for conservationists, foresters, and decision makers. Therefore, I will use the gained knowledge in this thesis to evaluate current conservation efforts and forestry practices and recommend adjustments or complementary actions, where necessary. Lastly, I will provide an assessment in which aspects of the presented research a passing of the baton might be most fruitful or necessary.

IT'S THE EDGE THAT MATTERS!

Edge Effects As Central Motif Shaping Forest Ecosystems In The Northern Palatinate Highlands – The edge/interior contrast, one essential component in habitat fragmentation (Wirth et al. 2008, Tabarelli et al. 2008), can easily be spotted as the main factor influencing forest biota in the Northern Palatinate highlands. One look at the conceptual illustration (**Figure 1**) is enough to confirm edge proliferation as the central influence on practically all studied biotic responses. While this graphical representation is partly biased (forest management was not specifically addressed in all chapters), the strong imbalance between edge and pure fragmentation effects is still striking. Small fragments had positive effects on (warmer/dryer/lighter) microclimatic requirements, but showed intermediate responses in all other aspects. Drawing a representative picture, forest edges in the Northern Palatinate highlands are composed of rich and variable woody plant communities, with diverse and rather high radiation regime requirements. Edge herbivore communities are equally diverse, with relatively high degree of host specialization. The resulting food webs are complex and functionally redundant, making edge ecosystems stable and particularly robust against climate change. Further, insect communities in edge canopies are rather species rich and display noticeable compositional variability. On the other hand, interior forests (particularly those under silviculture) are diametrically opposed: Tree assemblages are species poor and taxonomically highly homogenized, with pronounced shade/cold adaption. Consequentially, herbivore assemblages are equally impoverished, with high degrees of polyphagy. Naturally, resulting food webs are simplified, and collapse quickly under climate change. Compositional constraint is further

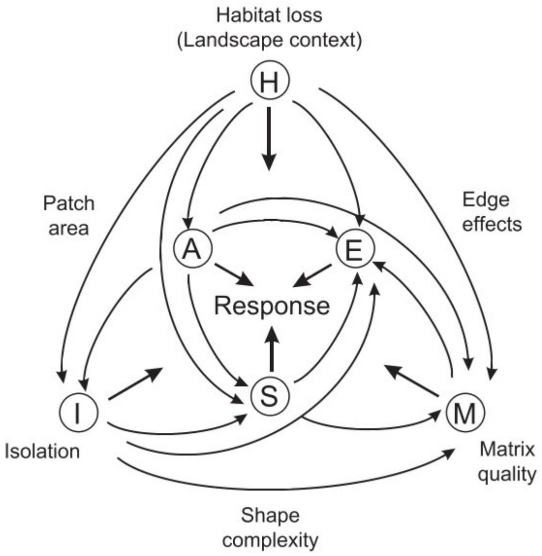

Figure 2: A conceptual model of interdependent drivers in forest fragmentation. The outer variables, (**I**)solation, (**H**)abitat loss, and (**M**)atrix quality, characterize the spatial arrangement, habitat quantity, and quality in a landscape, in turn influencing patch-scale attributes, namely patch (**A**)rea, (**S**)hape complexity, and (**E**)dge effects. Arrows indicate possible causal directions. From Didham et al. (2012).

noticeable within arboricolous insect communities.

Forest fragmentation is usually not perceived synonymously with edge effects, but rather seen from a landscape-scale perspective, with overall habitat loss and the following spatial arrangement of remaining habitat patches driving biotic responses (landscape changes causing biotic changes, Fahrig 2003). Naturally, landscape-scale fragmentation is inherently related to patch-scale attributes, such as patch area, shape complexity, and eventually edge effects (all, again, interdependent), which makes it hard to distinguish the individual components at work (**Figure 2**, Didham et al. 2012, Döbert et al. 2014). Yet it seems that patch-scale effects (patch area, and much more, edge effects) might often be of higher relevance for forest ecosystems, as demonstrated in this thesis, and in other works (Laurance & Lovejoy 2002, Wirth et al. 2008, Tabarelli et al. 2008, Döbert et al. 2014). For instance, in tropical realms the proliferation of forest edges is the predominant factor during forest fragmentation, driving ecosystems towards biotically homogenized communities (establishment of early-successional states, Laurance & Lovejoy 2002, Tabarelli et al. 2008, 2012) and inter-species interactions (e.g. hyperabundance of ecosystem engineers, i.e. leaf-cutting ants, Wirth et al. 2007, Meyer et al. 2009, 2011). With respect to temperate biomes, however, this thesis supports the available limited insights, which suggest partly different responses and further influences of non-fragmentational anthropogenic disturbances. Therefore, a mechanistic understanding of which proximate landscape parameters are of ecological relevance and how they affect ultimate operating (abiotic and biotic) drivers of biodiversity is essential for process-oriented generalizations, conservation considerations, and management recommendations in temperate forests (Didham et al. 2012).

What Are The Underlying Mechanisms Driving The Edge/Interior Contrast? – Although the various variables distinguishable in forest fragmentation may have tremendous effects on forest biota (**Figure 1**), it is important to note that none of them ever is an ultimate effect variable of biotic responses, but rather proximate, acting through abiotic or biotic mechanisms (Didham et al. 2012, Tuff et al. 2016). I deem four (partly related) mechanisms responsible for the pronounced edge/interior contrast of plant-herbivore diversity and interactions: (i) edge creation alters microclimates (increasing radiation regimes), (ii) altered microclimates and open forests shape plant (and herbivore) diversity, (iii) plant assemblages determine the associated herbivore communities, their ensuing interactions, and further biotic agents (e.g. top-down control), and (iv) silvicultural management differently affects edge- and interior floras.

(i) Forest fragmentation alters forest microclimates, with increased light and drought conditions, as well as temperature extremes in forest edges and small fragments. The mechanism originates from the physical contrast between intensively vegetated patches vs. the much more open matrix, resulting in opening of the forest. This fact is so well established in fragmentation research, it is bordering the trivial (Murcia 1995, Laurance & Lovejoy 2002, Tuff et al. 2016). Yet, fragmentation research has been deemed able to further profit from further integration of thermal biology (Tuff et al. 2016). While microclimatic variables were not directly measured in this thesis, the quantification of plant species abundances and the corresponding Ellenberg indicator values allowed for a clear microclimatic characterization of (fragmentation affected) forests (**Chapter 2**). The use of these values is well established (Diekmann 2003). And since they have been shown to correlate well with actual physical data, and since they were integratively derived from large European ecoregions, they do not suffer from circular reasoning (Diekmann 2003, Schmidtlein 2005).

(ii) Microclimate is an abiotic variable affecting forest biota during fragmentation. This mechanism has been shown abundantly in the literature, across species, communities, interactions, and ecosystem functions (Tuff et al. 2016). The prime example for plant communities is the degradation of tropical forests to early-successional pioneer floras, which are better suited for the harsh microclimates prevailing in forest edges and small fragments (Laurance & Lovejoy 2002, Laurance et al. 2006, Tabarelli et al. 2008). Temperate forest edges similarly promote pioneer and hedge species (*edge species*) which are adapted to intensive light/temperature/drought regimes (Honnay et al. 1999, 2002, Flückiger et al. 2002, **Chapter 2**). However, in these biomes we observe increased species richness and community heterogeneity, (Honnay et al. 2002, **Chapter 2**). A consistent pattern is becoming apparent. While microclimate is the primary ultimate variable, there are several mechanisms at work. For one, the natural species pool which is selected by edge microclimates is inherently species rich. Second, radiation regime requirements are not the only plant trait selecting edge communities. Entomophily and zoochory are further potential facilitators of edge species, as edge communities were composed to a noticeable degree of *Rosaceae*, *Sambucus* spp. and other insect-attended and fruit-bearing species (**Chapter 2**). Hence, this functional group of plants further benefits from microclimates via positive effects of temperature on insects. Warmer, sunnier conditions increase insect activity times, and metabolism, and decrease mortality (Cappuccino & Martin 1997, Lindner et al. 2010, Tuff et al. 2016). Furthermore, various pollinator (e.g. butterflies, *Lepidoptera*) and seed-disperser (e.g. frugivorous birds) groups prefer forest edges over interiors (Kusch et al. 2005, Lindell et al. 2007, Albrecht et al. 2013). Naturally, herbivores equally benefit after liberation from energy limitiations (increased activity times, metabolism, decreased mortality, Cappuccino & Martin 1997, Lindner et al. 2010, Tuff et al. 2016), with possibly positive consequences for food web construction.

(iii) High woody plant diversity and community heterogeneity in edges and small patches may be a primary result of abiotic factors, but is by itself a biotic variable shaping herbivore communities in a bottom-up fashion. The importance of plant diversity in this thesis can easily be derived from the conceptual network of abiotic and biotic variables in **Figure 1**. Variables with many dependencies are portrayed proportionally larger than others, and it is straightforward that plant diversity affects herbivore assemblages in various biodiversity components, across physical strata, and in their interaction patterns. The strong dependence of insect herbivores on their host plants, as elucidated in **Chapter 3**, is mainly rooted in the necessity to circumvent plant defenses, which facilitates trophic specialization and niche differentiation (Ehrlich & Raven 1964, Jaenike 1990, Rausher 2001). Hence, herbivores react sensitively to changes in host plant assemblages. I deem this the strongest argument for mirrored reactions by herbivores to plants under forest fragmentation. This point is further modulated by plant identity, as edge floras comprise species with many specialist herbivores (in turn increasing average specialization degree, niche differentiation and herbivore diversity, **Chapters 3** and **5**), such as many *Rosaceae* (Böhme 2001). Additional modulating effects by biochemical and physiological properties of plant tissues remain elusive. It may have been shown for tropical realms that plants in forest edges are more palatable to chewing herbivores due to higher nutritious value arising from higher concentrations of stress-related osmolytes (e.g. proline) and non-structural carbohydrates (*plant-stress hypothesis*, White 1984, Meyer et al. 2006). However, studies in temperate forests are practically nonexistent. There is little evidence for positive edge effects on leaf-traits and subsequently on chewing herbivores (Dohm 2009), and non for sap-sucking herbivores (arguing that edge conditions increase phloem quality for sap-suckers, Petry 2013). Apart from bottom-up forces on herbivores, plant diversity could also act via top-down controls. The *enemies hypothesis* predicts higher predator abundances in rich plant communities, due to high habitat availability and prey variability (Root 1973, Russell 1989). In the case of this thesis, this hypothesis is counteracted by the *trophic-level hypothesis* predicting reduced predatory pressure in fragmented habitats via unfulfilled habitat requirements (Holt 1996, Tscharntke et al. 1998, Kruess & Tscharntke 2000). Consequently, empirical evidence in the Northern Palatinate highlands remains inconclusive: while top-down control was not addressed in this thesis, Kelch et al. found reduced mortality of the beech gall midge (*Mikiola fagi*, *Cecidomyiidae*) to ectoparasitoids in forest edges (Kelch et al. 2016). Opposed to this, Schmidt (2011) saw no fragmentation/edge effects on predation rates on artificial herbivores whatsoever. To obscure the role of top-down control on edge herbivores in the Northern Palatinate highlands even further, spider densities measured in **Chapter 3** (not shown) were threefold increased in edges vs. the forest interior (linear regression, $F_{2,33} = 19.41$, $p < 0.001$***, $R^2 = 0.54$). As natural enemies are a pivotal element of herbivore control, it remains to future studies to illuminate the patterns in the Northern Palatinate highlands.

(iv) The final proposed mechanism causing the edge/interior contrast focuses on the largely opposite forestry regimes practiced in edge and interior forests. The forest interior is managed for high productivity of a few commercially relevant (shade/cold tolerant) tree species, with often homogeneous age structures (Boch et al. 2013, Schulze et al. 2015). Ensuing poor species richness and community homogenization equally causes poor herbivore communities and simplified food webs (**Chapters 2**, **3**, and **5**). On the other hand, best practice of silvicultural institutions in forest margins aims at promotion of taxonomical richness and structural complexity. Less common tree species are spared, while late successional species are felled, which in turn promotes habitat openness and sets back succession (Coch 1995, Landeswaldgesetz Rheinland-Pfalz 2000, Bartsch & Röhrig 2016). The reason mainly lies in a perceived ecological and recreational gain outweighing economic losses. Hence, silvicultural management and forest fragmentation act in unison, both respectively amplifying the found edge/interior contrast. This is all the more important, as silviculture is a pervasive element of forests of the Northern Palatinate, being noticeable even in the smallest forest fragments (**Chapter 2**). Hence, future studies in fragmented temperate landscapes cannot exclusively address isolated aspect of human landscape modification.

Why Did I Hardly See Any Influence Of Fragmentation *Per Se* (i.e. Patch Isolation)? – It is intriguing that pure fragmentation effects (mainly measured via the integrative fragmentation index, **Chapters 2** and **3**) scarcely contributed in explaining plant and herbivore reactions to human landscape modification. We have reason to attribute this to three interrelated aspects: first, the high autocorrelation of habitat loss and isolation, second, the role of minimum fragment size for maintenance of biodiversity, and third, the age of Central European forest fragments.

