Fakultät für Biologie der Universität Würzburg

Temporal development of communities

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With a focus on insects, in time series of one to four decades

Entwicklung von Artengemeinschaften in der Zeit

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Mit einem Fokus auf Insekten in Zeitreihen von einer bis vier Dekaden

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Dissertation zur Erlangung des naturwissenschaftlichen Doktorgrades
Julius-Maximilians-Universität Würzburg

Vorgelegt von
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Geboren in Nürnberg
Würzburg 2021

Submitted/Eingereicht ....

Members of the doctoral committee/Mitglieder der Promotionskommission:

Chairperson/Vorsitzender: ....

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Referee /Gutachter: Prof. Dr. Jan Christian Habel

Defence/ Tag des Promotionskolloquiums: ....

Date of Receipt of Certificates/Doktorurkunde ausgehändigt am: ....

“To a rough approximation and setting aside vertebrate chauvinism, it can be said that essentially all organisms are insects.”

(Robert M. May)

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Summary

Changes and development are fundamental principles in biocenoses and can affect a multitude of ecological processes. In insect communities phenological and density changes, changes in species richness and community composition, as well as interactions between those changes, are the most important macro processes. However, climate change and other factors like habitat degradation and loss alter these processes leading to shifts and general biodiversity declines. Even though knowledge about insect decline in central Europe increased during the last decades, there are significant knowledge gaps about the development of insect communities in certain habitats and taxa. For example, insect communities in small lentic as well as in forested habitats are under-sampled and reported to be less endangered than communities in other habitats. Furthermore, the changes within habitats and taxa are additionally influenced by certain traits, like host or feeding specialization. To disentangle these influences and to increase the knowledge about the general long-term development of insect communities, comprehensive long-term monitoring studies are needed. In addition, long-term effects of conservation strategies should also be evaluated on large time scales in order to be able to decide on a scientific base which strategies are effective in promoting possibly declining taxa. Hence, this thesis also tackles the effects of an integrative conservation strategy on wood dependent beetle and fungi, beside the development of water beetle and macro moth communities over multiple decades.

In Chapter 2 I present a study on the development of water beetle communities (Dytiscidae, Haliplidae, Noteridae) in 33 water bodies in Southern Germany from 1991 to 2018. Time-standardized capture per waterbody was used during three periods: between 1991 and 1995, 2007 and 2008, and 2017 and 2018. Results showed annual declines in both species number (ca. -1%) and abundance (ca. -2%). In addition, community composition shifted over time in part due to changing pH values. Hence, the recorded changes during the 28-year study period partly reflect natural succession processes. However, since also moor-related beetle species decreased significantly, it is likely that water beetles in southern Germany are also threatened by non-successional factors, including desiccation, increased nitrogen input and/or mineralization, as well as the loss of specific habitats. The results suggest, that in small to mid-size lentic waterbodies, current development should aim for constant creation of new water bodies and protection of moor waterbodies in order to protect water beetle communities on a landscape scale.

In Chapter 3 I present an analysis of the development of nocturnal macro moth species richness, abundance and biomass over four decades in forests of southern Germany. Two local scale data sets featuring a coppiced oak forest as well as an oak high forest were analysed separately from a regional data set representing all forest types in the temperate zone of

Central Europe. At the regional scale species richness, abundance and biomass showed annual declines of ca. 1 %, 1.3 % and 1.4 %, respectively. These declines were more pronounced in plant host specialists and in dark coloured species. In contrast, species richness increased by ca. 1.5 % annually in the coppiced forest, while no significant trends were found in the high forest. In contrast to past assumptions, insect decline apparently affects also hyper diverse insect groups in forests. Since host specialists and dark coloured species were affected more heavily by the decline than other groups, habitat loss and climate change seem to be potential drivers of the observed trends. However, the positive development of species richness in the coppiced oak forest indicates that maintaining complex and diverse forest ecosystems through active management might compensate for negative trends in biodiversity.

Chapter 4 features a study specifically aiming to investigate the long-term effect of dead-wood enrichment as an integrative conservation strategy on saproxylic beetles and fungi in a central European beech forest at a landscape scale. A before–after control–impact design, was used to compare assemblages and gamma diversities of saproxylic organisms (beetles and fungi) in strictly protected old-growth forest areas (reserves) and previously moderately and intensively managed forest areas. Forests were sampled one year before and a decade after starting a landscape-wide strategy of dead-wood enrichment. Ten years after the start of the dead-wood enrichment, neither gamma diversities of saproxylic organisms nor species composition of beetles did reflect the previous management types anymore. However, fungal species composition still mirrored the previous management gradient. The results demonstrated that intentional enrichment of dead wood at the landscape scale can effectively restore communities of saproxylic organisms and may thus be a suitable strategy in addition to permanent strict reserves in order to protect wood dependent organisms in Europe.

In this thesis I showed, that in contrast to what was assumed and partly reported so far, also water beetles in lentic water bodies and macro moths in forests decreased in species richness, abundance and biomass during the last three to four decades. In line with earlier studies, especially dark coloured species and specialists decreased more than light-coloured species and generalists. The reasons for these declines could partly be attributed to natural processes and pollution and possibly to climate change. However, further studies, especially experimental ones, will be needed to achieve a better understanding of the reasons for insect decline. Furthermore, analyses of time series data should be interpreted cautiously especially if the number of sampling years is smaller than ten years. In addition, validation techniques such as left- and right- censoring and cross validation should be used in order to proof the robustness of the analyses. However, the lack of knowledge, we are still facing today, should not prevent scientists and practitioners from applying conservation measures. In order to prove the effectiveness of such measures, long-term monitoring is crucial. Such control of success is essential for evidence based and thus adapted conservation strategies of threatened organisms.

Zusammenfassung

Veränderungen und Entwicklung sind grundlegende Prinzipien in Biozönosen und können eine Vielzahl von ökologischen Prozessen beeinflussen. In Insektengemeinschaften stellen Veränderungen in der Phänologie und Dichte, Veränderungen des Artenreichtums und der Artenzusammensetzung sowie die Wechselwirkungen zwischen diesen, die wichtigsten Makroprozesse dar. Klimawandel und andere Faktoren wie der Verlust von Lebensräumen oder deren Qualitätsverschlechterung beeinflussen diese Prozesse jedoch und führen zu Veränderungen und allgemeinen Rückgängen der Biodiversität. Auch wenn die Erkenntnisse zum „Insektensterben“ in Mitteleuropa in den letzten Jahrzehnten zugenommen haben, gibt es erhebliche Wissenslücken über die Entwicklung von Insektengemeinschaften in bestimmten Lebensräumen und Taxa. Beispielsweise ist die Entwicklung von Insektengemeinschaften in kleinen, stehenden Gewässern und in Wäldern wenig erforscht. Darüber hinaus werden die Veränderungen innerhalb von Habitaten und Taxa zusätzlich durch bestimmte Merkmale, wie Wirts- oder Nahrungsspezialisierung, beeinflusst. Um diese verschiedenen Einflüsse auseinanderhalten zu können und das Wissen über die allgemeine Langzeitentwicklung von Insektengemeinschaften zu vergrößern, sind umfassende Langzeitstudien erforderlich. Darüber hinaus sollten auch die langfristigen Auswirkungen von Naturschutzstrategien über lange Zeiträume evaluiert werden, um auf wissenschaftlicher Grundlage entscheiden zu können, welche Strategien zur Förderung bedrohter Taxa wirksam sind. Daher befasst sich diese Arbeit neben der Entwicklung von Wasserkäfer- und Großschmetterlingsgemeinschaften über mehrere Jahrzehnte auch mit den Auswirkungen einer integrativen Naturschutzmaßnahme auf xylobionte Käfer und Pilze.

In Kapitel 2 stelle ich eine Studie über die Entwicklung von Wasserkäfergemeinschaften (Dytiscidae, Haliplidae, Noteridae) in 33 Gewässern Süddeutschlands von 1991 bis 2018 vor. Die zeitstandardisierte Erfassung pro Wasserkörper erfolgte in drei Zeiträumen: zwischen 1991 und 1995, 2007 und 2008 sowie 2017 und 2018. Die Ergebnisse zeigten einen jährlichen Rückgang sowohl der Artenzahl (ca. -1%) als auch der Abundanz (ca. -2%). Darüber hinaus verschob sich die Artenzusammensetzung im Laufe der Zeit zum Teil aufgrund sich ändernder pH-Werte. Daraus lässt sich schlussfolgern, dass die erfassten Veränderungen während des 28-jährigen Untersuchungszeitraums teilweise natürliche Sukzessionsprozesse widerspiegeln. Da aber auch an moorige Gewässer gebundene Käferarten deutlich abgenommen haben, ist es wahrscheinlich, dass die Wasserkäfer Süddeutschlands auch durch Faktoren wie Austrocknung, erhöhten Stickstoffeintrag und/oder Mineralisierung sowie durch den Verlust spezifischer Lebensräume bedroht sind. Aufgrund dieser Entwicklungen ist es empfehlenswert, auf

Landschaftsebene auf die ständige Schaffung neuer Gewässer und den besonderen Schutz von Moorgewässern zu setzen, um Wasserkäfergemeinschaften erfolgreich schützen zu können.

In Kapitel 3 präsentiere ich eine Analyse der Diversitäts-, Abundanz- und Biomassenentwicklung von nachtaktiven Großschmetterlingen über vier Jahrzehnte in Wäldern Süddeutschlands. Neben einem bayernweiten Datensatz, der alle typischen Waldtypen der gemäßigten Zone Mitteleuropas beinhaltet, wurden zwei lokale, besonders regelmäßig besammelte Gebiete getrennt analysiert. In diesen Gebieten werden die Eichenwälder als Hoch- bzw. als Mittelwald bewirtschaftet. Bayernweit wiesen Artenreichtum, Abundanz und Biomasse jährliche Rückgänge von ca. 1 %, 1,3 % bzw. 1,4 % auf. Diese Rückgänge waren bei Wirtspflanzenspezialisten und bei dunkel gefärbten Arten besonders stark ausgeprägt. Im Gegensatz dazu nahm der Artenreichtum im Mittelwald jährlich um ca. 1,5 % zu, während im Hochwald keine signifikanten Trends festgestellt werden konnten. Im Gegensatz zu früheren Annahmen betrifft der Insektenrückgang offenbar auch hyperdiverse Insektengruppen im Wald. Da Wirtspflanzenspezialisten und dunkel gefärbte Arten vom Rückgang stärker betroffen waren als andere, scheinen Lebensraumverlust und Klimawandel potentielle Treiber der beobachteten Trends zu sein. Die positive Entwicklung des Artenreichtums im Mittelwald zeigt jedoch, dass der Erhalt komplexer und vielfältiger Waldökosysteme durch aktives Management, negative Biodiversitätstrends zum Teil kompensieren könnte.