In theory, patch isolation does not necessarily preclude habitat loss (Fahrig 2003), but in reality, both processes naturally operate in sync and are barely distinguishable (**Figure 2**, Tscharntke et al. 2012). Accordingly, the fragmentation index mentioned above incorporated (among others) both patch area and isolation metrics. Likewise, numerous studies in the field of fragmentation hardly distinguished fragmentation and overall habitat loss (Fahrig 2003, Lindenmayer & Fischer 2007, Tscharntke et al. 2012). However, it has been hypothesized that fragmentation itself has been overestimated as driver of landscape-scale biodiversity, and instead other factors (e.g. habitat area) might be more important (Tscharntke et al. 2012). In this case it is noteworthy that small fragments in this study were investigated in their center, hence the smaller the fragment, the higher the influence of edge effects. Therefore, other components of forest fragmentation need to be of high relevance in order to be analytically observable.

Let us remain on the matter of patch size for a second point: insects are orders of magnitudes smaller than their focal forest patch, no matter how fragmented it is. Yet, island biogeography theory maintains that species richness and abundances are negatively related to fragment size (MacArthur & Wilson 1967). And, furthermore, forest fragments usually are much bigger than e.g. herbaceous habitat patches, where many other fragmentation studies were performed (Steffan-Dewenter & Tscharntke 2000, Tscharntke et al. 2002, Haynes & Crist 2009). Hence, Ribas et al. (2005) have rightfully asked '*how large is large enough for insects?*'. While they found support for the ability of several small forest remnants to host equal species richness to single large remnants in Brazil (for further theoretical background, compare the *single large or several small* (SLOSS) *debate*, Simberloff & Abele 1976, Ribas et al. 2005), their findings also indicated smaller total species richness of ants within individual small remnants, compared to larger ones. Opposed to this, and although the smallest fragment in this study being 1.9 times smaller than their smallest one, I even found *higher* species richness in smaller fragments (not shown in **Chapter 3**; Pearson correlation between herbivore diversity and size of small fragments, t = -2.0731, df = 18, p-value < 0.05*, r = -0.44). This pattern was even stronger for woody plants (not shown in **Chapter 2**; t = -3.4169, df = 8, p-value < 0.01**, r = -0.77) indicating that even small fragments in the Northern Palatinate highlands are sufficient to sustain both plant- and herbivore diversity, and extinction risks of fragment populations might therefore be small. The main mechanism probably again is in the intensification of edge effects with decreasing patch size (as detailed above).

What are possible causes for low influence of patch isolation? Isolation is usually associated with high biotic heterogeneity via the sampling effect, as well as via increased species turnover, and decreased alpha diversity via imbalances between immigration and extinction rates (Brown & Kodric-Brown 1997, Laurance & Lovejoy 2002, Benedick et al. 2006). However, for herbivores in small fragments there neither was indication for decreased alpha nor beta diversity (**Chapter 3**). Similarly, plant communities in this habitat were even less variable than e.g. those in edges, with slightly higher microclimatic tolerances (both probably due to missing complementarity by core areas). To explain this, I argue that (i) spatial heterogeneity upon deforestation was of lesser importance, and (ii) that time since deforestation resulted in balanced states of immigration and extinction. Firstly, in tropical realms, plant communities (and hence associated herbivore assemblages) are relatively more patchy than in the temperate (Stevens 1989, Koleff et al. 2003). Hence, upon deforestation, sample effects in the temperate were of lesser importance than in other fragmented landscapes. A further factor for high species heterogeneity, namely variability in geological conditions, can be excluded from further considerations. While it may be true that the Northern Palatinate highlands are indeed geologically heterogeneous, forest remnants were nevertheless consistently kept on infertile soils, and within this thesis, geological factors were excluded as insignificant in exploratory analyses (**Chapter 2**). Secondly, consider that fragmentation in the European temperate zone is centuries old (Bhagwat 2014, Finger et al. 2014, Laurance 2014). Hence, immigration and extinction, deemed driving forces in island biogeography and, by extension, in fragmentation research (MacArthur & Wilson 1967, Brown & Kodric-Brown 1997, Fahrig 2003, Tscharntke et al. 2012), were prevailing since the Middle Ages and might have long reached a steady state. Hence, it is reasonable to assume that communities might have experienced a complete turnover, with no noticeable effects of inter-patch distances. In the study system at hand this is supported by missing correlation between physical distance and plant similarity of plot-pairs (not shown in **Chapter 2**; Pearson correlation, t = -0.16641, df = 43, p-value > 0.05, r = -0.03). Similarly, Dumortier et al. and Jacquemyn et al. highlighted the importance of patch age on vascular plant diversity and similarity in fragmented oak forests of differing age (Jacquemyn et al. 2001, Dumortier et al. 2002). Although the equilibrium theory predicts less alpha diversity and high dissimilarity in far, isolated islands (MacArthur & Wilson 1967, Simberloff 1974), certain attributes of fragmented temperate forest landscapes might mitigate immigration/extinction processes. The apparent ability of the landscape to retain biodiversity even in small fragments was already detailed above, indicating low extinction rates. However, the opposite requirement, high immigration, needs to be met as well, and hostility of the matrix must not be overestimated (there is indeed indication for lower matrix importance in temperate realms, Sodhi et al. 2007, Franklin & Lindenmayer 2009, Tscharntke et al. 2012). Furthermore, for plants, one might argue that isolation effects might not yet be noticeable due to extinction debts (i.e. prolonged existence in a patch, but inevitable extinction in the future, e.g. via clonal growth or long lifespans, Honnay et al. 2005). However, considering that most plants in this study reproduce sexually, and many of them are wind-dispersed, I deem immigration rates to be relatively high in Central European landscapes. This is supported by Butaye et al. (2001), who detected striking immigration into 35 years old fragments from within a 1,000 m radius in a Belgian cultural landscape.

IS THIS THESIS A PROJECTION OF FUTURE SCENARIOS FOR TROPICAL BIOMES UNDER CURRENT DEFORESTATION?

Throughout this thesis, the Northern Palatinate Highland and its biota were characterized as an exceptional example of a landscape under forest fragmentation. Most often this was done by contrasting it with what is known from other heavily fragmented biomes, the tropics in general and the Atlantic Forest in particular (da Silva & Tabarelli 2000, Barbosa et al. 2005, Santos et al. 2008). Apart from other aspects, one of the most striking differences lies in the great temporal divide between the respective deforestation stages. Of course, forest clearance is a process and does not occur instantaneously. Particularly in Europe, it gradually intensified over the course of centuries (even millennia). Nevertheless, we can in good conscience set maximum European deforestation and fragmentation stabilization to 700 years ago (Williams 2000, Büntgen et al. 2011, Schulze et al. 2015). Exemplary for many tropical biomes, colonist-driven deforestation of the Atlantic Forest of Brazil might have started as early as 1500 AD, but did not intensify until the 18th century and is still ongoing (Meyer 2008, Joly et al. 2014). Hence, one might argue that the study landscape at hand might be suitable to predict (at least in aspects) the future fate of other fragmented landscapes. In this subsection, I will therefore explore this matter by first synthesizing communalities between tropical and temperate forest fragmentation, then contrasting their essential differences, and finally providing educated guesses for future scenarios. Despite this promising applicability, a comprehensive comparison between (the consequences of) tropical and temperate forest fragmentation has hardly been done in the past (Finger et al. 2014), inducing Tscharntke et al. (2012) to rightfully call this '*likely to be a worthwhile endeavor*'.

Commonalities Of Tropical And Temperate Forest Fragmentation – The spatial component (deforestation and creation of forest islands) naturally is identical in both systems. While cover varies more than twofold (Atlantic Forest 7 - 16% vs. 34% in the Northern Palatinate highlands, Ribeiro et al. 2009, Paul 2015), fragmentation parameters are still comparable in their order of magnitude. Agriculture is the main land-use in both regions, with extensive sugarcane plantations on the one hand and a more fine-grained mixture of cereals, rape, pasture, and meadows on the other. In both cases fragmentation led to edge proliferation and increased edge effect. Similarly, the edge/interior contrast of microclimates came into play, with edges being lighter, dryer, and more extreme in temperatures (Murcia 1995). This is equally reflected in functional attributes of the woody plant assemblages: Both consist of light-adapted, drought/heat-resistant, successional species and are hence pioneer communities (**Chapter 2**, Santos et al. 2008, Tabarelli et al. 2008).

What Are The Most Essential Differences Between Tropical And Temperate Forest Fragmentation? – The manifold (and sometimes fundamental) differences outweigh the commonalities, further highlighting the peculiarity of historically fragmented temperate forest landscapes under silviculture. The most striking ones are described in the following.

Historical components should be addressed first, as they massively influence all following aspects. Central European forest fragmentation, as outlined in **Chapter 1** was a continuous process over centuries and reached a steady state around 700 years ago (Williams 2000, Büntgen et al. 2011, Schulze et al. 2015). Although this was accompanied by technological advancement and hence felling speed, logging of a particular site was still much slower than in contemporary industrialized tree-harvesting systems (Williams 2000). Therefore temperate forest biota had more time to react to altering environmental conditions in such 'softer' labor-intensive logging-

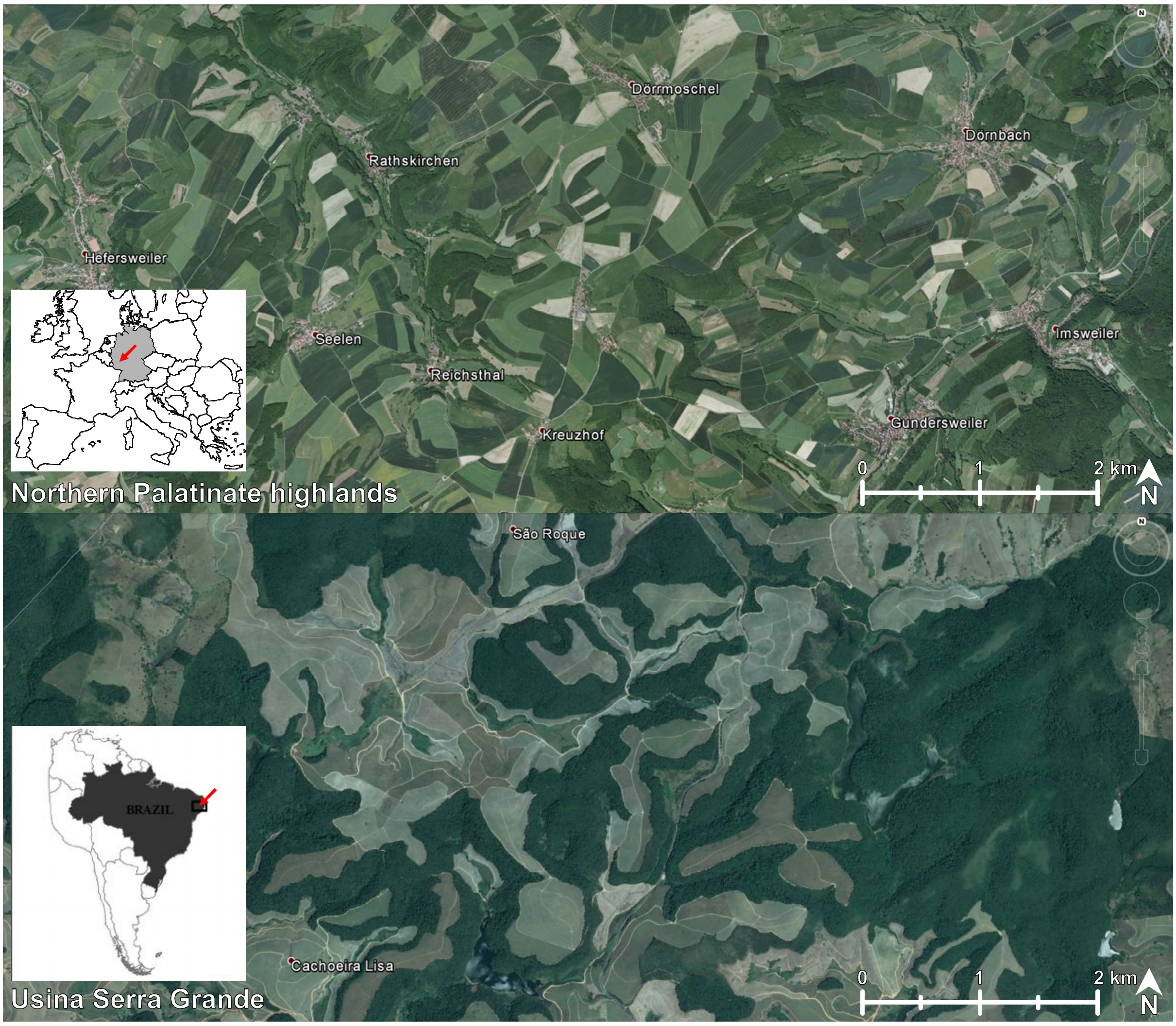

Figure 3: Spatial arrangement of two exemplary temperate and tropical landscapes under forest fragmentation. Top: the Northern Palatinate highlands, a cultural landscape in SW Germany (small b/w picture) display a pronounced small-scale arrangement of variably used matrices surrounding forest fragments, with relatively high density of settlements (large picture). **Botom:** the Usina Serra Grande, a highly deforested landscape in the Atlantic Forest biome of East Brazil (small b/w picture), shows high homogeneity in matrix use with extensive sugarcane plantations (large picture). Please note that both maps have identical scales. Map of Brazil modified after Filgeueiras et al. (2015). Satellite maps from Google Earth (2016, version 7.1.5.1557).

regimes (Finger et al. 2014). This may partially explain why European ecosystems lost only few forest plant species over the centuries, while deforestation is a major threat to biodiversity in the tropics (Wright & Muller-Landau 2006, Schulze et al. 2015).

Forest use was and still is fundamentally different in both biomes. While ecosystem services of tropical forests to the local natives might share similarities to ancient European forest use (hunting, grazing, wood extraction, slash-and-burn agriculture), modern day forestry in Europe is an extensive, systematic, and (most importantly) proactive management of all forested areas across all spatial scales (Schulze et al. 2009, 2015, Forest Europe 2011). Hence, while some native methods of forest use can be considered intensive (e.g. wood pastures, slash-and-burn), tropical forests are likely to be subjected to less intensive human use than in the temperate zone. However, mitigating effects may arise from close-to-nature forestry, including practices such as selective logging, tree species choice according to site conditions, dead wood management, etc.

Matrix use is a key feature in fragmented landscapes, as it determines matrix hostility and hence matrix/forest contrasts and species dispersal (Haynes & Cronin 2004, Franklin & Lindenmayer 2009, Cousins 2013). Determining factors in agroeconomically used matrices are field extent, type, and spatial homogeneity. In this respect, the Nothern Palatinate highlands are an excellent example of a European cultural landscape, with small-scale arrangement of differently used patches (**Figure 3**). Around forest fragments, several different kinds of matrix use can easily be identified, diversifying the matrix, and hence increasing species mobility (Ricketts 2001, Goulart et al. 2015). On the other hand, while the role of polycultures as matrix receives increasing attention (Goulart et al. 2015), fragmented tropical landscapes still often are subjected to large-scale utilization, with little crop variation across large distances (**Figure 3**). Furthermore, matrix microclimates in Europe are much milder than those of lower latitudes. Taken together, there is evidence that matrix hostility in the temperate is comparatively low, with beneficial consequences for species dispersal and matrix usability.

Functional attributes of edge floras and herbivore faunas partly differ between biomes. Concerning tropical herbivores, there is evidence for detrimental fragmentation effects on herbivore specialization, explained by facilitation of generalist species in fragmented habitats. When host species are lost, generalist herbivores can flexibly utilize other hosts, whereas specialists decline (*specialization disturbance hypothesis*, Vázquez & Simberloff 2002, Cagnolo et al. 2009). Opposed to this, edge herbivores in the Northern Palatinate highlands were much less generalist than their counterparts in the interior, due to several causes, e.g. facilitation through bottom-up effects and opportunities for pronounced niche differentiation (**Chapters 3** and **5**). Concerning tropical and temperate edge floras, both are composed of pioneer communities (light-loving, heat- and drought-resistant, fast growing, Santos et al. 2008), with an underrepresentation of large-seeded species with large animals as main dispersers (Santos et al. (2008) for trees, Kolb & Diekmann (2005) for herbs). However, woody plant assemblages in forest edges and small fragments in the Northern Palatinate highlands displayed a pronounced increase in abundance of insect-pollinated and zoochorous plant species (not shown in **Chapter 2**; insect pollination: seventeenfold increase edge vs. interior; animal dispersion: fivefold increase), which is further evidenced by identified indicator species (**Chapter 2**). Again, I deem sunnier and warmer conditions responsible, as the lenient environment facilitates animal activity. The seemingly contradictory prevalence of non-wind dispersed plants in such open forest habitats is a further indication for their comparatively good dispersal ability across forest patches, as they probably experience low matrix hostility. A further highly relevant pattern when comparing biomes seems to be the latitudinal gradient in species richness of functional groups (compare **Chapter 2**). While pioneers in tropical evergreen forests are strikingly inferior in their natural species pool compared to shade-tolerant interior species, this pattern reverts into the temperate zone. Latitudinal gradients are well described in ecology (particularly for biodiversity, Wiens & Donoghue 2004, Novotny et al. 2006). However, differences in species pools of functional groups are completely undescribed (Leuschner 2016, personal communication), the existing literature barely alluding to the topic (Hawkins et al. 2003, 2014). The mechanistic explanation provided in **Chapter 2** focused on limiting water and energy availability. Closed tropical forests are equally hot and moist, whereas open habitats may be hot, but are water deficient. Hence speciation is more probable in the less limiting interior conditions. Vice versa, closed forests in the temperate zone are relatively moist, but much colder than open habitats. Here, edges and small fragments exhibit lenient conditions, as water deficiency is less of an issue, compared to the tropics. Instead, plants need to deal with cold winters and are naturally much more energy-limited (Whittaker et al. 2006, Shiono et al. 2015). Nevertheless, the issue remains practically unexplored and might highly benefit from synergies between ecological and historic biogeographical research (Wiens & Donoghue 2004). Another explanation might be the availability of open vs. closed forest habitats in geological timescales. The tropical rainforests, encompassing the equator, formed a continuously forested area for millions of years. On the other hand, the *megaherbivore hypothesis* states that in the Holocene grazing by large herbivores (large herbivores > 45 kg, megaherbivores > 1,000 kg, Bakker et al. 2015) kept European landscapes fairly open and park-like (Sandom et al. 2014, Bakker et al. 2015). Although the hypothesis is not unanimously accepted (Vera et al. 2006), it still helps to explain high species richness in plants adopted to open conditions. The megaherbivores might have vanished due to humans, but one might argue that anthropogenic landscape cultivation over the centuries somehow compensated this ecosystem engineering by continuous facilitation of mentioned functional plant groups (Williams 2000). Beyond this, the natural prevalence of warm-adapted plants, as well as much more variable climatic conditions in past geological epochs of today’s Europe provide evidence for potentially higher ecosystem robustness against climate change, another support for the findings presented in **Chapter 5**. Moreover, the involved plant and herbivore species faced ever-changing climatic conditions in the past (Sprick & Floren 2008, Finger et al. 2014), hence suggesting future resistance. Opposed to this, decreased adaptive capacities in tropic systems are likely, as they were more climatically conserved in the past (Hooghiemstra & van der Hammen 1998, Leigh et al. 2004). It is hence reasonable to assume that climate change will be less detrimental for biota and their interactions in fragmented forests of temperate Europe than for those in the tropics.

The Predictive Suitability Of Fragmented Temperate Forests For Other Systems Is Limited – The Northern Palatinate highlands as an example of a fragmented temperate forest landscape might share certain attributes with fragmented landscapes from other biomes. However, as described, the many differences in temporal deforestations, modes of land-use, and inherent natural history of species easily outweigh the commonalities. This further highlights the notion that general coherencies in forest fragmentation must be described with caution and that it is essential to account for the individual peculiarities of the ecosystem at hand (compare discussions of **Chapters 2**, **3**, and **5**). Nevertheless, the comparison above, particularly the many differences, might still enable us to learn something about the possible future of fragmented tropical landscapes.

For instance, we can deduce that the relatively high rate of forest conversion, together with the low adaptive capabilities of species will have much more devastating effects than in Europe. Species traits are temporarily fixed in human time scales, and hence need to be seen as given. Therefore, the only recommendation in this respect is as trivial as it is difficult to implement: stop the deforestation.

It follows that we need to focus on variables which are within human spheres of influence. It was mentioned that tropical matrices are much more hostile due to extreme microclimates, low heterogeneity and comparatively less dispersal abilities of species. Mitigating practices have already been numerously described, such as creation of habitat corridors and stepping stones (Sodhi et al. 2007). Beyond this, small-scale variations of matrix use might have alleviating effects, as well as crop mixtures (Goulart et al. 2015). This might be hard to communicate/implement, as both proposals impair the abilities of landowners to utilize the matrix in an industrialized way. Otherwise, strong isolation effects will depauperate biodiversity in the long run, much more than it ever was in the temperate zone.

Silviculture has been a fundamental driving force of European forest ecosystems for centuries and is an intrinsic feature of practically all forest tracts. However, there is little evidence for synergistically detrimental effects in unison with forest fragmentation (**Chapter 2**). Changing the biome, at present, much of tropical forest-use (not deforestation) is due to native populations, with is often associated with smaller impacts. But what if demographic growth, economic demands, and silvicultural commercialization lead to similar extensive and intensive management of fragmented forests? I argue that tropical forest ecosystems will not hold up as well as Europeans do. Typical processes in forestry, tree species selection and forest opening via tree extraction, will further depauperate biodiversity, particularly among shade-adapted plants and insects (opposed to European forests). Hence, we will probably observe amplifying effects of forest fragmentation and silviculture. Counter-measures can only be strict protection of already fragmented forests (land sparing perspective, Klein et al. 2014), or at least application of low-impact forestry (land sharing perspective, Klein et al. 2014). In this last respect, the ongoing debate about close-to-nature forestry in Europe might provide helpful guidelines for the future. Further research is indeed needed, as commercial timber concessions (the main form of forest use by many post-colonial forestry departments) failed to achieve sustainability objectives, even under a policy of selective logging (Barr et al. 2014). Overexploitation might further be aggravated by weak law enforcement, widespread corruption, and dominance of commercial forestry by political and military elites (Barr et al. 2014).

As mentioned, fragmented tropical forest ecosystems might be more susceptible to climate change than temperate ones, due to low adaptive capabilities and heat tolerance of many species. There are a few recommendations as to how to stabilize plant assemblages against global warming, e.g. supplementation of local populations with pollen from more drought/heat tolerant specimens from the distributional border, or by planting climatically preadapted species (Lindner et al. 2010, Corlett 2014). However, considering the tropical megadiversity across all taxonomic groups, it seems that only little can be done at the whole.

Taken together, the Northern Palatinate highlands might not be a suitable projection of future scenarios for tropical forests under current deforestations. However, the study of the unique responses of fragmented temperate forests under silviculture enable us to contrast them with other fragmented forest systems and subsequently make assumptions if these will react similarly/differently, or better/worse. Concerning tropical forests, e.g. the Atlantic Forest of Brazil, it is reasonable to assume that fragmentation effects will be strikingly more severe in the long run, compared to the Northern Palatinate highlands. Mitigating measures are highly in order, limited as they may be.

IMPLICATIONS FOR CONSERVATIONISTS, FORESTERS, AND DECISION MAKERS

The thesis at hand is a piece of basic research, through and through. But this is not to say we cannot extract additional utility for practical application out of it. Therefore, I would deem this work incomplete, if it would not provide advice on how to treat human-modified forest landscapes in Europe in the future. The wealth of results gained across the chapters enable us to give specific recommendations for several target groups. If we separate them by underlying motives, three main parties emerge: conservationists (who strife for preservation of biodiversity, ecosystem functioning, or naturalness), foresters (which are torn between ecological sustainability, economical profitability, and recreational quality provision), and decision makers (who ultimately implement guidelines in forestry and landscape planning). In the following, I will elucidate recommendations for each group separately.

Conservationists: Shouldn't We Further Fragment The Forest? – This provocative questions pops to mind considering the essence of results pointing towards beneficial effects of forest fragmentation on almost all considered ecological attributes. Yet I think it is crucial to answer this question in order to adequately regard the unique position the Northern Palatinate highlands (and by extension all Central European forests) have in fragmentation research. The short answer is '*no*'. The proper answer is (of course) more complicated and needs to pay respect to the historic development from a natural to a cultural landscape. As already described in detail, European forests historically underwent a transformation from naturally open forests in the early Quaternary, to closed ones in the early Holocene, and finally to heavily used and deforested remnants in modern times. Hence, compared to the past, modern landscapes may be similarly 'open' in a very general sense, but are anthropogenically shaped in every way imaginable. That means that edge habitats, as promoted as they may be, are surrogate habitats in the absence of continuous open forests. This is further underlined by the small average edge-depth (< 5 m in Switzerland, Krüsi et al. 1996), making forest edges essentially a one-dimensional habitat on a two-dimensional surface. Hence, in the reality of heavily used interior forests and agroeconomically exploited matrices, forest edges and small fragments constitute a surrogate reservoir of biodiversity, biotic heterogeneity, and species interactions. It is therefore not a question of whether we should further promote this habitat, but rather, what we can do to ecologically valorize it and its adjacent habitats.