Kapitel 4 enthält eine Studie, die die Langzeitwirkung von Totholzanreicherung als integrative Naturschutzmaßnahme auf xylobionte Käfer und Pilze in einem mitteleuropäischen Buchenwald auf der Landschaftsebene untersucht. Dabei wurde die Gamma-Diversität und die Artenzusammensetzung dieser beiden Gruppen anhand einer Vorher-Nachher Untersuchung mit Kontrollflächen (Naturwaldreservate) untersucht. Die bewirtschafteten Flächen wurden weiterhin in zuvor mäßig und intensiv bewirtschaftete Flächen eingeteilt. Die Wälder wurden ein Jahr vor und ein Jahrzehnt nach Beginn einer Totholzanreicherungsstrategie auf Landschaftsebene beprobt. Zehn Jahre nach Beginn der Totholzanreicherung spiegelten weder die Gamma-Diversität der xylobionten Organismen noch die Artenzusammensetzung der Käfer die früheren Bewirtschaftungstypen wider, und wiesen keine Unterschiede mehr zu den Naturwaldreservaten auf. Die Pilzartenzusammensetzung spiegelte jedoch noch immer den früheren Bewirtschaftungsgradienten wider. Die Ergebnisse zeigen, dass Totholzanreicherung auf Landschaftsebene positive Effekte auf xylobionte Artengemeinschaften haben kann. Somit stellt Totholzanreicherung eine Naturschutzmaßnahme dar, die zusätzlich zu permanenten Schutzgebieten, eine Grundlage schaffen kann, um holzabhängige Organismen in Europa zu schützen.

In dieser Arbeit habe ich gezeigt, dass im Gegensatz zu dem, was bisher angenommen und zum Teil berichtet wurde, auch Wasserkäfer in stehenden Gewässern und nachtaktive Großschmetterlingen in Wäldern in den letzten drei bis vier Jahrzehnten an Artenreichtum, Abundanz und Biomasse abgenommen haben. In Übereinstimmung mit anderen Studien nahmen vor allem dunkel gefärbte Arten und Spezialisten stärker ab als hell gefärbte Arten und Generalisten. Die Gründe für diese Rückgänge konnten zum Teil auf natürliche Prozesse, Umweltverschmutzung und möglicherweise auf den Klimawandel zurückgeführt werden. Es sind jedoch weitere Studien, insbesondere experimentelle, erforderlich, um die Gründe für das „Insektensterben“ besser zu verstehen. Darüber hinaus sollten Zeitreihendaten mit Vorsicht interpretiert werden, insbesondere wenn die Anzahl der besammelten Jahre kleiner als zehn Jahre ist. Darüber hinaus sollten Validierungstechniken wie Links- und Rechts-Zensierung und Kreuzvalidierung eingesetzt werden, um die Robustheit der Analysen nachzuweisen. Der Mangel an Wissen, mit dem wir heute noch konfrontiert sind, sollte Wissenschaftler und Praktiker jedoch nicht davon abhalten, Naturschutzmaßnahmen anzuwenden. Um die Wirksamkeit solcher Maßnahmen nachzuweisen, ist eine langfristige Überprüfung von entscheidender Bedeutung. Solche Erfolgskontrollen sind für evidenzbasierte und damit angepasste Erhaltungsstrategien bedrohter Organismen unerlässlich.

Chapter 1: General introduction

1.1 Development of communities and types of development

Development is a fundamental principle in biological systems which can be found from cellular up to macroecological levels. Development always implies a change of a certain study object or system. In ecology it is often an individual, species, species community or their attributes (traits, genetic structure etc.) which are studied. Studying the abundance of a single species remains fairly straightforward in terms of possible outcomes at a certain sampling point (increase – constant – decrease). Communities, on the other hand, are complex structures in which not only species number and abundance can vary in time but also species identities and interactions may fluctuate. The disappearance of species from communities with a simultaneous or subsequent appearance of other species is called turnover and is a topic which was addressed since the beginning of ecological research d. Currently one of the most challenging tasks in community research is the differentiation between (anthropogenically caused) long-term trends and natural fluctuations or short to mid-term phenomena like weather variations (Fewster et al., 2000; Benton et al., 2002; Hallmann et al., 2019). Note, that even when environmental and other conditions are static, communities change through demographic stochasticity (ecological drift) (Vellend, 2010; Sgardeli et al., 2016). This phenomenon is called neutral turnover. Indications of negative trends of species abundance and community developments in the Anthropocene increased the pressure on gaining knowledge about processes of community development, beyond the general scientific interest in exploring such processes. Especially the effects of land use change, pollution and climate change on wildlife has become an important scientific issue. Since the 1990 high impact journals started to concentrate on these topics (e.g. Global Change Biology 1995, Nature Climate Change 2011). While in animals, research on a human-induced biodiversity crisis has focused a lot on vertebrates (Ceballos et al., 2015), recently the negative trends in insect communities have raised concerns in the scientific community as well as policy makers and the general media (Habel et al., 2019a; Kunin, 2019; Thomas et al., 2019). As insects provide a multitude of ecosystem services as well as disservices, their long-term development produced interest for a long time (Sabrosky, 1953) and was increasingly studied since the 2000s (Parmesan & Yohe, 2003; Chapman, 2009; Stork, 2018). Studies on long-term development of insect communities include different types and causes of long-term changes, which will be introduced below. The following section will also comprise the identification of knowledge gaps in central Europe, which in turn will lead to the study questions of this this thesis.

1.1.1 Phenology and Phenological changes

One of the most basic temporal patterns in insect communities are seasonal phenologies i.e. seasonal life cycles. For most insect imagines in temperate regions, there is one or more peaks of abundance at a certain point of the growing season (Scott & Epstein, 1987). As these peaks differ from one species to another, community compositions at certain locations vary along the course of the season (Brito et al., 2014; Plant et al., 2018). In addition, phenological changes from year to year can occur as fluctuations (Martikainen & Kaila, 2004) or directed changes (e.g. Ellwood & Diez, 2012). Both are mostly modulated by external factors, like changes in temperature and water availability. Thus higher temperatures advance phenologies significantly in insect communities e.g. faster development of larvae (Menzel et al., 2006; Rosenzweig et al., 2008), as well as drought has been shown to advance the flight period (Forister et al., 2018). Furthermore, not only earlier flight periods, but factors like enhanced winter survival rates and an acceleration of development rates can affect the phenologies of insect species (Robinet & Roques, 2010; Sheppard et al., 2015). These trends are not harmful for insect populations per se. However, if these shifts imply shifting away from, for example, a food resource or possible mates, phenological changes can highly affect insect populations (Dixon, 2003; Memmott et al., 2007; Forkner et al., 2008; Hegland et al., 2009; Altermatt, 2010). On the other hand, some insects show only little or no response to e.g. increasing temperature (Parmesan & Yohe, 2003; Visser, 2008).In fact, insect phenologies show very variable and contradictory trends within and among species, and also at different study sites (Primack et al., 2009; Hodgson et al., 2011). For instance there are long-term data sets indicating an advancement of the phenologies in insects which exceeds even the advancement of their hostplants (e.g. Gordo & Sanz, 2005) while others suggest a later phenology even with rising temperatures (e.g. Ellwood & Diez, 2012). These non-intuitive patterns indicate that there are other factors influencing the phenology e.g. a general population decline. Furthermore, even when synchronies are being temporarily disrupted, they can likely be restored by adaptive genetic processes (Robinet & Roques, 2010). Although these phenological changes are still not understood, this thesis only uses the phenology (day of sampling) as a control variable and does not focus on this aspect of temporal development.

1.1.2 Density changes

Phenology directly influences the recorded density of species, as a higher density (number of specimens) of a species can be detected at its yearly maximum or maxima. Consequently if there are mismatches in the phenology between e.g. host and herbivore, it can have negative impacts on the herbivores densities (Ellwood & Diez, 2012 and references therein). However, there are also other factors regulating species density. Insect density can for example be regulated by predators (top-down), e.g. aphids and coccinellids. Frazer & Gilbert

(1976) showed that the predation rate of coccinellids on aphids increased with increasing temperatures, which should therefore control the aphid populations even more with ongoing climate change (Skirvin et al., 1997). Note that insect herbivores are generally strongly controlled top-down (Vidal & Murphy, 2018). Also extreme weather events can reduce insect density significantly, simply by killing a high proportion of the specimens (Koptur et al., 2002; Ewald et al., 2015), or enhance the density by favouring certain species after droughts or floods (Zhang et al., 2012; Tudoran et al., 2016). Other important weather extremes which increase with climate change are droughts (Dale et al., 2001; Trenberth, 2006). Especially when plants are planted at locations where the climatic conditions are not suitable it is likely that for example water stress leads to increasing densities of pest species (Rouault et al., 2006; Tudoran et al., 2016). Increasing temperatures will further intensify this phenomenon because insects as ectothermic organisms are likely to profit from warmer environments and thus develop faster with possibilities for shorter and more generations (Faccoli, 2009; Martín-Vertedor et al., 2010; Cornelissen, 2011). In this thesis, density changes are not addressed for single species but merely as total insect abundances or biomass.

1.1.3 Species richness

Measured species richness depends on space and time. While the space aspect is not the focus of this thesis, the temporal component is often linked to the factors introduced before - the phenology (especially in temperate climates) and the density. Species richness is often measured as number of species or its derivatives accounting for abundance (density) or differences between the abundances of species (evenness). Species richness is influenced by abiotic factors, such as water availability and elevation, and by biotic factors reaching from competition and predation to the influence of the mesoclimate established by e.g. a forest. These factors are also important for the community composition (see 1.1.4). One of the most natural changes in diversity at a specific location occurs during succession. Thus there are states of habitats where diversity is known to be especially high, which are often "mature" habitats like forests and ponds (Fairchild et al., 2000; Schmidl, 2003; Müller et al., 2008; Hilmers et al., 2018). Disturbance, which can also be part of natural succession is another factor influencing species richness in time which alters patterns of natural succession. Disturbance has a positive influence on species richness until a certain threshold (intermediate disturbance) (Grime, 1973; Horn, 1975; Connell, 1978). During the last century however, habitat conversion, pollution, and climate change have increased disturbance events to a level which is far beyond having positive effects on species richness (see below). The development of species richness in consideration of abiotic and biotic factors is one of the main study questions in this thesis and will be addressed in greater detail in Chapters 1.2,2,3,4,5).

1.1.4 Change of composition

The temporal development of communities – a community being an assemblage of species populations co-occurring in space and time (Begon et al., 2005) - can be shaped by different processes including changes during the phenology, and changes in density and diversity. In general, three basic principles, dispersal constraints, environmental constraints and internal dynamics underlie the formation of communities (Belyea & Lancaster, 1999). This means that a species can occur in a community if it is capable of reaching a location and it is not (completely) excluded by competitors, predators, parasites or by random events (Hanski, 1998; Begon et al., 2005). Thus, the development of an assemblage depends e.g. on whether the community is founder or dominance controlled (Yodzis, 1986). In order for a species to thrive at a location it also needs the resources and climatic conditions necessary to live and procreate (Ettema & Wardle, 2002). Consequently, communities change along environmental gradients like temperature or between habitats like forests and open lands (Gibbs & Stanton, 2001; Brito et al., 2014). But also, within habitat changes influence communities. The most natural within habitat changes in composition apart from random events occur due to succession, as not only diversity (see 1.1.3) but also species identities tend to change during succession (Horn, 1981; Fairchild et al., 2000; Habel et al., 2019b). Communities can be altered or even artificially maintained in less mature states by exploitation (Müller et al., 2008). Natural and anthropogenic disturbances can shape not only insect richness but also insect communities. Long-term changes in the management or in the environment also influence community composition in insects (Habel et al., 2016a). Increasing the knowledge of changes in insect community compositions over ten and more years is one of the major goals of this thesis (Chapters 2,3,4).