Specific recommendations for conservationists to achieve this should aim at small, yet feasible, actions on a local scale. I imagine punctual interventions, such as deliberate planting of shrubs where young forest margins are still disclosed, preferably rare, thermophilous species. However, where site conditions differ (e.g. forests bordering a riparian area), choices of better fitting species have of course higher priority. This procedure also enhances edge heterogeneity, which has been shown to be a distinct feature of the Northern Palatinate highlands (**Chapter 2**). Furthermore, e.g. private owners of pastures adjoining forests can enhance ecological edge quality by managing for deeper edges with pronounced herb and shrub fringes. However, on larger scales, it will need foresters and governmental decision makers to have extensive impacts.

Foresters: Off To A Good Start, But Much More To Go – Europe's forests have a long history of exploitation, deforestation, and plantation-forestry. However, the recent past saw progressive improvement. For instance, forestry institutions in the Northern Palatinate highlands did a noteworthy job in implementing increasingly close-to-nature forestry in the second half of the 20th century. This is well illustrated by the comparably high amounts of lying dead wood found in managed stands (21.00 ± 11.71 m^3/ha, Christmann 2014) compared to the rest of Rhineland-Palatinate or Switzerland (12.88 m^3/ha, MULEWF 2014; 11.5 ± 1.4 m^3/ha, Bütler & Lachat 2009). Nevertheless, utilizing insights gained in previous chapters, recommendations for the identified types of forest habitats can be made.

As already described, forest edges are habitats of particular conservation value in the reality of cultural landscapes, and there are several possible silvicultural interventions to further enhance their ecological value. As already hinted, edge depths usually are rather small, with the commercial forest starting within the first few meters towards the interior. 4.7 meters edge depth from Switzerland are equally representative for forests of Rhineland-Palatinate (Krüsi et al. 1996). Ideal values are 25 – 40 m, including the shrub and herb fringe (Krüsi et al. 1996). Increasing edge depths, particularly herb and shrub fringes, might significantly enhance edge quality via increases in structural complexity and biodiversity, hence making them true ecological reservoirs for the surrounding landscape. However, foresters are always torn between commercial profitability and ecological necessities. Hence, it is important to ask how much commercially usable forest would be lost if we arbitrarily set the recommended minimum depth to 25 m as goal. Assuming a current 4.7 m edge depth as given, and considering a total edge length of 5,700 km in the Northern Palatinate highlands (**Chapter 1**), edges would then take up 142.5 km^2 from the total forest cover of 528.9 km^2 (hence 26.9%). This would be striking rise in edge portion from 5% before (assuming 4.7 m), naturally caused by the high inherent fragmentation degree of the landscape. That would make it hard for forestry institutions to meet both demands. However, if we only consider the seven largest fragments (all > 1,000 ha, totaling 727.7 km^2), we would only see a proportional rise of edge habitat from 0.5 to 2.5%, reducing the commercial forest by 14.7 km^2. However, this is no economically lost area. Edges may incorporate tree species with valuable wood, like wild cherry (*Prunus avium*). Hence, in the case of large forest fragments, increasing edge depth can enhance ecological value without sacrificing significant commercial profits. Moreover, deep edges with pronounced shrub and herb fringes harbor more insect pollinated plants (increasing pollinator diversity) and incorporate more microhabitats for predators, increasing food web complexity at the whole. This might even have positive spillover effects into the matrix with increased pollination success of crops and higher top-down control of crop pests. Furthermore, silvicultural facilitation of site-specific tree species may help to increase heterogeneity of edge assemblages of all taxonomic groups. Lastly, enhancing edges as described above, will massively increase their visual appeal to forest visitors, serving foresters' third task, namely cultivating the forests' recreational value.

Small forest fragments have been shown to be nearly as diverse in species and species interactions as edges, as described within this thesis. However, whereas edges of large remnants gradually transform into core forest, when moving to the center, small fragments lack any interior core whatsoever. They are often entirely dominated by heat adapted tree and shrub species, with low commercial value (**Chapter 2**). Furthermore, 85% of patches in the Northern Palatinate highland are smaller than 0.1 km^2 and only contribute 8.5% to total forest cover in the landscape (**Chapter 1**). Hence, small fragments can be considered to be of practically no economic interest. It is further plausible to argue that wood extraction in small remnants might be detrimental for ecological functions related to soil, such as soil stability and water retention capacity. Therefore, cessation of silviculture in small fragments (where in state-possession) might help prevent ecological harms without serious economic losses. Furthermore, foresters might preferably aim to increase inter-patch mobility by cultivation of hedgerows seaming agricultural patches in the matrix. As the matrix in the study landscape is particularly patchy (**Figure 3**), seaming in such a way might generate a complex network of habitat corridors, which might further mitigate isolation effects.

In the case of managed interior forests, foresters naturally have the highest impact. During many personal conversations, I noticed considerable commitment from the majority of forestry-members to close-to-nature practices, despite having to meet both ecological and economical standards. Nevertheless, within the Northern Palatinate highlands, age class forestry is still a defining feature of many tracts (Hubert 2016). Of course, efforts should be made to keep moving away from this practice, as it was repeatedly shown within this thesis and in the past that monotonous forests constrict biodiversity and simplify species assemblages, as well as their interactions. Instead, continued implementation of close-to-nature forestry should be encouraged. There are various specific aspects, of which the following might be the most promising. Firstly, concerning spatial arrangement of tree species and their selection, small scale richness and heterogeneity should be aimed for, in order to prevent detrimental effects of monodominant stands, as explained above. Furthermore, functional traits of species should match site conditions in order to encourage formation of natural phytosociological forest types (e.g. lime-oak forests, ravine forests, etc., EEA 2006), to in turn increase forest type heterogeneity across the landscape. A further benefit is increased fitness and productivity of tree specimen. Secondly, mimicking of natural gap dynamics might help to increase heterogeneity of microclimates, age structures, and successional stages. Large scale clearings, such as clear-cutting, might be somewhat similar to other major disturbances, such as fires. However, clear-cutting has been predominantly deemed detrimental, e.g. for soil quality or forest pest control. On the other hand, single-tree extraction creates gaps similar to natural collapses, with only slight opening of the canopy. Indeed, group-wise extractions might create gaps similar to windthrow, significantly opening the forest without the negative consequences of larger clearings. This practice might facilitate early-successional species and hence benefitting beta diversity. However, foresters might rightfully argue that successional setback of this magnitude requires several tree generations to reach successional climax and reestablish valuable tree species of harvestable age, in turn decreasing stand profitability. Succession might even be further delayed, if cleared stands are left unattended, which can cause growth of thick grass and bramble covers, in which trees hardly establish. Until a better solution emerges, I recommend a compromise of locally retaining grove-like groups of early succession, but keeping single tree extraction as major type of gap/disturbance dynamic. Lastly, successional stages are not solely defined by tree community composition, but also by tree age and physical forest context. To be precise, at harvest age, a tree is far from reaching its maximum life span (e.g. beech: 120 -160 a vs. maximal 200 - 300 a; pedunculate oak: 180 - 300 a vs. maximal 500 - 800 a). However, the associated fauna and flora posses their own successional progression, with many species only occurring at later stages of a trees life cycle (Moning & Müller 2009). These species require crevices, arboreal duff accumulations, or dead branches. While the deliberate retention of valuable trees is already an established concept in close-to-nature forestry, the spatial density of such trees is a matter of debate (Niedermann-Meier et al. 2010). Customary recommendations of five trees per hectare would lead to losses of about 770 € per hectare and year, increasing the tension between ecological needs and profitability (Niedermann-Meier et al. 2010, Ministerium für Umwelt, Landwirtschaft, Ernährung 2011). It is well known that many species requiring old-growth forest conditions are limited in their mobility, hence decreasing the density of target trees would impact these species the most. It is unknown, what distance can be seen as threshold for the majority of species, and future research might illuminate this matter. A reduction from five ecologically valuable trees per hectare to just one increases distances from 45 to 100 m, which might still be feasible, considering that even high-priority species in conservation, such as *Osmoderma eremita* (*Scarabaeidae*) easily traverse larger distances (Zauli et al. 2014). But why recommending lower densities of target trees for the sake of profitability? Because, instead of establishing a fairly dense system of stepping-stone trees, forestry departments could try a group-wise arrangement of ecologically valuable trees together with similarly important structures, e.g. dead wood accumulations, or shady stand conditions. The importance of open forest conditions was discussed in depth in this thesis (particularly **Chapter 2**), and the deliberate use of disturbances for heterogeneous light conditions as well (**Chapters 2**, **6**). However, open forest structures are only half of the story, because in order to cover all possible habitat types within large forests, the opposite conditions must be present as well. Or in short: it must be dark and moist at least somewhere. Hence, a more clustered distribution of old-growth conditions might further enhance alpha and beta diversity across all taxonomic groups. This promotion of heterogeneity in tree species and microclimatic conditions was described in such depth because the pronounced biotic homogenization of interior forests is one of the key outcomes of this thesis (**Chapter 2**). This small-scale diversity will further propagate through other trophic levels, increasing biodiversity at the whole with potentially beneficial effects for ecosystem functions and services. For instance, in **Chaper 5**, it was shown that species rich plant communities are part of particularly stable ecosystems. In turn, high general diversity and ecosystem stability might help to regulate processes such as herbivory, as herbivores then would neither experience relaxed bottom-up, nor top-down regulation (Haddad et al. 2011). This is highly relevant for foresters, as decreased background herbivory might benefit tree productivity, as trees can invest more energy into growth and wood formation (Zvereva et al. 2012). Furthermore, diminished variability in herbivory reduces the probability of calamities, which in turn decreases harvesting losses. There is indeed evidence for positive effects of plant diversity on herbivory reduction. Dohm (2009) found a more than twofold reduction in folivory in diverse forest edges, compared to the depauperate interior. Similarly to herbivores, bark beetles and tree pathogens might be less effective in diverse forests, as well.

In the case of unmanaged natural reserves, foresters, by definition, have comparatively limited possibilities for interventions. Yet, the forest strips bordering reserves certainly lie within their professional domain. In theory, these strips are managed as buffer zones around reserves, minimizing disturbances from the managed forest parts into the reserve, and should have a generous breadth of 100 m (Landesforsten 2016). However, stand structure and naturalness of these buffer zones seems to vary considerably across reserves and even within the perimeter of individual reserves (personal observation). This is partly explainable by the varying age of reserves, as some of them were expanded over the years, generating borders younger than 20 years. These time scales are plainly too short to allow cultivation of appropriate buffer zones. Nevertheless, creation of such transitional zones is elementary, as old-growth stands have been shown to be strikingly susceptible to external disturbances from the surrounding managed forest (which functions as a matrix, in this case) (Wesołowski & Rowiński 2006). In conclusion, as the formally set guidelines cannot yet be met due to insufficient time since reserve establishment, the recommendation is rather trivial: to strive for continued cultivation of buffer zones, until ecological criteria are fulfilled.

As a final recommendation, I would like to suggest to consider the management index, which was used in **Chapter 2** to assess the management intensity in a forest stand. As unmanaged forests are still fairly young, we still have no adequate controls. Hence, the use of a continuous index is useful, as it is able to quantify the *relative* management intensity. There are multiple published measures which integrate several management proxies (Schall & Ammer 2013). However, I deem the presented management index, based on the PCA-approach of Martorell and Peters (2005) particularly useful, as it elegantly deals with autocorrelation by embracing it.

Decision Makers: Laying The Foundation For Future Biodiversity – The majority of forests in Rhineland-Palatinate are in public possession, either by municipalities (46%), the federal state (26%), or the federal republic (2%) (BMEL 2016). Furthermore, the public institutions are the primary agent for regional planning on landscape-scale. Hence, it is these organs that should be addressed with large-scale recommendations on land-use, forest-arrangement, and regulatory changes in forestry.

Concerning small forest fragments, the potential of establishing hedgerow systems was already mentioned above. Whereas foresters could participate in a practical manner (bottom-up approach), institutions operating at landscape-scale could complement this by regional planning (top-down approach).

On the matter of managed interior forests, not much can be said concerning regulatory requirements. Official management principles already laid a sound foundation for the implementation of close-to-nature forestry, and there is noticeable evidence for increasing commitment of higher public institutions to ecologically sustainable silviculture. If the rate of innovations and their implementation remain the same (e.g. reserve establishments, introduction of the BAT concept, creation of the National Park Soonwald, just to name a few, MULEWF 2011), it will be a matter of time to see ecological responses. Hence, continued scientific companionship is essential to evaluate the significance of individual reforms and to provide advice.

Regarding unmanaged forests, I will address both unmanaged forest reserves and private forests. Firstly, Germany's natural forest reserves are noticeably small, as less than 10% of them are larger than 1 km^2 (BfN 2016). For illustration, similarly, only 3% of forest fragments in the Northern Palatinate exceed this size. Hence, if we consider these reserves as patches within a non-patch landscape, the typical forces of habitat fragmentation prevail again. This is all the more important, as it was already mentioned that habitat continuity matters, even for old-growth forests within regular forest tracts (Wesołowski & Rowiński 2006). Therefore, expansion of natural reserves, as it can be observed in Rhineland-Palatinate (e.g. reserve *Wildensteinertal*, expansions in 1994 and 1999) should continue. Secondly, if we place reserves in the context of habitat fragmentation, it is important to note that they are usually hardly comparable, as they are often tremendously different in forest type. This lies in the tendency to conserve forest types deemed particularly worthy of protection (e.g. pedunculate oak–

hornbeam forests). A further motivation for this selection practice is that many of these forests are on unprofitable stands (e.g. due to poor soil conditions or limited accessibility). Under these circumstances, the most prominent natural forest types of Europe, mixed beech forests with high dominance of beech, are underrepresented. This is illustrated by my difficulties finding representative beech stands in natural forest reserves for inclusion in this thesis (own observation), and by low dominance of beech across reserves in Rhineland-Palatinate (41 ± 32%, Landesforsten 2016). By comparison, unmanaged forests in this thesis, which were chosen as representative beech stands, had a dominance of 61 ± 28 %. Hence, future reserve selection should regard the need to develop natural old-growth beech forests. Lastly, and now switching to private forests, I would like to point out their potential value in reserve selection. A characterizing feature of the Northern Palatinate highlands is the existence of local assemblages of small, privately owned forest parcels. The likelyhood of historic wood extractions and other forms of management diminishes with decreasing size and increasing remoteness. For instance, single plots used in this thesis, which were situated in such forests, were unmanaged for over sixty years, easily surpassing any forest reserve. The importance of such '*informal reserves*' has already been demonstrated e.g. by Bhagwat et al. (2005), who found similar biodiversity in formal reserves and nearby sacred groves in India. A further benefit of privately owned forests is the inherent heterogeneity in historic forest use. Many stands were once structure-rich coppice forests, which are rarely found nowadays. Naturally, the question emerges, if these forest parcels might not be promising locations for future reserves. They often occur in clusters, so that a reserve establishment would require the simultaneous acquisition of several parcels. However, while many may be part of a family's inheritance for several generations, often owners will show low attachment or even hardly remember ownership (personal observation). Hence, group-wise acquisition might be feasible. Therefore, in conclusion, the proactive acquisition of privately owned forests and their subsequent transformations into reserves is a promising prospect for decision makers in forestry.

OUTLOOK

I would like to conclude this thesis by providing prospects for future research activities, which emerged. These range from rather specific recommendations for variable selection to general directions of research.

Apart from the integration of concrete microclimatic measurements (instead of reliance on indicator species), future studies in the Northern Palatinate highlands might also incorporate the role of predators in the ecosystem. Within this thesis, emphasis was laid on bottom-up forces shaping herbivores and their interactions in human modified landscapes. However, predatory pressure naturally is a major driving agent of herbivores as well. This is all the more important, as the role of predators on herbivores in this study landscape remains inconclusive (Schmidt 2011, Kelch et al. 2016).

Furthermore, the main mode how herbivores influence other ecosystem components is, of course, herbivory. While the relation of forest fragmentation and insect herbivory was already evaluated in the Northern Palatinate highlands (Dohm 2009), a more intricate analysis incorporating the variables generated in the meantime might make a major contribution in illuminating the role and relationships of herbivory.

Concerning interaction networks, two major enhancements are conceivable. One would be the inclusion of climate change susceptibility of herbivores. This would make networks more dynamic and might increase predictive abilities. While no proxies exist for herbivore susceptibility, as is the case for plants, the literature may still deliver qualitative information, which could prove usable. Another aspect is rewiring, i.e. the formation of new host-herbivore interactions, when a former host is lost. This increases the robustness of real food webs, but is underrepresented in most theoretical networks. Incorporating the documented feeding range of herbivores might enable network modeling to better assess network robustness.

The final recommendation, which is detached from this thesis the most, is the discussed latitudinal gradient in functional group species richness (**Chapters 2** and **6**). The observation that heat and shade adapted plants seem to strikingly differ in their respective species richness along a latitudinal gradient is practically unreported. However, it seems to be a very general pattern, which is easily explainable by limitations of water and energy in the respective environment. For higher latitudes, data acquisition is fairly simple, as functional traits for practically all plant species are documented in depth. On the other hand, comparison to plant species pools in lower latitudes might be aggravated by increasing, but still limited knowledge on the occurring plant species. Nevertheless, the matter is highly intriguing and warrants further/deeper investigation.

In conclusion, research activities on ecological responses to human forest modification in the Northern Palatinate highlands were extensive and sufficed to create a comprehensive conceptual picture. Nevertheless, there are still questions unresolved and aspects not taken into consideration. Future studies (and analysis of recent data) will help to complete the picture and might hopefully contribute to the ecological quality of this unique landscape.

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Chapter 7

Appendix

Things in tow:
cross-forest transportation can take a heavy toll on a car.

Appendix 1: Effects of human forest modification on dead wood in forests of the Northern Palatinate highlands – an excursion

Appendix 2: Poster "Can forest fragmentation promote food web complexity? A case of plant-herbivore networks in (silviculturally managed) temperate forests"

Appendix 1: Effects of human forest modification on dead wood in forests of the Northern Palatinate highlands – an excursion

INTRODUCTION

Retrospectively, dead wood (particularly coarse woody debris, CWD) was an elementary variable in the determination of management intensity within this thesis (compare e.g. **Chapter 2**). The reason lies in the strong causal relationship between CWD and silviculture (Christensen et al. 2005, Lachat et al. 2013). Furthermore, CWD is an elementary component of temperate forest ecosystems in terms of biodiversity, ecosystem functioning and services (Christensen et al. 2005, Müller-Using & Bartsch 2009, Bauhus et al. 2009).

For one, CWD serves as ressource, as well as habitat for a wide array of forest arthropods (Grove 2002, Varady-Szabo & Buddle 2006). These encompass a multitude of higher taxa and corresponding life history strategies, including xylo(detriti)phages throughout all life stages (e.g. many *Anobiidae*, such as *Ptilinus pectinicornis*, compare **Chapter 4**), predators which roam wood galleries as larvae and mature into pollinators as adults (e.g. many *Dasytidae*, such as *Dasytes plumbeus*, compare **Chapter 4**), or xylo(detriti)phages which turn into pollinators upon maturation (many *Scraptiidae*, such as *Anaspis maculata* compare **Chapter 4**). This determines a huge diversity of insects bound to coarse woody debris. In Germany, for example, more than 1,400 beetle species are considered to be dead wood specialists (Seibold et al. 2015). As CWD is usually limited in managed forests (Erdmann & Wilke 1997, Christensen et al. 2005, Müller et al. 2008), many of those specialists are indicator species for more pristine forest conditions (Urwald relict species, Müller et al. 2005). Hence, many of them are also threatened as well (Grove 2002, Möller 2009, Seibold et al. 2015). For example, from aforementioned ca. 1,400 coleopteran CWD specialists, 1,064 species are recorded in the German Red List (Seibold et al. 2015). Quantity is not the only aspect determining the ecological relevance of CWD as ressource or habitat. CWD diameter, species, and decompositional stage are essential, as well (Erdmann & Wilke 1997, Lachat et al. 2013). Furthermore, standing dead tree trunks (snags) are considered as important complements, as decomposition is slower and microclimatic conditions are different (e.g. dryer) (Jonsell & Weslien 2003, Bouget et al. 2012). Apart from resource and habitat provision for various (often rare) arthropods (Grove 2002, Christensen et al. 2005), further functions include microclimatic buffering, as decomposing wood retains moisture, and continuous nutrient release (Christensen et al. 2005, Lachat et al. 2013). Another pivotal ecosystem service is, without doubt, the sequestration of carbon, as CWD retains organic compounds for many decades before full decomposition (Müller-Using

& Bartsch 2009, Pan et al. 2011). European forests accumulate roughly 2 million tons of carbon each year through dead wood formation (Pan et al. 2011). Accordingly, forests in Rhineland-Palatinate show a positive carbon balance, hence functioning as carbon sink (MULEWF 2014). Therefore CWD is an important ecosystem component in climate change contexts (Milad et al. 2011, Pan et al. 2011).

Yet, anthropogenic silviculture (ca. 99.8% of European forests are silviculturally used, Frank et al. 2009) diminished CWD abundance and quality, as the major point of human forest management is the extraction of woody biomass (Christensen et al. 2005). For instance, Erdmann & Wilke (1997) reported 9.3 m^2/ha CWD for managed German beech forests. By comparison, European natural forest reserves (with ceased silviculture) showed on average 1,400% higher amounts (130 m^3/ha), ranging from 6 to 550 m^3/ha (Christensen et al. 2005). It is noteworthy, that this mentioned study incorporated fairly old reserves (the oldest being unmanaged since 1838) and time since establishment was highly related to CWD volume (Christensen et al. 2005). Consequently, other studies failing to show higher CWD amounts in unmanaged stands attributed this mainly to the relatively young age of forest reserves (Blaser et al. 2013). Hence, CWD accumulation is a comparably slow process, associated with the rather sedate life cycle of trees (Vandekerkhove et al. 2009). Remaining wood residues after tree extractions are a further factor why managed forests might show similar CWD amounts than recently unmanaged forests, although these remnants are usually much smaller in diameter and of lesser ecological quality (Balcar 2013, Lachat et al. 2013). Differences might be further leveled by recent advances in silvicultural practice, such as the *BAT Konzept*. This conceptual framework aims at retaining and facilitating old, morbid trees of high ecological quality and subsequent CWD increase in managed stands (MULEWF 2011).

While silviculture affects dead wood mainly via the extraction of trees, the main mechanism in forest fragmentation is the increase in dead wood via changes in tree mortality due to small forest fragments and forest edges being more strongly exposed to wind and extreme microclimates (Harper et al. 2005, Jönsson et al. 2007). Hence, fragmentation-affected forest habitats might display higher CWD amounts. Yet, as opposed to forest management, studies on the effects of forest fragmentation on dead wood are rare at best (Esseen 1994, Jönsson et al. 2007).

For all these reasons ((i) the important role of CWD in this study, (ii) not least because of its pivotal role in forest ecosystems, (iii) and the poor empirical evidence concerning fragmentation effects) a more detailed analysis concerning fragmentation and management effects on dead wood quantities and qualities in forests of the Northern Palatinate highlands was necessary.

METHODS

For this purpose, a master's thesis in 2014 systematically censused lying CWD, snags, and stumps (all CWD types > 10 cm diameter, Nordén et al. 2004, Müller-Using & Bartsch 2009), as well

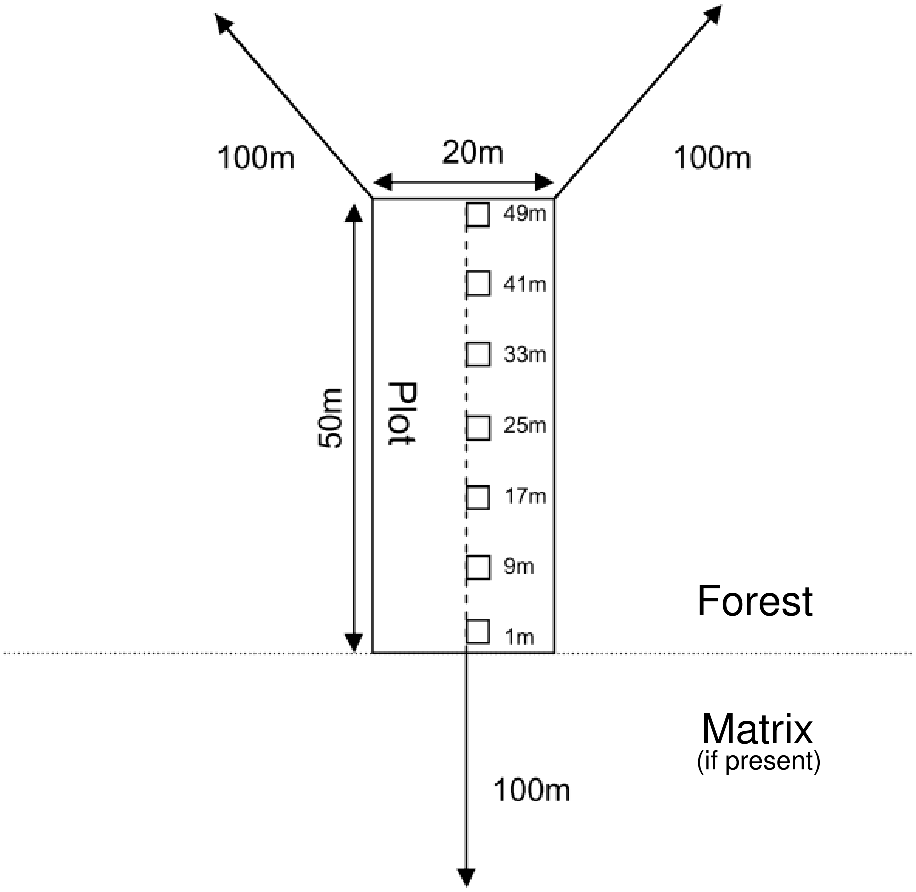

Figure A1: Conceptual sampling framework for recording coarse woody debris (CWD) and fine woody debris (FWD) in permanent plots in forests of the Northern Palatinate highlands. Lying CWD was recorded following the line intersect method (Marshall et al. 2000) along the three equiangular 100 m transects leaving the plot. Snags and stumps were measured within the 1,000 m² plot. FWD was sampled in seven subplots à 0.25 m² (small squares along the dashed line). Modified from Christmann (2014).

as fine woody debris (FWD, between 1 and 10 cm diameter, Nordén et al. 2004, Müller-Using & Bartsch 2009) across all 57 permanent biomonitoring plots described in this thesis (Christmann 2014). This incorporated 10 small forest fragments, 19 forest edges, 12 managed and 16 unmanaged forest sites (compare **Chapters 1** and **2**). Lying CWD volume was measured along three 100 m transects (totaling 17.1 km across the study landscape), leaving the plots in an equiangular triangle (**Figure A1**) and recording length, diameter, and angle to ground of all lying CWD pieces following the line intersect method described by Marshall et al. (2000). Snags and stumps were quantified within the 1,000 m² plot (totaling 5.7 ha) by measuring and estimating maximum and minimum diameter, as well as height of tree trunks, assuming a conical shape. For FWD quantification, per plot seven subplots were established along a 50 m transect (**Figure A1**). Within each subplot, all FWD pieces were collected and volume calculated assuming a cylindrical shape, totaling 99.75 m² of area sampled for FWD. Summing fine and coarse woody debris, 3,950 individual pieces of dead wood were measured and recorded.