1.2 Current knowledge of development of insect communities

More and more studies show a decline in insect communities during the last decades (Habel et al., 2019c; Hallmann et al., 2019; Seibold et al., 2019). The global climate is changing and humans continue to alter biota and physical properties at an accelerating rate (Steffen et al., 2007; Rockström et al., 2009a, 2009b; Stocker et al. 2013). Climate change is often blamed for changes in insect communities and for cross-taxon, country-wide insect declines (Asher et al., 2001; Thomas et al., 2004b; Conrad et al., 2006; Wagner, 2020). These studies show that many of the declines began in the 1950s. However, besides the pure climatic changes like increasing temperatures and changes in precipitation, other factors like pollution and land conversion co-occur with climate change. The following section summarizes the current knowledge of the development of insect communities with regards to different driving forces.

1.2.1 … with changing climate

The first studies on insect responses to climate change mainly focused on climate warming and showed range shifts and later community shifts correlating with increasing temperatures (Mikkola, 1997; Parmesan et al., 1999; Hill et al., 2002; Devictor et al., 2012). Nearly all observed species expanded their limits northwards. Similar range shifts have been recorded along elevational gradients (Stange & Ayres, 2010 and references therein). Due to the ectothermic nature of insects a rise of temperature leads to a faster metabolism (Gillooly et al., 2002; Clarke & Fraser, 2004) and thus faster development. This influences and amplifies the population dynamics (Bale et al., 2002; Gillooly et al., 2002). Additionally warmer winters can reduce winter mortality in populations (Ayres & Lombardero, 2000), but only if higher temperature variance especially in spring does not lead to increasing mortalities because of "premature" insect activity (Karl & Trenberth, 2003; Dukes et al., 2009). Furthermore, reduced snow cover can reduce survival rates, which in turn leads to insect decline (Harris et al., 2019). The direct influence of rising temperatures on community composition and diversity was mainly assessed in mesocosm experiments which did may (Perdomo et al., 2012) or did not (Dossena et al., 2012) find changes in diversity but at least in community compositions. However in some cases increasing temperatures can have beneficial effects on insect communities, as it may compensate for lower amounts of resources (Müller et al., 2015). This is in line with the prediction, that temperature increase per se should affect insect communities in temperate regions less than in tropical regions (Deutsch et al., 2008). In addition to the direct effects of temperature on insects there is a multitude of indirect effects, like changes in habitat, food availability or predation, or other between species interactions mediated through climate change (Stange & Ayres, 2010 and references therein). Thus, elevated carbon dioxide levels may alter plants nutritional values and/or the concentration of secondary plant chemicals, which can have negative effects on insect herbivores and pollinators (Coviella & Trumble, 1999; Hunter, 2001; Ziska et al., 2016). Furthermore, climate change increases the frequency of disturbance events (Seidl et al., 2011; Senf & Seidl, 2020), which can have positive impacts on species richness (Bouget & Duelli, 2004) and may create patches of different habitats in the landscape supporting a greater gamma diversity (Schall et al., 2017). Note that in general certain species profit from disturbance while others do not (see 1.2.3), as shown for forest insects in case of drought (Rouault et al., 2006).

1.2.2 … with other factors

Nitrogen deposition accelerated during the last century and will probably continue to increase (Galloway et al., 2004). This can also have negative effects on insect populations, e.g. increased nitrogen content in plants can increase mortality of certain Lepidoptera species (Kurze et al., 2018). Furthermore, it can have indirect effects through species loss in vegetation communities or nitrogen deposition in water bodies (Holden et al., 2007; De Schrijver et al., 2011; Habel et al., 2016b). Another anthropogenic factor driving insect decline is intensification. Especially land use intensification in the agricultural context is known to lead to insect decline and homogenization (Sala et al., 2000; Allan et al., 2014; Gossner et al., 2016). These negative effects also extend to adjacent protected areas (Hallmann et al., 2017). However, also intensive management in forests leads to reduced diversity and altered community composition (Müller et al., 2008). In water bodies a higher fish biomass due to intensive stocking density reduces insect diversity significantly (Fairchild et al., 2000). The most drastic form of intensification is conversion of land to another type of land (land use change), which has negative effects on insect communities (2018; Kremen & Merenlender, 2018; Habel et al., 2019c). Land use change in Europe is especially common in agricultural systems, but in a way happens also in forest. The conversion of deciduous forests to coniferous or mixed forests with high proportions of planted spruce trees has negative impacts on wood-dependent species adapted to deciduous trees (Goner 2004). In addition to changes of the management of a site, "land loss" via urbanization and light pollution is another cause for diversity decline in insects (Knop et al., 2017; Van Langevelde et al., 2018; Sánchez-Bayo & Wyckhuys, 2019). Finally, another factor which is linked to the intensification is the use of pesticides and insecticides. Insecticides are directly linked to the decline of species richness (Fairchild & Eidt, 1993; Hallmann et al., 2017), and thus also seriously threaten pollinators and the respective ecosystem services they perform (Goulson et al., 2015).

1.2.3 … according to their taxonomic group and their traits

Not all insect species are threatened equally. Thus, trends are dependent on the taxonomic group and may additionally depend on the habitat type under study (De Schrijver et al., 2011; Stefanescu et al., 2011a). Open habitat species tend to be more threatened in Europe due to a higher degree of intensification with more insecticide usage (Reif et al., 2008). Forest species, on the other hand tend to be less endangered, because forest management did not change drastically over the last decades in central Europe (Hunter et al., 2014; Juslén et al., 2016a; Potocký et al., 2018 but see Seibold et al. 2019). At some individual locations species richness even increased in forests during the last decades (Thomsen et al., 2015; Ubach et al., 2020 but see Seibold et al., 2019), possibly because of the stable and homogeneous habitat most forests offer nowadays in Central Europe (Schall et al., 2017). Interestingly also fresh-water habitats are found to have stable or even increasing diversity trends in insect communities (Pilotto et al., 2020). Though decline (and increase) might not affect all taxa in the same way comparison between taxa are difficult because there is a bias in study numbers towards Lepidoptera and Apidae (Wagner, 2020). Beside the taxon there are certain traits which are associated with decline. Thus, large body or wing-size is associated with a higher threat and greater decline (Seibold et al., 2015b; Coulthard et al., 2019). Furthermore, cold adapted species suffer more from climate change (Haase et al., 2019), and habitat and dietary specialists as well as IUCN red listed species are in greater danger (Potts et al., 2010; Habel et al., 2016b; Wagner, 2020). In contrast, common and wide-spread species seem to be affected at least (Fox et al., 2014).

Recent reports in the media showed quite alarmistic trends of around 75% insect decline based especially on a study of insect biomass in Germany (Hallmann et al., 2017) and an alarmistic review by (Sánchez-Bayo & Wyckhuys, 2019). The latter was criticized in the scientific community for exaggerating the actually provable trends (e.g. Komonen et al., 2019).

A global meta-analysis on insect decline revealed a 45% decline of insect abundance (Coleoptera, Lepidoptera, Hymenoptera) (Dirzo et al., 2014). Similar decline rates were shown for Sweden, the UK and Germany (Conrad et al., 2006; Franzén et al., 2007; Habel et al., 2019c). However, considering recent findings these trends might be overestimated, at least for certain taxonomic groups in certain habitats. Bell & Shortall (2020) showed a decline of moths by 35 percent between 1969 and 2016 in the UK while there was no significant trend in aphids. Furthermore, the negative trend of moths depended on the habitat, as moths only declined significantly in woodland, moorland, urban and costal habitats, but not in scrubland, parkland and farmland. Macgregor et al. (2019) recently showed that moth biomass increased and decreased over 50 years in the UK, with a 2-fold net gain in the last decades. Freshwater diversity also increased by 8.5 and 39 percent, respectively, in two European studies (Haase et al., 2019; Baranov et al., 2020). An also recent meta-analysis, which affirms these trends indicates a 9 percent decline per decade in terrestrial and an 11 percent increase in fresh-water insects (Pilotto et al., 2020; Van Klink et al., 2020).

1.3 Knowledge gaps

Though now there is a multitude of studies on temporal development of insect and their decline, it is a phenomenon which is, with some exceptions, poorly understood (Didham et al., 2020; Wagner, 2020). Until recently development of insect communities was still often assessed using chrono-sequences instead of "real" time series (Palik et al., 2001; Marchetti et al., 2010; Miguel-Chinchilla et al., 2014). Furthermore, a lot of time series are either restricted in their temporal or spatial extent (or both) (Habel et al., 2016b; Seibold et al., 2019). In addition, the recently published meta analyses on insect decline lack proper information on certain taxa in certain habitats (Pilotto et al., 2020; Van Klink et al., 2020), which makes some of the conclusions doubtful. For instance, fresh-water insects seem to have increased during the last decades in central Europe (Haase et al., 2019; Baranov et al., 2020). However, these long-term datasets mostly represent data from streams and coastal waters and are mainly restricted to northern Europe (Pilotto et al., 2020; Van Klink et al., 2020). Furthermore, especially small water bodies are rarely investigated (Biggs et al., 2017) and some taxa like beetles are underrepresented in these data (Vogel, 2017). On the other hand, taxa like moths are well studied, but the observed time series are quite restricted to northern countries, open habitats, or only few forest locations (Bell & Shortall, 2020; Wagner, 2020). Furthermore long-term studies on forests mostly concentrate on species considered pest-species and not general forest insect communities (Klapwijk et al., 2013; Pureswaran et al., 2018). Last but not least, with all surveys aiming to quantify or explain insect decline, less effort is put in analysing the effect of conservation measures on insect communities (Lindenmayer et al., 2013). This is not true for all habitat types, as for instance in agricultural landscapes there is considerable research on flowering strips (Boetzl et al., 2019; Krimmer et al., 2019) but in forested habitats there is only few studies considering a time span of at least 10 years (Heikkala et al., 2016a). This, however, would be of crucial importance to gain knowledge how to counteract the declines, however huge they may be.

1.4 Objectives of the study

Based on the knowledge gaps, this work concentrates on three aspects of temporal development of insect communities (one chapter features an additional analysis on wood-dwelling fungi). The objectives of this study were to contribute to the closure of the above-mentioned knowledge gaps based on three case studies with the following focus:

(1) Do the increasing trends in species richness and abundance found in freshwater insects also apply to water beetles living in small to middle-sized water bodies in southern Germany?

(2) Can the general assumption, that forest dwelling species are less declining than species in open lands be affirmed by analysing development of moth diversity in Bavarian forests?

(3) How effective is a conservation strategy aiming at dead-wood dependent organisms for saproxylic beetles and wood dwelling fungi?

1.5 Data sets and methods (study designs)

1.5.1 Study area(s)

All fieldwork was conducted in the federal state of Bavaria, Southern Germany (Fig. 1.1). Bavaria is a suitable study area in order to address temporal development of insect communities in Central Europe. It features a lot of different habitats and provides the

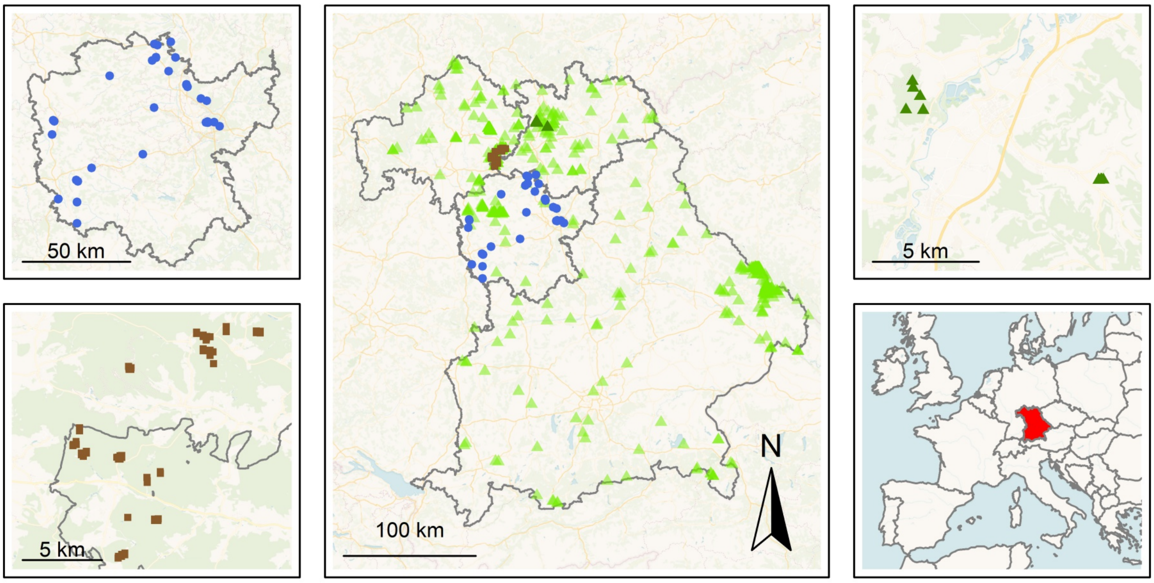


Fig. 1.1: Study areas within Europe (bottom right) and the federal state of Bavaria, Germany (center). Detailed maps of the location of the 33 sampled water bodies (top left), the two core areas of moth sampling (top right) and the 69 plots on which saproxylic organisms were sampled in beech forest (bottom left). Blue dots represent the water bodies sampled for Chapter 2, the green triangles the plots sampled for Chapter 3, an the brown squares the plots sampled for Chapter 4.

possibility to study patterns along extend elevational gradients. Chapter 2 investigates water-beetle diversity (see 1.5.2) in 33 small to mid-size water bodies, which were sampled over three decades (2-3 years per decade) from the 1990s to the 2010s. Chapter 3 features 531 forest plots in whole Bavaria which were sampled in 41 years spanning 1978 to 2018 and along an elevational gradient of 1500 m asl. Additionally, two core areas in northern Bavaria were constantly sampled between 1979 and 2018 with 283 plot-dates in a coppice with standards forest and 118 plot-dates in an oak high forest, respectively. Last but not least for Chapter 3, 69 beech forest plots belonging to three categories of management intensities (intensively managed, moderately managed, and forest reserves) were sampled in north-western Bavaria in 2004 and 2014. All plots were in European beech (*Fagus sylvatica*) forests.

1.5.2 Study systems

In the studied "pond-scape" (Chapter 2) I concentrated on small to mid-sized water beetles belonging to three different families (Dytiscidae, Haliplidae, Noteridae). The management of the water bodies did not change substantially during the time, hence it could be ruled out as possible driver of changes in the communities. Chapter 3 features plots in all common forest types of Central Europe and is therefore also representative for the latter. In addition to overall macro-moth community development I analysed the three most abundant families (Geometridae, Noctuidae, Erebidae) separately, in order to check for consistency of patterns across the Lepidoptera taxonomy. In Chapter 4 the three management types refer to a former management, which shaped saproxylic organism communities before the implementation of a landscape-wide integrative management concept in the managed parts of the forest. The forest reserves could thus serve as a control for the before-after comparison of the managed plots (BACI). In this I focused on distinct functional groups rather than on certain families. In Chapter 2, 3 and 4 I also analysed the data regarding different traits. Thus, in Chapter 2 I analysed if the global patterns differ for species belonging to raw-soil, mature pond or moor associations, respectively. In Chapter 3, I analysed if lighter moths differ from the trends in darker moths, and if dietary specialists differ from generalists. In Chapter 4 I tested if saproxylic organisms specialized on fresh dead wood, old dead wood and wood fungi differ in their patterns and in their response to the conservation strategy.

Chapter 2: Long-term monitoring reveals decreasing water beetle diversity, loss of specialists and community shifts over the past 28 years

This Chapter is published as: Roth, N., Zoder, S., Zaman, A. A., Thorn, S., & Schmidl, J. (2020). Long-term monitoring reveals decreasing water beetle diversity, loss of specialists and community shifts over the past 28 years. Insect Conservation and Diversity, 13(2), 140-150.

2.1 Summary

Lentic freshwater organisms are influenced by a multitude of factors, including geomorphology, hydrology, anthropogenic impacts and climate change. Organisms that depend on patchy resources such as water beetles may also be sensitive to anthropogenic habitat degradation, like pollution, eutrophication, water level or management alteration. To assess composition and ecological trends in the water beetle communities of Central Europe, we sampled water beetles (Dytiscidae, Haliplidae, Noteridae) in 33 water bodies in Southern Germany from 1991 to 2018. We used manual, time-standardized capture during three periods: between 1991 and 1995, 2007 and 2008, and 2017 and 2018. During the 28-year survey period, we captured a total of 81 species. We found annual declines in both species number (ca -1%) and abundance (ca -2%). Also, community composition showed significant changes over time. The significant impact of pH on the community composition suggests that the recorded changes through time partly reflects natural succession processes. However, a pronounced decline of beetle species belonging to the moor related beetle associations indicated that Central European water beetles are also threatened by non-successional factors, including desiccation, increased nitrogen input and/or mineralization, and the loss of specific habitats. This trend to physiographical "homogenization" resulted in corresponding community composition shifts. To effectively protect endangered species, conservation strategies need to be aimed at regularly creating new water bodies with mineralic bottom substratum, and maintenance of moor water bodies that represent late successional stages.

2.2 Introduction

Species declines accompanying climate change have been recorded for many taxa including insects, and in many regions and their respective habitat types (Thomas et al., 2004b; Barnosky et al., 2011; Sánchez-Bayo & Wyckhuys, 2019). A recent study in Central Europe reported large declines in terrestrial insect biomass in protected areas embedded in agricultural landscapes, presumably due to increasing land-use intensification (Hallmann et al., 2017). This biomass-related study highlights the overall trend, but the interpretation (politically and practically) is controversial in terms of the mechanistic causes of decline, as the specific biology and population trend of most of the affected species is not taken into account in such large-scale studies. Also specific species declines in insects have been shown for different target taxa and habitats (e.g. Seibold et al. 2019), and species extinctions are often reported to be non-random, reflecting trait-mediated selective processes (Cardillo et al., 2005; Seibold et al., 2015b; Habel et al., 2016b). However, major freshwater groups like water beetles received little attention and analyses so far.

Lentic inland water bodies form discrete habitat patches in landscapes (Pope et al., 2000; Hof et al., 2008) and are influenced by factors that include geomorphology (e.g., sinks, pondages, barriers), hydrology (e.g., water inflow and runoff, drainage, inundation, precipitation, evaporation), succession, sedimentation, and anthropogenic impacts (e.g., utilization, pollution, water management, fishery, recreation). The main drivers of their physicochemical features are the chemistry of the subsoil (Molinari et al., 2012), evaporation (Townsend, 2002) and the "collective nature" of a water body resulting from the surface flume of its catchment area (Sioli, 1975). Organisms dwelling and breeding in lentic inland water bodies are inescapably subject to their physicochemical and structural characteristics (Hansch & Fujita, 1963; Rohr & Crumrine, 2005). Consequently, anthropogenic influences (Fairchild & Eidt, 1993; Dudgeon et al., 2006; Perrett et al., 2006; Mcmahon et al., 2012) and/or climate change (Stocker et al., 2013; Richman et al., 2015), threatening these lentic water bodies, can lead to species losses at rates comparable to those in tropical forests (Ricciardi & Rasmussen, 1999). Moreover, different species may differ in their response to habitat change. For example, moor specialists may be negatively affected by high nitrogen levels (Smith et al., 1999; Galloway et al., 2004; Holden et al., 2007), while, in general, species dwelling in small water bodies are relatively insensitive to compounds that contribute to eutrophication (Rosset et al., 2014).

The identification of true declines in arthropods requires standardized long-term data (Jeffries, 2011; Ewald et al., 2015; Habel et al., 2016b). Yet, in most studies on lentic water bodies either the survey was conducted for only a few years (Jeffries, 1994; Chase, 2007; Florencio et al., 2009; Ripley & Simovich, 2009 but see, e.g., Ovaskainen, 2019), or a space-for-time substitution approach was used across chronosequences of successional stages (Palik et al., 2001; Marchetti et al., 2010; Sferra et al., 2017). Accurate estimates of the biodiversity in various water bodies must take into account not only temporal but also spatial scales (Cayrou & Céréghino, 2005). Small lentic water bodies constitute a mosaic of different conditions at a regional scale (Rosset et al., 2014). In these "pond-scapes", a high gamma diversity is achieved as a result of a high beta diversity among ponds (Davies et al., 2008). Accordingly, by obtaining samples from different types of small lentic water bodies at a regional scale, both the diversity and the trends of their water-dwelling organisms can be assessed.

Water beetles form a diverse invertebrate group (Jäch & Balke, 2008) and their ecology, especially that of the family Dytiscidae, has been well-studied (Wesenberg-Lund, 1943;

Galewski, 1971; Yee, 2014; Miller & Bergsten, 2016). In freshwater ecosystems water beetles have been used as indicators of biodiversity and ecosystem health (Bilton et al., 2006; but see Rosset et al., 2014). Among the factors that influence water beetle diversity are latitude, elevation, subsoil, and beetle life history (Flechtner, 1983; Vamosi et al., 2007; Abellán et al., 2012), temperature, pH, and conductivity (Heino, 2000; Schmidl, 2003; Gutiérrez-Estrada & Bilton, 2010) as well as fish density and the species composition of water plants (Fairchild et al., 2000; Gioria et al., 2010).

To determine whether there was a change in diversity and change of composition of water beetle communities we used the water beetle association concept of Schmidl (2003), which relates species assemblages to successional stages of vegetational and physiographical development of water bodies. We carried out time-standardized, repeated surveys of water beetle communities (Dytiscidae, Haliplidae and Noteridae) in water bodies of different habitat types and successional status, within one region and over 28 years (1991-2018). These surveys covered the whole range of available natural or near-to-nature water bodies in the study area, comprising early successional water bodies with no or little vegetation and mineralic substratum (the corresponding term for the typical water beetle association in these water bodies is "mineralic substratum association"), pools and ponds in open landscape rich in vegetation and with a substratum made of sludge and coarse detritus ("detritus association"), and mature old fen and moor water bodies ("moor association") with a soil substratum made of dense and thick layers of vegetation and detritus which chemically separates the water body from the subsoil. To disentangle the effects of this natural succession pathway, climate change and land-use intensification, we analysed physical and chemical parameters in parallel with our water beetle monitoring.

We predicted that (1) water beetles species of the "mineralic substratum association" would disappear nearly completely from the sampled water bodies because of the natural succession of vegetation and accumulation of detritus over the 28 years of the study; (2) moor dwelling species ("moor association") would also be negatively affected, due to increased eutrophication which shifts community composition towards detritus related species associations ("detritus association"); thus (3), these species associations typical for detritus-rich waterbodies would be the least affected.