RESULTS AND DISCUSSION

While forest fragmentation decreased lying amounts of dead wood, cessation of management generally had beneficial effects on all components of CWD. FWD, on the other hand, was entirely unaffected by any aspect ofanthropogenic forest modification (**Figure A2**).

FWD volumes were markedly similar, with on average 9.12 ± 6.34 m^3/ha across the entire study region. These values are comparable in magnitude to another study reporting FWD volumes from a European mixed forest (11.2 ± 5.1 m^3/ha, Nordén et al. 2004). This might imply high homogeneity in FWD production across European forest systems, regardless of forest and predominant disturbance types. This is surprising, as in managed forests brushwood is often left behind after tree fellings, suggesting increased amounts. On the other hand, this mechanism might be weakened by comparably higher decomposition rates, as FWD decomposes roughly twice as fast as CWD (18 vs. 35 a, Müller-Using & Bartsch 2009). Another confounding factor might be deliberate extraction of FWD in the form of woody residue following felling events, as FWD might become more profitable with increasing economical prevalence of fuel wood use (Riffell et al. 2011).

Across the study landscape, volume of coarse woody debris varied markedly, ranging from 6.58 to 170.66 m^3/ha (more than 25fold), with an average of 41.13 ± 33.83 m^3/ha. Contrary to expectation, forest fragmentation decreased volume of lying CWD, although there was evidence for increased volume and diameter of snags (**Figures A2** and **A3**). This pattern might be explicable by the following reasoning: First, the fact that I did not see generally increased CWD volumes might be due to the age of forest fragments and forest margins. The studies reporting elevated tree mortality due to fragmentation were usually conducted in forests of recent deforestation (Laurance & Lovejoy 2002, Laurance et al. 2006, Jönsson et al. 2007). However, fragmentation of the Northern Palatinate highlands occurred centuries ago, and the flora of fragmentation-affected habitats verifiably responded to the accompanying abiotic conditions (compare **Chapter 2**). It is hence reasonable to assume that these floras show mortality levels comparable to interior communities, rather than floras of recently fragmented forests. Second, decreased levels of lying CWD might be due to the relatively higher decomposition rate of lying vs. standing dead wood and the predominance of pioneers. As these tree species usually exhibit softer woods, they decompose more quickly. These two aspects lead to faster degradation of lying CWD in fragmented forest habitats. Third, slightly (not significantly) higher volumes and diameters of snags in small forest fragments is in line with findings from other small European forest fragments. There, fragmentation led to higher mortality of trees with larger diameters, as well as to replacement of uprooting as primary mode of mortality by standing death (Jönsson et al. 2007).

Furthermore, in this study region, smaller fragments are more likely to be owned privately (**Chapter 1**, **Table 1**), increasing the probability that snags are not extracted by foresters for *silvicultural hygiene* reasons.

Cessation of management had substantial effects on volume and

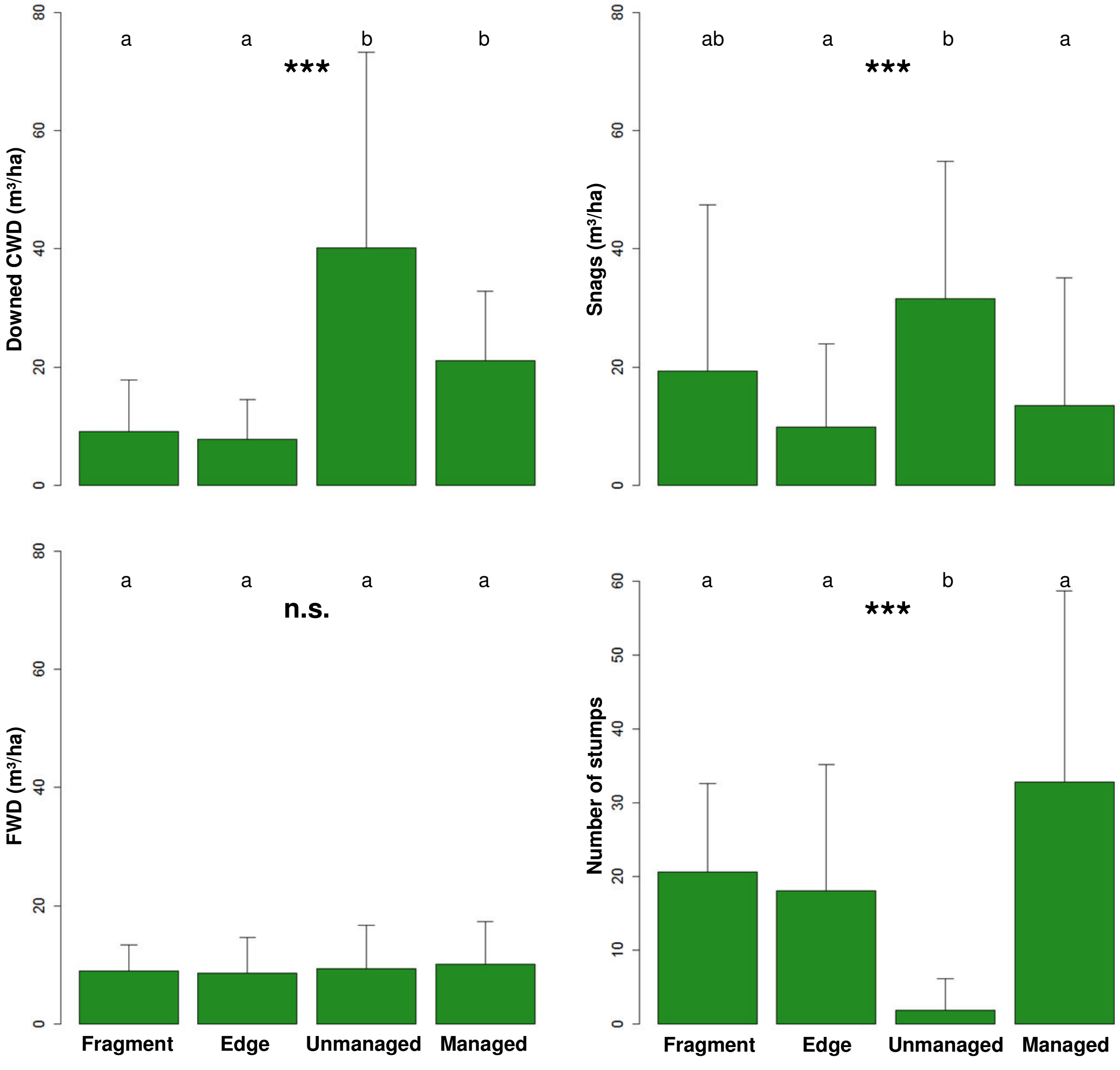

Figure A2: Effects of human forest modification on volume of dead wood (downed coarse woody debris (CWD), snags (standing CWD), fine woody debris (FWD), and abundance of stumps) in forests of the Northern Palatinate highlands. Anthropogenic modification is represented by silvicultural management (*Managed*, with ceased management as control, *Unmanaged*), as well as forest fragmentation (small forest fragments, *Fragment* and forest edges, *Edge*). Log-transformed data, one-way ANOVAs, all df = 3 & 53 and $p < 0.001^{***}$ (where significant). Significance letters were assigned according to Tukey`s HSD post-hoc test. Modified after Christmann (2014).

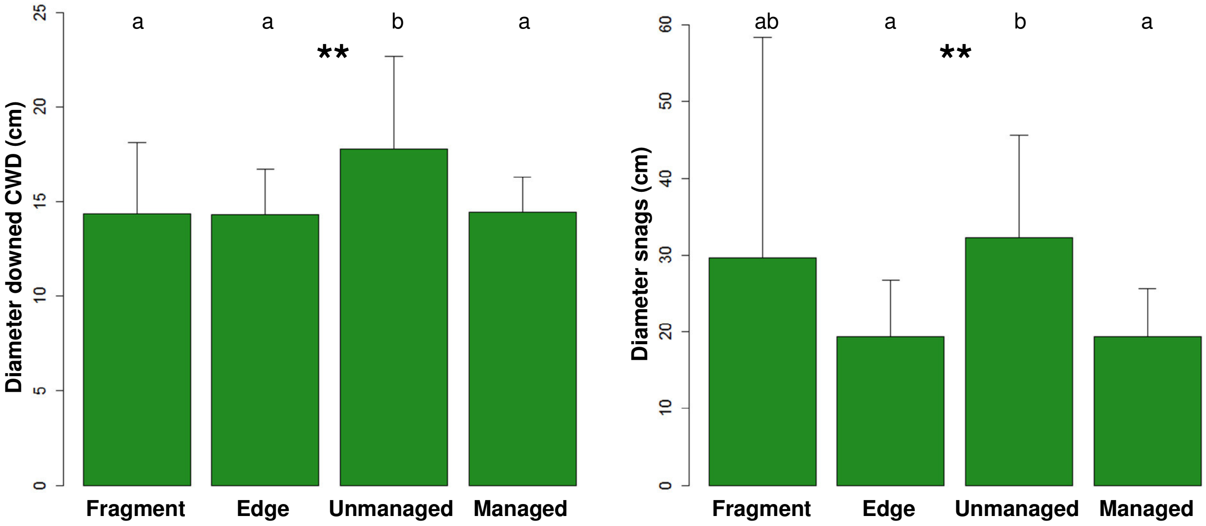

Figure A3: Effects of human forest modification on diameter of downed and standing (snags) coarse woody debris (CWD) in forests of the Northern Palatinate highlands. Anthropogenic modification is represented by silvicultural management (*Managed*, with ceased management as control, *Unmanaged*), as well as forest fragmentation (small forest fragments, *Fragment* and forest edges, *Edge*). Kruskal-Wallis tests, all df = 3 & 53 and $p < 0.01^{**}$. Significance letters were assigned according to Nemenyi-Damico-Wolfe-Dunn post-hoc test. Modified after Christmann (2014).

diameter of downed and standing CWD, as well as on the abundance of stumps (**Figures A2** and **A3**). Compared to managed forests, unmanaged stands roughly doubled in their amount of lying CWD (91%, 21.00 ± 11.71 m^3/ha vs. 40.13 ± 33.17 m^3/ha) and snags (134%, 13.43 ± 21.57 m^3/ha vs. 31.53 ± 23.31 m^3/ha). Volumes of standing CWD in unmanaged forests are similar to those from a study in NW Germany, reporting 33 m^3/ha (von Oheimb et al. 2005) and exceed the European average for lowland/submontane beech forests (24.9 m^3/ha, Christensen et al. 2005). Furthermore, snags in unmanaged stands were 67% larger in diameter (32.3 ± 13.3 cm) than their counterparts from managed forests (19.4 ± 6.2 cm), although they were substantially below the average across several European near-natural beech forests (56.4 cm, Ódor et al. 2006). While snag volume was markedly reduced in managed stands (13.43 ± 21.57 m^3/ha), it still was more than 2.5 times higher than the average for Rhineland-Palatinate (4.85 m^2/ha, MULEWF 2014), which might be attributable to consequent implementation of close-to-nature forestry. Although volume of downed CWD was increased in unmanaged forests (40.13 ± 33.17 m^3/ha), just as the volume of snags, it was still considerably lower than values reported from other studies on beech forest reserves located in Germany (61 m^3/ha, von Oheimb et al. 2005), Switzerland (78 m^3 /ha, Bütler & Lachat 2009), and the whole of Europe (83.2 m^3/ha, Christensen et al. 2005). This shows that 40 years of silvicultural abandonment are sufficient to increase lying CWD (**Figure A4**), although it takes much longer to reach higher levels, as most of the referenced reserves were much older than those in the Northern Palatinate highlands. Nevertheless, time since reserve establishment allowed trees in this study to mature into later phases of their life cycle, as shown by significantly larger diameters of downed CWD in unmanaged stands (23%, 17.8 ± 4.9 cm) over managed ones (14.4 ± 1.9 cm). While tree extraction kept the amount of lying CWD in managed forests on a comparatively low level (21.00 ± 11.71 m³/ha), it was still higher than average managed forests of Switzerland (55%, 11.5 ± 1.4 m³/ha, Bütler & Lachat 2009) and Rhineland-Palatinate (61%, 12.88 m³/ha, MULEWF 2014). This further strengthens the impression of consequent application of close-to-nature practices in the Northern Palatinate highlands. This notion is further illustrated by the role played by cut stumps. While stump volume constitutes nearly a quarter of total CWD in Rhineland-Palatinate (23%, MULEWF 2014), stumps from managed forests in this study region only contribute 10% to the respective CWD (not shown).