2.3 Material and methods

2.3.1 Study sites

From 1991 to 2018, 33 lentic water bodies were monitored over a spatial extent of ~120 km2 in southern Germany (Figure S2.1). The mean annual temperature in the study region is 11–13°C, with an annual rainfall of 600–960 mm (Dietmar et al., 2007) (See Figure S2.2 for annual mean temperatures and rainfall in the study area from 1991 to 2018). The investigated water bodies ranged from very small and partially ephemeral pools (6 m^2) to mid-size ponds (1 ha). Fifteen water bodies were in open land, 15 in forests, and three were old sand pit water bodies. Eight of the 33 water bodies were extensively managed carp ponds.

Initially, in 1991 the 33 water bodies could be assigned to the following different successional stages and categories of habitat types (see above): four mineralic substratum water bodies, 14 moor and fen water bodies in forests, and 11 ponds in open landscape (eight carp ponds and three unmanaged ponds), with four water bodies being in a transitional stage between mineralic and detritus-accumulated substratum. The sites were sampled in 1991, 1993 and 1995, in 2007 and 2008, and in 2017 and 2018. In the 1990s, 12 of the 33 water bodies were resampled between one and five times, yielding 75 survey events. In the 2000s, 16 of the 33 sites were resampled once each, for a total of 49 data sets. During the last survey decade, seven of the 33 water bodies were either desiccated or no longer existed (four moor and fen water bodies, two ponds, and one mineralic substratum pool). Thus, only 26 sites could be resampled in 2017 and 2018. In this decade, three ponds were resampled once each, resulting in 29 additional data sets. In total, 153 surveys were conducted from 1991 to 2018 (see Table 2.1).

Table 2.1: Number of surveys per water body and year

Water body/Year	1991	1993	1995	2007	2008	2017	2018
1	1	0	0	2	0	1	1
2	3	0	0	2	0	1	0
3	0	0	1	2	0	1	0
4	0	0	1	2	0	1	0
5	3	3	0	1	0	1	1
6	3	2	0	1	0	1	1
7	1	0	0	1	0	1	0
8	1	0	0	2	0	1	0
9	1	0	0	1	0	1	0
10	0	3	0	2	0	1	0
11	3	3	0	1	0	0	0
12	1	3	0	2	0	0	1
13	3	3	0	2	0	0	0
14	1	3	0	2	0	0	0
15	1	0	0	2	0	1	0
16	3	3	0	2	0	0	0
17	1	0	0	2	0	1	0
18	0	1	0	2	0	0	1
19	1	0	0	1	0	1	0
20	0	1	0	2	0	1	0
21	2	0	0	1	0	1	0
22	0	1	0	1	1	1	0
23	1	0	0	1	0	0	0
24	0	3	0	1	0	1	0
25	0	1	0	1	1	0	0
26	1	0	0	1	0	1	0
27	1	0	0	0	1	0	0
28	3	3	0	0	1	1	0
29	0	1	0	0	1	1	0
30	0	1	0	0	1	1	0
31	1	0	0	0	1	1	0
32	0	1	0	0	1	1	0
33	0	1	0	0	1	1	0

2.3.2 Beetle sampling and classification

Water beetles were collected using a time-standardized direct search, and always either collected or supervised by JS. Each water body was sampled by hand for 90 min, using a colander (25 cm diameter and 0.7 mm mesh size) in water containing dense vegetation, and a net (20 cm diameter, 1.0 mm mesh size) in open water bodies. All captured beetle specimens were collected. Collecting was done during the day, between 12:00 and 18:00, but not on rainy days. This ensured comparable data, with respect to the water parameters (see below). Only water beetles belonging to the Hydradephaga were considered, but Gyrinidae (whirligig beetles) were excluded as these require different collecting methods. Specimens from the hydradephagan families Dyticidae (excluding the genera Dytiscus and Cybister), Haliplidae, and Noteridae were determined to species level by JS. Nomenclature follows the catalogue of Nilsson & Hájek (2019). The water beetle association concept of Schmidl (2003) was used to classify species and associations ecologically, with respect to the physiographical status and successional gradient of water body and vegetation development, respectively.

This concept recognizes three main associations and eight sub-associations along the successional and pH-related gradient: Species of the "mineralic substratum association" (A-category) are found in new or disturbed water bodies devoid of detritus and vascular plants on the mineralic ground; therein, species within the "mineralophilous sub-association" (A1) require water bodies with an argillaceous, hardness-component-rich substrate, and those within the "psammophilous sub-association" (A2) water bodies with a sandy, hardness-component-poor substrate. With further succession of the vegetation, water beetle communities develop towards "detritus associations" (B-category), which occur in higher-successional-level water bodies in open landscape that are characterized by sludge and/or coarse detritus accumulation and decreasing pH values. The accrual of species of the "argillophilous sub-association" (B1) results in a transitional species community that is followed by a community of species of the "limnophilous sub-association" (B2). The latter species are typically found in mature meso- and eutrophic ponds and pools containing extensive vascular plant vegetation and organic detritus, thus shielding the water body from the mineralic subsoil. Species of the "acidophilic sub-association" (B3) are found in water bodies affected by siltation, fens and low moors with strong accumulations of detritus, and sub-dystrophic water caused by dissolved humus. The "marshland forest association" (B2/C1) is a transition between limnophilous detritus association B2 and acidic, oligo- to mesotrophic, shady forest water bodies of "umbrophilic moor associations" C1. "Moor associations" (C-category) may either be umbrophilic ("umbrophilic sub-association" C1), with species occurring mostly in small shady forest pools with a litter layer and a few algae, or sphagnophilic ("sphagnophilic sub-association" C2), comprising tyrphophilic or tyrphobiontic species that colonize peat bogs with significant Sphagnum spp. cover (over raised bog formations) and a low pH (see Table S2.1 for species list).

2.3.3 Water bodies and water parameters

The physical and chemical parameters of the water bodies were determined at each survey date. The maximum depth at 1 m from the edge and the elevation of the water body was recorded, and pH and temperature (°C) were measured using the pH 320 pH-meter fitted with a SenTix 41 pH-sensor (both from WTW, Weilheim). A WTW Oxi-Meter Oxi 320 and CellOx 325 electrode (both from WTW, Weilheim) were used to measure oxygen saturation (%). Furthermore, nitrite (mg/l) and chloride (mg/l) were determined using a PF 10 filter-photometer (Macherey-Nagel, Düren), and the conductivity (µS) using a LF 91 conductivity meter with a KLE1/T conductivity sensor (both from Macherey-Nagel, Düren). Total hardness (dH°) and carbonate hardness (dH°) were determined by titration. The water used in the chemical analyses was taken 1 m from the water's edge at a depth of 10–50 cm depending on the total depth of the water. Spearman correlation between the measured parameters were calculated using the "cor" function within the 'stats' package in R (R Core Team, 2018).

2.3.4 Statistical methods

Changes in water beetle communities through time were quantified using four measures: species richness, abundance, relative richness and community composition. Species richness and abundance of each association was calculated per survey in order to include association as an explanatory variable in the models.

Hierarchical generalized additive models (HGAM) sensu Pedersen et al., (2019) were used to model species richness and abundance. Relative richness was also modelled with species richness as dependent variable while abundance was included as explanatory variable. These models are extensions of the standard generalized additive model (GAM) framework (Hastie & Tibshirani, 1990) and allow smooth functional relationships between predictor and response to vary between groups (Pedersen et al., 2019). These are implemented in the 'mgcv' package (Wood, 2017) in R (version 3.5.2) (R Core Team, 2018) which was used for all statistical analyses. The year was modeled in an overall smoother and in an additional smooth term, which specified the group-level smooth terms in a factor-smooth interaction, in order to show group-specific deviations from the global function (see Supporting Information S2.3 for model formula). Elevation of the water bodies, water temperature, oxygen saturation, total hardness, carbonate hardness, nitrite concentration, chloride concentration, ph and conductivity as well as water depth and the day of the year (1-365 further referred to as "season") were included in the model as global smooth terms. Latitude and longitude were wrapped in the same smooth term (see Supporting Information S2.3). All the continuous variables used thin plate splines as basis function within the smoothers except for the season where cubic cycle splines were used as basis function. The initial waterbody type and the survey ID were wrapped in smoothers as discrete random effects. The survey-level random effect accounts for frequently observed overdispersion in models of count data (Harrison, 2014). Furthermore, it accounted for the fact that sampling intensity differed between the decades. A Tweedie error distribution with a log-link function was used which is appropriate for data with a non-zero probability of zero observations (Gilchrist & Drinkwater, 2000). Restricted maximum likelihood (REML) was used as the smoothing parameter estimation method. Finally, variable selection was performed with the 'gam' internal argument 'select = T'.

Canonical Correspondence Analysis (CCA) was used in order to analyse if the patterns found via the HGAMs translate into community composition shifts, while also controlling for explanatory variables using the 'cca' function within the 'vegan' package (Oksanen et al., 2018). Communities were computed at the survey level, temperature, oxygen saturation, conductivity, total and carbonate hardness, chloride and nitrite concentration, ph and temperature as well as the year were used as environmental variables. Variable selection was performed with a stepwise model selection using the ‘ordistep’ function.

2.4 Results

In total, 19,232 specimens (average 126 per sample, range 4–487) were recorded, belonging to 81 different water beetle species (average 11 per sample, range 2–25) in all water bodies sampled since 1991 (see Table S2.2 for species list and abundance per survey year). Surveyed water bodies ranged from a minimum pH of 3.9, which is near the lower end of the pH range of natural water bodies (e.g. in raised bogs), and a maximum pH of 10.1, which is close to the upper end of the pH gradient of natural water bodies. pH and conductivity were positively correlated (Spearman rho = 0.56) in “real-time” comparison (Table S3).

2.4.1 Abundance and richness

The total abundance as well as the species richness of the water beetles per survey decreased by approximately 2% and ca 1%, respectively (Fig 2.1 & 2.2 a-c). Thus, mean abundance and species richness per survey decreased from 151 to 74 individuals (Fig. 2.1a), and from 13 to 7 species (Fig. 2.1b), respectively. Furthermore, abundance increased with increasing nitrite and total hardness and decreased with increasing temperature, pH, conductivity and depth (Table 2.2 & Figure S2.3). Species richness decreased with increasing elevation and conductivity (Table 2.2 & Figure S2.4). Relative richness decreased yearly and increased slightly with increasing depth of the waterbodies. It was also significantly influenced by the elevation (Table 2.2 & Figure S2.5). Survey ID had a significant effect on abundance, species richness and relative richness. The initial water body type had a significant effect on abundance and species richness.

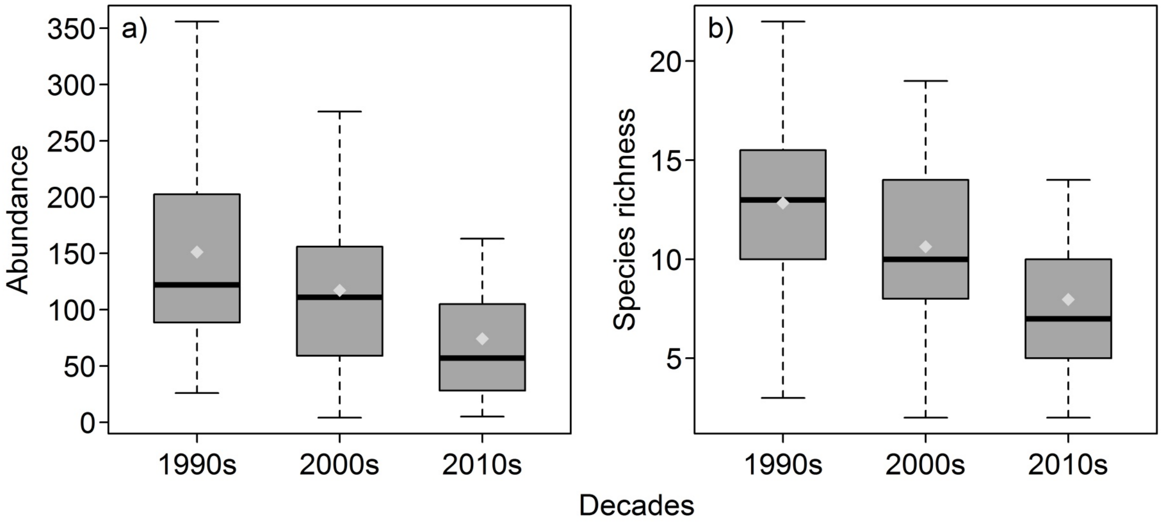


Fig. 2.1: Boxplots of water beetle abundance (a) and species richness (b) per survey and decade. Light grey rhombs indicate means.

2.4.2 Associations

Overall, we recorded five species belonging to mineralic substratum associations (A1/A2), 47 species belonging to detritus association (B1, B2, B3) and the transitional marshland forest association (B2/C1), and 16 species belonging to the moor association (C1/C2). The association - year interaction was significant for all three dependent variables and showed high effect sizes (Table 2.2). The group specific deviation from the overall temporal trend was most pronounced in mineralophilous and psammophilous water beetle associations (mineralic substratum sub-associations A1/A2) which indicates that the species belonging to these associations showed the greatest declines over time (Fig. 2.2 d-f). The species belonging to the umbrophilous and sphagnophilous species (moor sub-associations C1/C2) also deviated negatively from the overall trend, although the deviation was less pronounced than for the mineralic substratum associations (Fig 2.2 c-f). The trend for the species belonging to the "ecological mid-position" associations (detritus associations B1, B2, B3, and marshland forest association B2/C1) deviated positively from the overall temporal trend (Fig. 2.2 c-f). This means that species belonging to "detritus" sub-associations did not decrease, but show rather stable trends, in contrast to mineralic substratum and moor association related species. The deviation patterns from the overall trend were similar for abundance, species richness and relative richness.

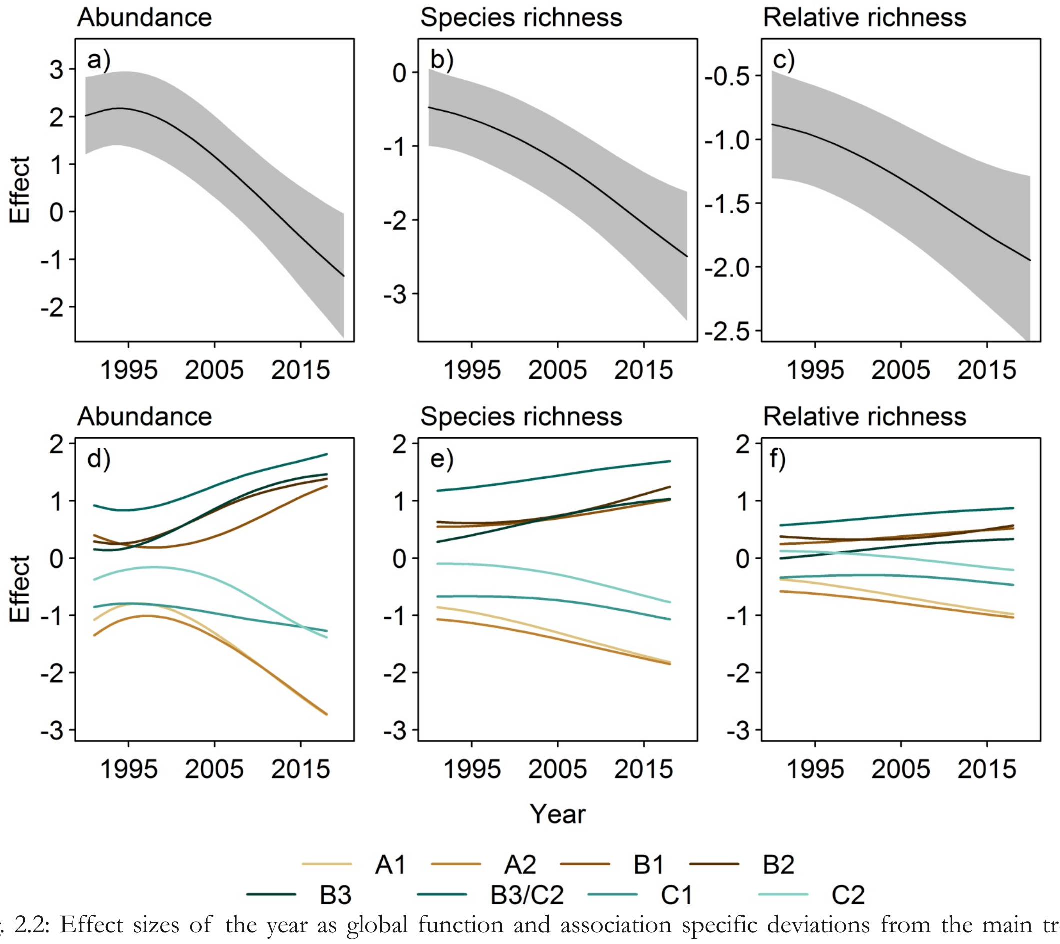


Fig. 2.2: Effect sizes of the year as global function and association specific deviations from the main trend for abundance (a,d), species richness (b,e) andrelative richness (c,f). The A-categories are mineralic substratum associations, the B-categories detritus associations and the C-categories moor associations.

Table 2.2: Summaries of hierarchical generalized additive models for the dependent variables abundance, species richness and species richness corrected for abundance (relative richness). Dashes indicate variables, which did not contribute to the according models and were thus excluded. NAs indicate variables which were not included in the according model from the start.

	Abundance		Species Richness		Relative Richness	
Term	F	Significance	F	Significance	F	Significance
Year	1.921	***	2.413	***	1.03	**
Year:association	8.64	***	21.788	***	4.966	***
Season	-		-		-	
Survey ID	0.509	***	0.989	***	0.471	***
Initial type	7.809	***	1.914	*	1.011	
Lon/Lat	0.431		1.337	*	-	
Elevation	-		3.373	**	4.513	*
Temperature	0.451	.	0.513		0.239	
Oxygen saturation	-		-		-	
Total hardness	2.579	**	-		-	
Carbonate hardness	-		-		-	
Nitrite	5.833	***	-		-	
Chloride	-		-		-	
pH	1.971	**	0.688		-	
Conductivity	2.608	***	0.837	.	-	
Depth	1.842	**	0.001		0.807	.
Abundance	NA	NA	NA	NA	102.705	***

2.4.3 Community Composition

The stepwise model selection for the CCA showed that all included parameters had a significant influence (Table S6). Thus, all of them were kept in the CCA. CA inertia was 11.55, CCA constrained 2.18 (19%). CCA axes 1-4 cumulatively explained 73% (30.3, 50.5, 62.6, and 73.0) of the total constrained variation (Table S4 & S5 for further details). The main gradient were defined by nitrite, pH and carbonate hardness (Fig. 2.3). Conductivity, chloride and total hardness gradients values are rising co-linear with pH and carbonate hardness. High values of nitrite are found mainly in young water bodies with mineralic substratum. Year (time) is another quite independent gradient in the community composition, with rising temperature being the most closely correlated parameter.

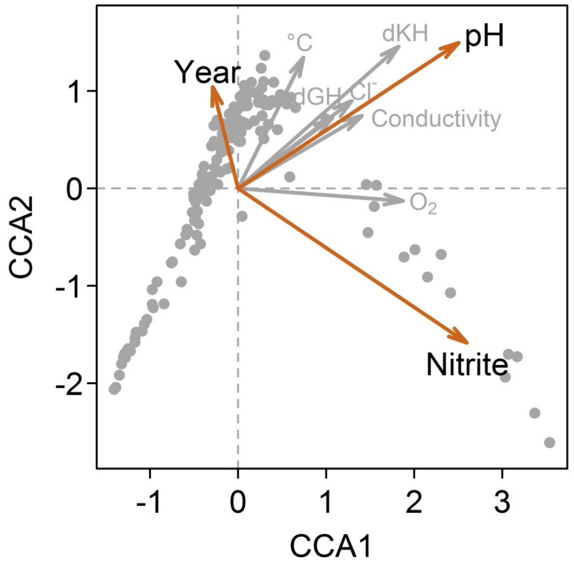


Fig. 2.3: CCA ordination with main gradients highlighted in orange.

2.5 Discussion

Within the total temporal range of our observation of 28 years, nearly 50% of all species belonging to the three water beetle families Dytiscidae, Haliplidae, and Noteridae recorded in Germany (Spitzenberg et al., 2016) were sampled. As the temperature had no significant effect on abundance and richness in our calculations, effects attributable to climate change may have been mediated by the observed decrease in water depth and by resulting increases in conductivity and total water hardness by concentration effects. Note that especially abundance was significantly influenced by these parameters. The negative effect of rising maximum depth (measured 1 m from the water's edge) on abundance can also be explained by the steep slopes at the banks of the surveyed water bodies (esp. ponds) with larger depths, resulting in fewer habitat structures and water plants, both of which provide breeding sites for water beetles (Nilsson et al., 1994; Fairchild et al., 2003). The decrease in richness with increasing elevation is in line with previous findings (Vamosi et al., 2007), although the maximal elevation difference in our study area was only ~100 m a.s.l..

2.5.1 Effects of pH and conductivity on water beetle abundance and richness

We found more specimens in water bodies with lower pH, which is in line with previous studies (Nilsson & Soderberg, 1996; Batzer et al., 2004 but see Arnott et al., 2006). However, although our samples covered nearly the entire gradient of the naturally occurring pH range, we could not detect a clear threshold at which this trend decreased or changed (Figure S2.3). In near-to-nature lentic water bodies, pH is mainly influenced by the geological substratum and the amount of plants and detritus (succession). Under natural conditions, a lower pH correlates with increases in the amounts of plant matter and humus (Vuorenmaa et al., 2006) and increasing isolation of the water body from geological underground (Schmidl, 2003, but see Carvalho, Thomaz, & Bini, 2005 for laboratory conditions and Yee & Juliano, 2007 for rotholes). Detritus accumulation in turn enlarges the structural diversity of a habitat and therefore water beetle abundance (Schmidl 2003).