Stump abundance, a direct proxy of recent tree fellings, was more than eighteen times higher in forests under silviculture (3.28 ± 2.59 ha^{-1}) than their unmanaged counterparts (0.18 ± 0.42 ha^{-1}) (**Figure A2**). For further illustration, 10 out of 16 plots in unmanaged forests did not contain any stumps whatsoever. This further underlines the already successful and still ongoing convergence of unmanaged forest reserves to near-natural beech forests.

In synthesis, I can conclude that both forest fragmentation, and even more forest management, affect volume, diameter, and spatial structure of coarse woody debris. Forest fragmentation slightly decreased lying CWD and increased volume and diameter of snags, probably via edge-adapted floras, increased decomposition rates, and shifts in mortality modes. This finding signifies the previous scientific neglect of forest fragmentation as important driver of CWD in European temperate forests and therefore invites for further research. Cessation of forest management (as demonstrated by much smaller amounts of stumps) allowed natural continuation of tree life cycles with subsequent increases in CWD diameters and volumes. Although CWD was substantially more abundant in unmanaged stands, volumes only partially exceeded European averages, indicating need for further reserve maturation. On the other hand, unmanaged forests displayed noticeable higher CWD amounts in German and pan-European comparison. This can be seen as evidence for successful implementation of close-to-nature practices in the studied forestry districts. Forests of the Northern Palatinate highlands were already shown to be suitable habitats for a wide array of xylobiont insects (**Chapter 4**). The results of this CWD census further underline the importance of the study region for dead wood dependent organisms, as both managed and unmanaged forest stands might further increase in their suitability in the future.

Figure A4: Accumulated downed and standing coarse woody debris (CWD) in a remote, privately owned forest parcel. The study plot within this parcel was classified as *unmanaged* within this thesis. Note the variety of diameters and decomposition stages, as well as the frequent snags (dead, yet not downed tree trunks).

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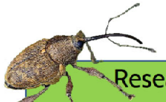
Appendix 2: Poster (next page) "Can forest fragmentation promote food web complexity? A case of plant-herbivore networks in (silviculturally managed) temperate forests" presented at the 1st Student Conference of the Faculty of Biology, Kaiserslautern by Kevin Bähner & Rainer Wirth. First price in the poster competition. Please follow the QR code/link to see the corresponding article in the Unispectrum 13/1.

http://tiny.cc/hnzcby

Can forest fragmentation promote food web complexity?

-A case of plant-herbivore networks in (silviculturally managed) temperate forests -

Kevin Bähner & Rainer Wirth



Research gaps in our backyard

Habitat fragmentation has been globally shown to be a major cause of loss and simplification of biodiversity and species interactions[1], yet the underlying mechanisms are still far from being understood. Trophic interaction networks are able to describe the complexity (e.g., measured as *Interaction Diversity*[2]) and the degree of host specialization[3] between communities. Among those, the interplay between herbivores and their plant hosts is most important, because both have a wide array of ecosystem functions[4] and are the basis of the trophic pyramid.

Forest fragmentation is known to drastically alter plant communities[5]. Because of the high evolutionary dependence of herbivores on their plant hosts, it is reasonable to assume, that the complexity and degree of specialization of herbivore-plant interaction networks is highly affected by forest fragmentation. So we asked:

How does forest fragmentation affect the complexity and specialization of herbivore-plant interaction networks?

To address the two key drivers of forest fragmentation (fragmentation *per se* and edge effects), the study design consisted of forest fragments and - edges and the interior of continuous forests as control.

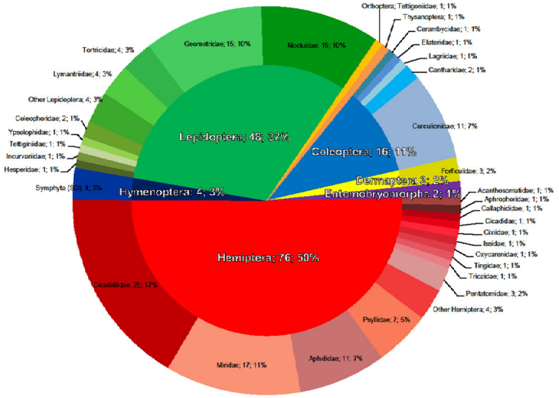
Our study region, the hyperfragmented landscape of the North Palatinate Uplands (Nordpfälzer Bergland, > 1,500 km²), near Eßweiler. Insect samples were obtained by beeting vegetation in the understory of beech forests in permanent monitoring sites (20 x 50 m) of our department.

Huge diversity and complex networks

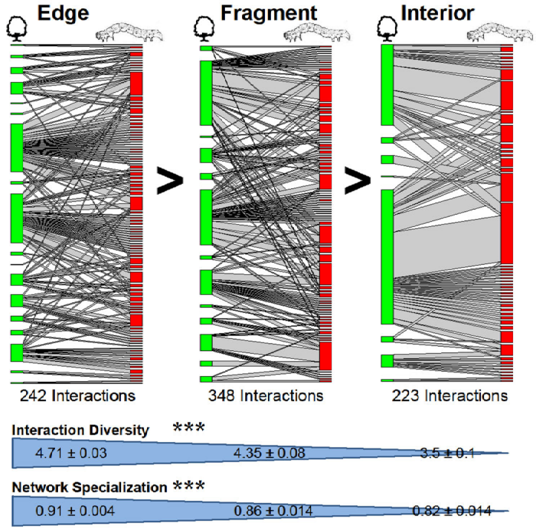
Over 200 hours of sampling of over 1300 woody plants from 28 plant species returned 1187 herbivores in at least 151 taxa and 31 families. Hence, herbivore diversity was huge, with a big dominance of Hemipterans.

1) Network complexity...
...diminished from forest edges over fragments to the forest interior, which is supported by highly significant differences in interaction diversity.

2) Trophic specialization on network level...
...was highest in edge habitats, compared to forest fragments and the forest interior (highly significant).



Herbivore diversity was enormous in the North Palatinate Uplands. *Hemiptera* are the most dominant group in the community, with *Lepidoptera* (Butterflies) and *Coleoptera* (Beetles) being second and third.



Bipartite interaction networks show a decline of complexity and specialization from forest edges over fragments to the forest interior.
Both Kruskall-Wallis-tests, n = 100, p < 0.001

Cutting edge results and implications

Forest edges were **1) more complex** and **2) more specialized** than forest fragments and the forest interior. But why, and what does that imply?

1)
- Higher floristic diversity in edges may offer more interaction possibilities for generalists, thus creating larger complexity within the networks.
- The highly impoverished communities in the forest interior may stem from extensive silvicultural management, while forest edges are generally undisturbed.

2)
- Higher floristic diversity in forest edges results in more rare plant species. Specialist herbivores might benefit from this [6]. On the other hand they have a higher risk of local extinction in the simplified interior communities.

We conclude that fragmentation-affected habitats may serve as reservoirs for species diversity and their ecosystem functions in managed forests in Europe.

But to fully understand the effects of anthropogenic habitat effects, it is also essential for future research to address silvicultural management as well. This will be integrated into my PhD-thesis on the topic.
So: **Stay tuned!**

A most peculiar herbivore: The Lobster Moth (*Stauropus fagi, Notodontidae*) is a trophic generalist, feeding on a wide range of woody plants, like beech, oak and hazel. It is one of the more bizarre insects in our forests. It supposedly benefits from higher floristic and structural diversity in forest edges, as it can forage on a wider range of nutrients.

Want to learn more?

If you have more questions and I'm not around, just scan the QR-Code with your smartphone and get a .pdf-file of my state examination thesis this poster is based on.

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Summary

Human forest modification is among the largest global drivers of terrestrial degradation of biodiversity, species interactions, and ecosystem functioning. One of the most pertinent components, forest fragmentation, has a long history in ecological research across the globe, particularly in lower latitudes. However, we still know little how fragmentation shapes temperate ecosystems, irrespective of the ancient status quo of European deforestation. Furthermore, its interaction with another pivotal component of European forests, silvicultural management, are practically unexplored. Hence, answering the question how anthropogenic modification of temperate forests affects fundamental components of forest ecosystems is essential basic research that has been neglected thus far. Most basal ecosystem elements are plants and their insect herbivores, as they form the energetic basis of the tropic pyramid. Furthermore, their respective biodiversity, functional traits, and the networks of interactions they establish are key for a multitude of ecosystem functions, not least ecosystem stability. Hence, the thesis at hand aimed to disentangle this complex system of interdependencies of human impacts, biodiversity, species traits and inter-species interactions.

The first step lay in understanding how woody plant assemblages are shaped by human forest modification. For this purpose, field investigations in 57 plots in the hyperfragmented cultural landscape of the Northern Palatinate highlands (SW Germany) were conducted, censusing > 4,000 tree/shrub individuals from 34 species. Use of novel, integrative indices for different types of land-use allowed an accurate quantification of biotic responses. Intriguingly, woody tree/shrub communities reacted strikingly positive to forest fragmentation, with increases in alpha and beta diversity, as well as proliferation of heat/drought/light adapted pioneer species. Contrarily, managed interior forests were homogenized/constrained in biodiversity, with dominance of shade/cold adapted commercial tree species. Comparisons with recently unmanaged stands (> 40 a) revealed first indications for nascent conversion to old-growth conditions, with larger variability in light conditions and subsequent community composition. Reactions to microclimatic conditions, the relationship between associated species traits and the corresponding species pool, as well as facilitative/constraining effects by foresters were discussed as underlying mechanisms.

Reactions of herbivore assemblages to forest fragmentation and the subsequent changes in host plant communities were assessed by comprehensive sampling of > 1,000 live herbivores from 134 species in the forest understory. Diversity was – similarly to plant communities - higher in fragmentation affected habitats, particularly in edges of continuous control forests. Furthermore, average trophic specialization showed an identical pattern. Mechanistically, benefits from microclimatic conditions, host availability, as well as pronounced niche differentiation are deemed responsible. While communities were heterogeneous, with no segregation across habitats, (small

forest fragments, edges, and interior of control forests), vegetation diversity, herbivore diversity, as well as trophic specialization were identified to shape community composition. This probably reflected a gradient from generalistic/species poor vs. specialist/species rich herbivore assemblages.

Insect studies conducted in forest systems are doomed to incompleteness without considering '*the last biological frontier*', the tree canopies. To access their biodiversity, relationship to edge effects, and their conservational value, the arboricolous arthropod fauna of 24 beech (*Fagus sylvatica*) canopies was sampled via insecticidal knockdown ('*fogging*'). This resulted in an exhaustive collection of > 46,000 specimens from 24 major taxonomic/functional groups. Abundance distributions were markedly negative exponential, indicating high abundance variability in tree crowns. Individuals of six pertinent orders were identified to species level, returning > 3,100 individuals from 175 species and 52 families. This high diversity did marginally differ across habitats, with slightly higher species richness in edge canopies. However, communities in edge crowns were noticeably more heterogeneous than those in the forest interior, possibly due to higher variability in environmental edge conditions. In total, 49 species with protective value were identified, of which only one showed habitat preferences (for near-natural interior forests). Among them, six species (all beetles, *Coleoptera*) were classified as '*priority species*' for conservation efforts. Hence, beech canopies of the Northern Palatinate highlands can be considered strongholds of insect biodiversity, incorporating many species of particular protective value.