We found a positive correlation of pH and conductivity (Table S2.3), and at the same time decreasing abundances and species richness with increasing conductivity (Supporting Information S2.3). This is in line with the above outlined, corresponding effects of detritus on pH, but is in contrast to the observations of some studies in which rising conductivity was shown to have a positive effect on species richness (Eyre et al., 1990; Heino, 2000; Bilton et al., 2006), at least up to a threshold of around 600 µS (Gutiérrez-Estrada & Bilton, 2010). Our results suggest that water bodies with lower abundances of water beetles and fewer species had conductivity levels exceeding this 600 µS threshold, however, there was no such clear threshold in our data set. Increasing levels of conductivity are often a result of a concentration effect (Townsend, 2002) arising from increased evaporation or a deficient water supply. Our finding of decreasing water levels comply with this, and may have led to water bodies that negatively influenced abundances and species numbers (Blasius & Merritt, 2002).

2.5.2 Effects of time on water beetle abundance and richness

For all of the surveyed water types, time (year) had a significant negative effect on abundance, species richness, and relative richness. A negative effect over time has been previously reported but variably interpreted. According to Nilsson (1984), succession in lentic water bodies is accompanied by a decline in species numbers, whereas Fairchild (2000) demonstrated higher diversities in older water bodies and other studies reported no change in species richness or abundance during succession (Spieles et al., 2006; Miguel-Chinchilla et al., 2014). Thus, while the reductions in abundance and diversity can in part be attributed to natural succession (see below), they cannot be clearly separated from time-related effects, such as trophic or structural disturbances or chemical disturbances such as insecticides (Fairchild & Eidt, 1993; Fairchild et al., 2000; Wood et al., 2003; Death & Zimmermann, 2005; Rohr & Crumrine, 2005). As habitat availability in lentic water bodies tends to influence beetle species richness positively (Dehling et al., 2010), the observed losses might also have resulted from habitat loss at the landscape level or by in situ losses of structural and vegetational diversity. Alternatively, the frequency of drought events may have increased as a consequence of climate change, as noted above. Drought has been shown to affect water beetles negatively by reducing the number and type of their habitats (Kholin & Nilsson, 1998). In fact, an attempt to start a similar monitoring program in moor water bodies in 2015 and subsequent years in the same study area failed, because nearly all water bodies were dried up in summer.

2.5.3 Association specific deviations from overall temporal trend

Over the 28 years of this study, the observed association range narrowed, with the opposing changes at both ends of the successional gradient shown in the year – association interaction (Fig. 2.2). Species belonging to the mineralic substratum associations (A1, A2) vanished naturally during progressive succession (Schmidl, 2003). At the other end of the successional gradient instead, species losses and decreases in total abundances occurred that could not be attributed to natural succession. Water bodies initially suitable for moor association species (C1, C2) gradually lost their specific habitat quality for the respective species sets. This might have been due to increases in air-borne nitrogen inputs (De Schrijver et al., 2011) or to the transient complete desiccation of these water bodies, accompanied by remineralization effects and "reverse" vegetational alterations (Limpens et al., 2011). Although eutrophication may not necessarily pose a major threat to water beetle diversity in small water bodies (Rosset et al., 2014), special habitats such as nutrient-poor moors and fens and their faunas suffer generally from eutrophication (Holden et al., 2007).

Declines both in mineralic substrate and moor associations led to a "bidirectional" homogenization (Fig. 2.2 & Fig 2.3) of communities towards "detritus" associations. This is in line with the general findings in insects of a loss of habitat specialists and the homogenization of insect communities in land habitats (Augenstein et al., 2012; Gossner et al., 2016). Both should be carefully considered in conservation strategies in which the creation and maintenance of water habitats are important issues and a practical tool for nature conservation (Davies et al., 2008; Brainwood & Burgin, 2009; Thiere et al., 2009; Gioria et al., 2010). Based on our results, conservation efforts should routinely include the creation of new water bodies with mineralic bottom substratum. In addition, moor water bodies should be actively promoted in suitable areas and soils and existing moor water bodies maintained. Restoration of moor and fen water bodies requires a long period of development until they become suitable for the typical species sets (Wiecek et al., 2013). Also, the presence of an appropriate source habitat is crucial for successful recolonization (Van Duinen et al., 2003). Accordingly, the conservation of water bodies and their fauna should be organized at a landscape scale to take also organisms into account which are poor dispersers (Kehl & Dettner, 2007; Lønsmann Iversen et al., 2013).

Our findings showed that "detritus associations" were not negatively affected over time. Ponds in open landscape are still used and maintained by humans for fishery, but also for nature conservation issues. Mature ponds with a high structural diversity (different reed and water plant formations, shallow water body sides, coarse detritus, etc.) and higher nutrition levels are still present in the study area, thus supporting higher species richness and abundances (Fairchild et al., 2000; Palik et al., 2001; Schmidl, 2003). While early successional pools with no or little vegetation and mineralic substratum are transitional by nature, the ecological "nodus" (sensu Ellenberg, 1988, see also Austin et al. 1989) of pond associations currently is enlarged in the successional continuum by the discussed nutrient input, which suppresses or retards the development towards dystrophic moor associations, or even reverses the latter back into the nutrient richer "detritus" habitat type.

2.5.4 Shifts in community composition

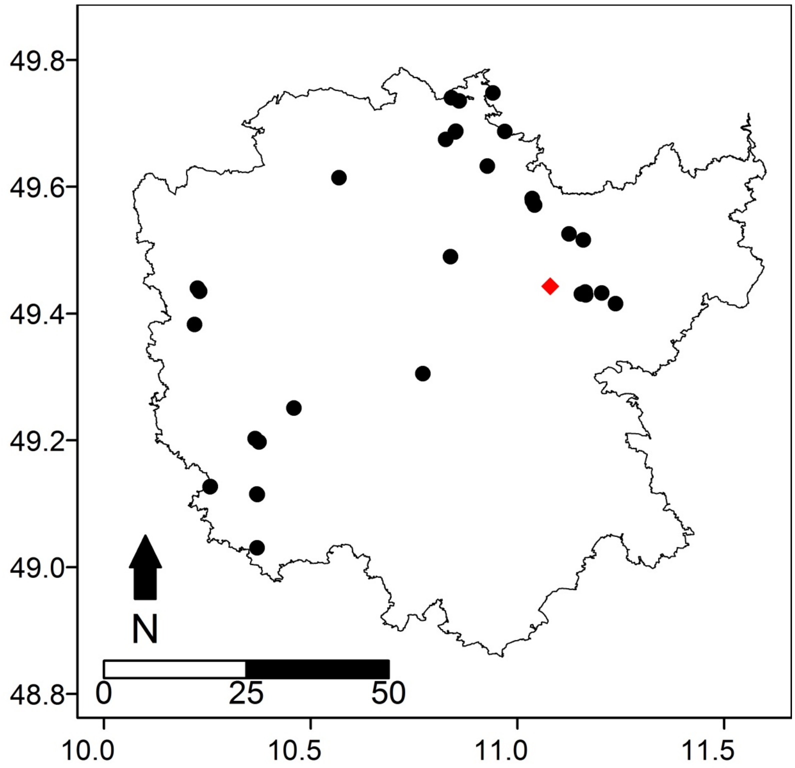
Community composition was strongly driven by pH (Fig. 2.3), which is a good proxy for succession (Schmidl 2003). This finding was in line with the results of earlier studies showing that pH is one of the most important chemical factors correlating with the species composition of small lentic water bodies (Larson, 1985; Eyre et al., 1990; Zikeli et al., 2002; Fritz et al., 2004). Nitrite was another key determinant of community composition in our study and its concentration decreased over time (Fig. 2.3). Nitrite accumulation is a prominent feature of fresh, mineralic substrate water bodies and it occurs before the bacterial flora has become established (Smith et al., 1997), i.e. the denitrification cascade is not well developed yet. Thus, as the sampled water bodies underwent succession, their nitrite levels naturally dropped, because of the decreasing pH, the development of the denitrifying bacterial flora and the pH-related transition of nitrite to ammonium (Suzuki et al., 1974; Grunditz & Dalhammar, 2001; Strauss et al., 2002; Jiménez et al., 2011).

2.5.5 Prospects

This study shows that especially mineralic substratum and moor water-beetle associations are facing threats and declines in diversity and abundance, correlating with changes in the physicochemical setting especially of these water types. Despite the fact that the time range of 28 years is a long survey period, some of the evaluated factors could be counterchecked by comparable surveys in forest areas, where changes on landscape (alteration of water catchment, agricultural nutrient input) or climate level are more moderate, compared to open landscapes. Methodologically, a more continuous survey would allow greater power to evaluate variation through time, and the regular inclusion of newly created water bodies with mineralic substratum to the surveying scheme would allow assessment of the status of the corresponding beetle associations at the landscape scale correctly. Furthermore, though time standardized collecting is a reliable tool for assessing water beetle fauna of small to mid-sized water bodies, a sampling with standardized traps would be a way of excluding sampler biases, which is especially important when considering long time spans and essential for establishing a general tool for bioindication.

2.6 Appendix

S2.1: Map of the study area



S2.1 Fig. 1: Study area in southern Germany. Scale bar indicates kilometers. The reference system is WGS84. Inset: location in Central Europe.

S2.2: Water beetle associations according to Schmidl (2003)

S2.1 Table 1: Species per associations and sub-associations, with additional character species for each association (if applicable)

Association	**Sub-association**	**Character species**	**Species**
A: mineralic substratum		*Nebrioporus canaliculatus*	*Hydroglyphus geminus*
			Coelambus confluens
			Coelambus nigrolineatus
			Hydroporus marginatus
			Scarodytes halensis
			Agabus nebulosus
			Dytiscus circumflexus
	A1: Mineralophilous	*Hydroglyphus geminus*	*Hydroglyphus geminus*
		Coelambus confluens	*Coelambus confluens*
		Scarodytes halensis	*Coelambus nigrolineatus*
			Hydroporus marginatus
			Nebrioporus canaliculatus
			Scarodytes halensis
			Agabus nebulosus
			Dytiscus circumflexus
	A2: Psammophilous	*Nebrioporus canaliculatus*	*Hydroglyphus geminus*
		Agabus nebulosus	*Coelambus confluens*
			Coelambus nigrolineatus
			Nebrioporus canaliculatus
			Agabus nebulosus
			Dytiscus circumflexus
B: Detritus		*Hydroporus palustris*	*Peltodytes caesus*
			Haliplus confinis
			Haliplus ruficollis
			Haliplus heydeni
			Haliplus flavicollis
			Haliplus fulvus
			Noterus clavicornis
			Noterus crassicornis
			Hyphydrus ovatus
			Coelambus impressopunctatus
			Hygrotus versicolor
			Hygrotus inaequalis
			Hygrotus decoratus
			Hydroporus angustatus
			Hydroporus umbrosus
			Hydroporus palustris
			Hydroporus striola
			Graptodytes granularis
			Graptodytes bilineatus

			Graptodytes pictus
			Porhydrus lineatus
			Laccophilus ponticus
			Laccophilus minutus
			Laccophilus hyalinus
			Agabus uliginosus
			Ilybius fenestratus
			Ilybius ater
			Ilybius fuliginosus
			Ilybius quadriguttatus
			Ilybius subaeneus
			Rhantus grapii
			Rhantus exsoletus
			Hydaticus transversalis
			Hydaticus seminiger
			Graphoderus cinereus
			Graphoderus zonatus
			Acilius sulcatus
			Acilius canaliculatus
			Dytiscus marginalis
			Dytiscus circumcinctus
			Dytiscus dimidiatus
			Cybister lateralimarginalis
	B1: Argillophilous	*None*	*Haliplus lineatocollis*
			Haliplus obliquus
			Haliplus sibiricus
			Haliplus immaculatus
			Haliplus laminatus
			Noterus clavicornis
			Hyphydrus ovatus
			Hygrotus inaequalis
			Graptodytes pictus
			Laccophilus minutus
			Ilybius fuliginosus
			Rhantus suturalis
			Rhantus notatus
			Colymbetes fuscus
			Dytiscus marginalis
	B2: Limnophilous	*Haliplus flavicollis*	*Haliplus flavicollis*
		Haliplus fulvus	*Haliplus ruficollis*
		Hydroporus angustatus	*Haliplus fulvus*
		Hydroporus palustris	*Noterus crassicornis*
		Hydaticus transversalis	*Hygrotus decoratus*
		Hydaticus seminiger	*Hygrotus versicolor*
		Graphoderus cinereus	*Hydroporus angustatus*