The intricacy of plant-herbivore interaction networks and their relationship to forest fragmentation is largely unexplored, particularly in Central Europe. Illumination of this matter is all the more important, as ecological networks are highly relevant for ecosystem stability, particularly in the face of additional anthropogenic disturbances, such as climate change. Hence, plant-herbivore interaction networks (PHNs) were constructed from woody plants and their associated herbivores, sampled alive in the understory. Herbivory verification was achieved using no-choice-feeding assays, as well as literature references. In total, networks across small forest fragments, edges, and the forest interior consisted of 696 interactions. Network complexity and trophic niche redundancy were compared across habitats using a rarefaction-like resampling procedure. PHNs in fragmentation affected forest habitats were significantly more complex, as well as more redundant in their realized niches, despite being composed of relatively more specialist species. Furthermore, network robustness to climate change was quantified utilizing four different scenarios for climate change susceptibility of involved plants. In this procedure, remaining herbivores in the network were measured upon successive loss of their host plant species. Consistently, PHNs in edges (and to a smaller degree in small fragments) withstood primary extinction of plant species longer, making them more robust. This was attributed to the high prevalence of heat/drought-adapted species, as well as to beneficial effects of network topography (complexity and redundancy). Consequently, strong correlative relationships were found between realized niche redundancy and climate change robustness of PHNs. This was both the first time that biologically realistic extinctions (instead of e.g.

random extinctions) were used to measure network robustness, and that topographical network parameters were identified as potential indicators for network robustness against climate change.

In synthesis, in the light of global biotic degradation due to human forest modification, the necessity to differentiate must be claimed. Ecosystems react differently to anthropogenic disturbances, and it seems the particular features present in Central European forests (ancient deforestation, extensive management, and, most importantly, high richness in open-forest plant species) cause partly opposed patterns to other biomes. Lenient microclimates and diverse plant communities facilitate equally diverse herbivore assemblages, and hence complex and robust networks, opposed to the forest interior. Therefore, in the reality of extensively used cultural landscapes, fragmentation affected forest ecosystems, particularly forest edges, can be perceived as reservoir for biodiversity, and ecosystem functionality. Nevertheless, as practically all forest habitats considered in this thesis are under human cultivation, recommendations for ecological enhancement of all forest habitats are discussed.

Zusammenfassung

Die menschliche Modifikation von Wäldern gehört global zu den größten Triebfedern terrestrischen Verfalls von Biodiversität, Artinteraktionen und Ökosystemfunktionsfähigkeit. Eine der einschlägigsten Komponenten, Waldfragmentierung, hat eine lange Geschichte ökologischer Forschung durchlaufen, insbesondere in den tiefen Breitengraden. Dennoch wissen wir noch immer wenig wie Fragmentierung temperate Ökosysteme formt, ungeachtet des antiken Status quo Europäischer Entwaldung. Weiterhin sind die Interaktionen zwischen Fragmentierung, und einer weiteren zentralen Komponente europäischer Wälder, Waldbewirtschaftung, praktisch unerforscht. Daher ist die Beantwortung der Frage, wie die anthropogene Modifikation temperater Wälder fundamentale Komponenten von Waldökosystem beeinflusst, essentielle Grundlagenforschung, die bislang vernachlässigt worden ist. Die grundlegendsten Ökosystemelemente sind dabei Pflanzen und ihre Insektenherbivoren, da sie die energetische/materielle Basis der trophischen Pyramide bilden. Weiterhin sind ihre Biodiversität, funktionellen Eigenschaften und ihre Interaktionsnetzwerke entscheidend für eine Fülle von Ökosystemfunktionen, nicht zuletzt Ökosystemstabilität. Daher war das Ziel dieser Arbeit die Entwirrung dieses komplexen Systems aus Interdependenzen zwischen menschlichen Einflüssen, Biodiversität, Arteigenschaften und zwischenartlichen Interaktionen.

Der erste Schritt bestand darin, zu verstehen, wie Gehölzgemeinschaften durch menschliche Modifikation von Wäldern geformt werden. Zu diesem Zweck wurden in der hyperfragmentierten Kulturlandschaft des Nordpfälzer Berglands Felduntersuchungen durchgeführt, indem über 4.000 Gehölzindividuen aus 34 Arten erhoben wurden. Die Nutzung neuartiger, integrativer Indizes für verschiedene Typen von Landnutzung erlaubte eine genaue Quantifizierung biotischer Reaktionen. Interessanterweise reagierten Gehölzgemeinschaften auf Waldfragmentierung auffallend positiv mit erhöhter Alpha- und Beta-Diversität, sowie einer Proliferation von hitze-/trocken-/lichtangepassten Pionierarten. Umgekehrt zeigten sich bewirtschaftete Waldinnengebiete homogenisiert/eingeschränkt hinsichtlich ihrer Biodiversität, mit ausgeprägter Dominanz von schatten-/kälteangepassten Baumarten mit kommerzieller Relevanz. Vergleiche mit unlängst unbewirtschafteten Beständen (> 40 a) offenbarten erste Anzeichen für eine einsetzend Wandlung hin zu primärwaldähnlichen Bedingungen, mit großer Variabilität von Lichtbedingungen und daraus folgenden Zusammensetzung von Gemeinschaften. Als zugrundeliegende Mechanismen wurden Reaktionen auf mikroklimatische Bedingungen, die Beziehung zwischen mikroklimatischen Arteigenschaften und den korrespondierenden Artenpools, sowie fördernde/einschränkende Effekte durch Förster diskutiert.

Die Reaktionen von Herbivorengemeinschaften auf Waldfragmentierung und auf anschließende Veränderungen von Wirtspflanzengemeinschaften wurden durch eine

umfangreiche Unterwuchsbeprobung von 1.000 lebend gefangenen Herbivoren aus 134 Arten evaluiert. Die Diversität war – ähnlich wie die Pflanzengemeinschaften - in fragmentierungsbetroffenen Habitaten erhöht, besonders in Rändern kontinuierlicher Kontrollwälder. Ferner zeigte die durchschnittliche trophische Spezialisierung ein identisches Muster. Mechanistisch werden Vorteile mikroklimatischer Bedingungen, Wirtsverfügbarkeit, sowie ausgeprägte Nischendifferenzierung für verantwortlich gehalten. Obwohl Herbivorengemeinschaften sehr heterogen waren, ohne jede Segregation über Habitate hinweg (kleine Waldfragmente, -ränder und Interior von Kontrollwäldern), wurden Vegetationsdiversität, Herbivorendiversität, sowie trophische Spezialisierung als formende Kräfte der Zusammensetzung von Gemeinschaften identifiziert. Dies reflektiert wahrscheinlich einen inhärenten Gradienten zwischen generalistischen/artenarmen und spezialisierten/artenreichen Herbivorengemeinschaften.

Insektenstudien, die in Waldsystemen durchgeführt werden, sind zur Unvollständigkeit verdammt, solange man die “*letzte biologische Grenze*“ ignoriert, die Baumkronen. Die Arthropodenfauna von 24 Buchenkronen (*Fagus sylvatica*) wurde mittels einer Insektizidbehandlung (”*fogging*”) beprobt, um deren Biodiversität, Reaktionen auf Randeffekte und naturschützerischen Wert zu evaluieren. Dies resultierte in einer umfassenden Sammlung von > 46.000 Individuen aus 24 wichtigen taxonomisch-funktionellen Gruppen. Die Abundanzverteilungen waren ausgeprägt negativ-exponentiell, was auf eine hohe Abundanzvariabilität in Baumkronen hindeutet. Individuen aus sechs einschlägigen Gruppen wurden auf Artniveau bestimmt, was > 3.100 Indivuen aus 175 Arten und 52 Familien ergab. Diese hohe Diversität unterschied sich geringfügig zwischen Habitaten, mit etwas größeren Artenreichtum in Waldrandkronen. Dennoch waren Insektengemeinschaften in Randkronen deutlich heterogener als solche im Waldesinneren, wahrscheinlich durch größere Variabilität von Umweltbedingungen in Waldrändern. Insgesamt wurden 49 schützenswerte Arten identifiziert, von denen eine nachweislich Habitatpräferenzen (für das Waldesinnere) zeigte. Von diesen wurden sechs Arten (alle Käfer, *Coleoptera*) als prioritäre Arten für Schutzmaßnahmen klassifiziert. Daher können Buchenkronen des Nordpfälzer Berglandes als Hochburgen insektischer Biodiversität, inklusive vieler schutzwürdiger Arten, betrachtet werden.

Die Komplexität von Pflanzen-Herbivoren Interaktionsnetzwerken und ihre Beziehung zu Waldfragmentierung sind praktisch unerforscht, besonders in Mitteleuropa. Eine Erhellung dieser Angelegenheit ist umso wichtiger, als ökologische Netzwerke relevant sind für Ökosystemstabilität, besonders im Antlitz zusätzlicher anthropogener Störungen, wie etwa Klimawandel. Daher wurden Pflanzen-Herbivoren Interaktionsnetzwerke (PHNs) auf der Grundlage von Gehölzen aus dem Unterwuchs und deren assoziierten, lebend-gefangenen Herbivoren erstellt. Herbivoren-Verifizierung erfolgte durch No-Choice-Feeding Assays, sowie durch Literaturreferenzen. Insgesamt bestanden Netzwerke (aus kleinen Waldfragmenten, Rändern und dem Waldinneren) aus 696 Interaktionen. Netzwerk-Komplexität und trophische Nischenredundanz wurden zwischen Habitaten mittels eines rarefaction-artigen Wiederbeprobungsverfahrens verglichen. PHNs in fragmentierungsbedingten

Waldhabitaten waren komplexer und redundanter in ihren realisierten Nischen, obwohl sie sich aus vergleichsweise spezialisierteren Arten zusammen setzten. Weiterhin wurde die Netzwerkrobustheit gegenüber Klimawandel quantifiziert, indem vier verschiedene Szenarien für die Anfälligkeit involvierter Pflanzenarten gegenüber Klimawandel angelegt wurden. In diesem Verfahren wurden die verbliebenen Herbivorenarten nach sukzessivem Verlust ihrer Wirtspflanzen gezählt. Konsistenterweise widerstanden PHNs in Rändern (und in kleinerem Umfang auch in kleinen Fragmenten) Primärextinktionen von Pflanzenarten länger, was sie als robuster kennzeichnete. Dies wurde auf die hohe Prävalenz hitze/trockenangepasster Arten zurück geführt, sowie auf förderliche Effekte von Netzwerktopographie (Komplexität und Redundanz). Konsequenterweise wurden daraufhin starke korrelative Beziehungen zwischen realisierter Nischenredundanz und Robustheit gegenüber Klimawandel gefunden. Dies war sowohl das das erste Mal, dass zur Messung von Netzwerkrobustheit biologisch realistische Extinktionen benutzt wurden, als auch dass topographische Netzwerkparameter als potentielle Indikatoren für Robustheit gegenüber Klimawandel identifiziert wurden.

Zusammengefasst muss, angesichts globalen biotischen Verfalls durch menschliche Waldveränderung, die Notwendigkeit zur Differenzierung beansprucht werden. Ökosysteme reagieren unterschiedlich auf anthropogene Störungen und es scheint als würden die besonderen Eigenschaften mitteleuropäischer Wälder (urtümliche Entwaldung, umfangreiche Bewirtschaftung, und, am wichtigsten, hoher Pflanzenreichtum von Offenwaldarten) zu teils umgekehrten Mustern als in anderen Biomen führen. Milde Mikroklimata und diverse Pflanzengemeinschaften in Waldrändern fördern gleichsam diverse Herbivorengemeinschaften, und damit komplexe und robuste Netzwerke, im Gegensatz zum Waldesinneren. Daher, in der Gegenwart umfassend genutzter Kulturlandschaften, können fragmentierungsbetroffene Waldökosysteme, besonders Waldränder, als Reservoir betrachtet werden für Biodiversität und Ökosystemfunktionalität. Nichtsdestoweniger, da praktisch alle in dieser Arbeit betrachteten Waldhabitate menschlicher Kultivierung unterliegen, werden Empfehlungen zur ökologischen Aufwertung aller Waldhabitate diskutiert.

Kevin Wilhelm Bähner

CV


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Education

Since 2012/03	PhD student in the department of Plant Ecology and Systematics (Dr. Rainer Wirth, Prof. Dr. Burkhard Büdel), Faculty of Biology, University of Kaiserslautern	
2005 – 2012	Study of biology and chemistry for teachers (gymnasium), University of Kaiserslautern	
	Graduation: state-examination for teachers (gymnasium, biology and chemnistry) (2012/02).	Grade: 1.4
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Declaration

Hiermit versichere ich, dass die vorliegende Dissertation von mir in allen Teilen selbstständig angefertigt wurde und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt wurden.
Darüber hinaus erkläre ich, dass die Dissertationsschrift weder vollständig, noch teilweise einer anderen Fakultät mit dem Ziel vorgelegt worden ist, einen akademischen Grad zu erlangen.

Kaiserslautern, den 30.06.2016

(Kevin Wilhelm Bähner)