			Hydroporus palustris
			Graptodytes pictus
			Porhydrus lineatus
			Laccophilus ponticus
			Ilybius quadriguttatus
			Ilybius subaeneus
			Rhantus grapii
			Hydaticus transversalis
			Hydaticus seminiger
			Graphoderus cinereus
			Graphoderus zonatus
			Acilius sulcatus
			Dytiscus marginalis
			Dytiscus circumcinctus
			Dytiscus dimidiatus
			Cybister lateralimarginalis
	B3: Acidophilic	*Hygrotus decoratus*	*Haliplus heydeni*
		Hydroporus umbrosus	*Bidessus unistriatus*
		Hydroporus striola	*Bidessus grossepunctatus*
		Graptodytes granularis	*Noterus crassicornis*
		Copelatus haemorrhoidalis	*Hygrotus decoratus*
		Acilius canaliculatus	*Suphrodytes dorsalis*
			Hydroporus umbrosus
			Hydroporus palustris
			Hydroporus incogntius
			Hydroporus striola
			Hydroporus elongatulus
			Hydroporus erythrocephalus
			Hydroporus rufifrons
			Graptodytes granularis
			Porhydrus lineatus
			Copelatus haemorrhoidalis
			Agabus uliginosus
			Agabus unguicularis
			Agabus labiatus
			Acilius sulcatus
			Acilius canaliculatus
	B2/C2: Marshland forest	*None*	*Haliplus ruficollis*
			Haliplus heydeni
			Noterus crassicornis
			Hyphydrus ovatus
			Coelambus impressopunctatus
			Hygrotus inaequalis
			Hydroporus angustatus
			Hydroporus palustris

			Hydroporus incognitus
			Hydroporus erythrocephalus
			Hydroporus memnonius
			Laccophilus minutus
			Agabus neglectus
			Agabus sturmi
			Agabus bipustulatus
			Ilybius ater
			Ilybius fuliginosus
			Acilius sulcatus
			Dytiscus marginalis
C: Moor		*Hydroporus incognitus*	*Hydroporus tristis*
			Hydroporus gyllenhali
			Hydroporus erythrocephalus
			Hydroporus obscurus
			Hydroporus nigrita
			Hydroporus memnonius
			Hydroporus melanarius
			Hydroporus longicornis
			Hydroporus neglectus
			Agabus subtilis
			Agabus melanarius
			Agabus affinis
			Agabus congener
			Ilybius crassus
			Ilybius aenescens
			Ilybius guttiger
			Rhantus suturellus
	C1: Umbrophilic	*Agabus subtilis*	*Hydroporus incognitus*
		Agabus melanarius	*Hydroporus memnonius*
			Agabus subtilis
			Agabus melanarius
	C2: Sphagnophilic	*Hydroporus tristis*	*Hydroporus tristis*
		Hydroporus gyllenhali	*Hydroporus gyllenhali*
		Hydroporus obscurus	*Hydroporus obscurus*
		Hydroporus neglectus	*Hydroporus neglectus*
		Agabus affinis	*Hydroporus longicornis*
		Agabus congener	*Hydroporus melanarius*
		Ilybius crassus	*Agabus affinis*
			Agabus congener
			Ilybius crassus
			Ilybius guttiger
			Ilybius aenescens
			Rhantus suturellus

S2.3: Details to hierarchical generalized additive model (HGAM)

S2.3.1 HGAM formulae:

Abundance:

```
 gam(abund ~ s(year,k=7,m=2)+s(year,asso,bs="fs",k=7,m=2)
            + s(date_cont,bs="cc")
            + s(id_neu,bs="re")+s(type,bs="re")
            + s(x,y)+s(elev)+s(temp)+s(o2)+s(gh)+s(kh)+s(no2)+s(cl)+s(ph)+s(cond)+ s(Tiefe)
            ,data=guilds,family = tw,method = "REML",select=T)
```

Species richness:

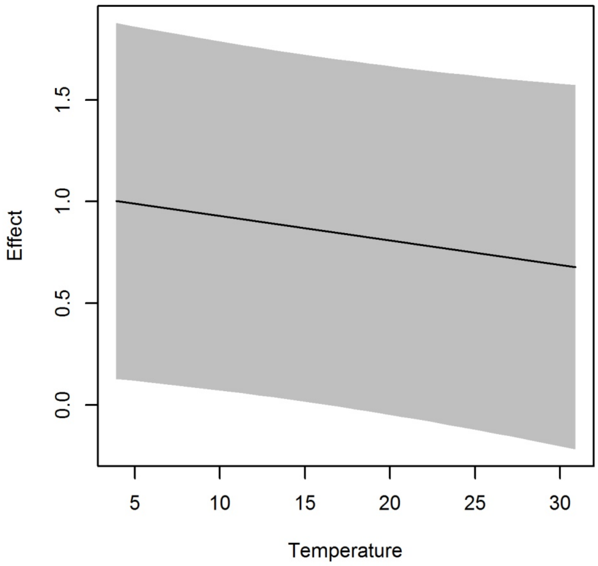
```
 gam(specnum ~ s(year,k=7,m=2,bs="gp")+s(year,asso,bs="fs",k=7,m=2)
             + s(date_cont,bs="cc")
             + s(id_neu,bs="re")+s(type,bs="re")
             + s(x,y)+s(elev)+s(temp)+s(o2)+s(gh)+s(kh)+s(no2)+s(cl)+s(ph)+s(cond)+ s(Tiefe)
             ,data=guilds,family = tw,method = "REML",select=T)
```

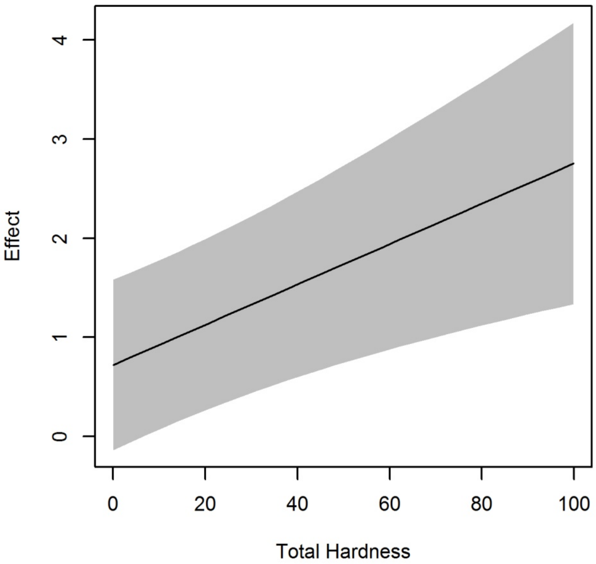
Relative richness:

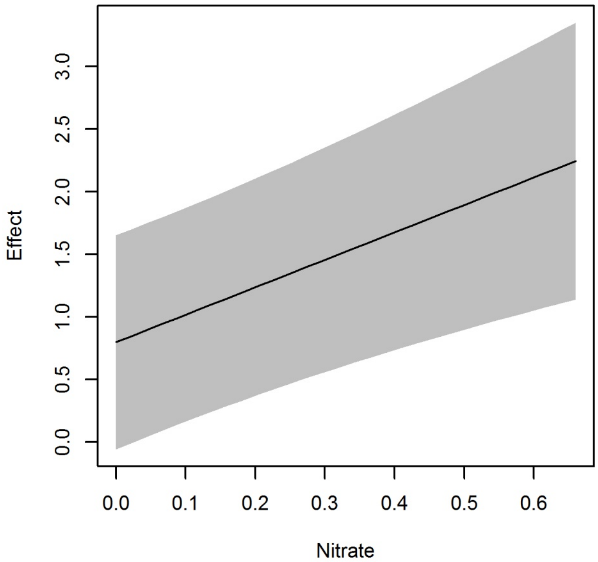
```
 gam(specnum ~ s(year,k=7,m=2)+s(year,asso,bs="fs",k=7,m=2)+s(abund)
            + s(date_cont,bs="cc")
            + s(id_neu,bs="re")+s(type,bs="re")
            + s(x,y)+s(elev)+s(temp)+s(o2)+s(gh)+s(kh)+s(no2)+s(cl)+s(ph)+s(cond)+ s(Tiefe)
            ,data=guilds,family = tw,method = "REML",select=T)
```

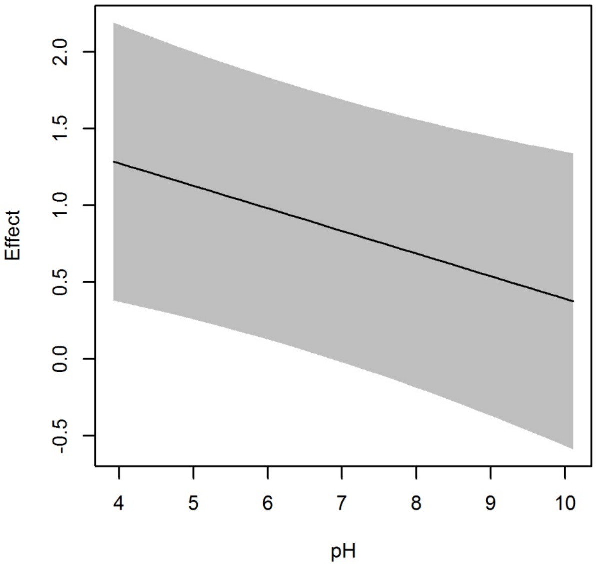
S2.3.2 Partial effect plots of significant variables of HGAMs

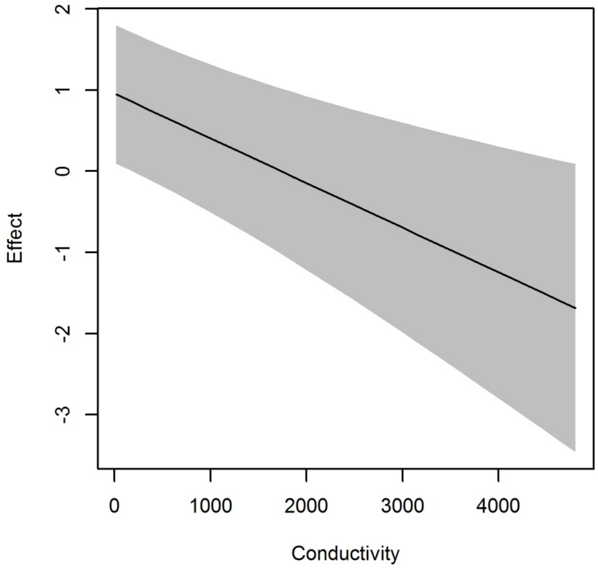
S2.3.2.1 Abundance:

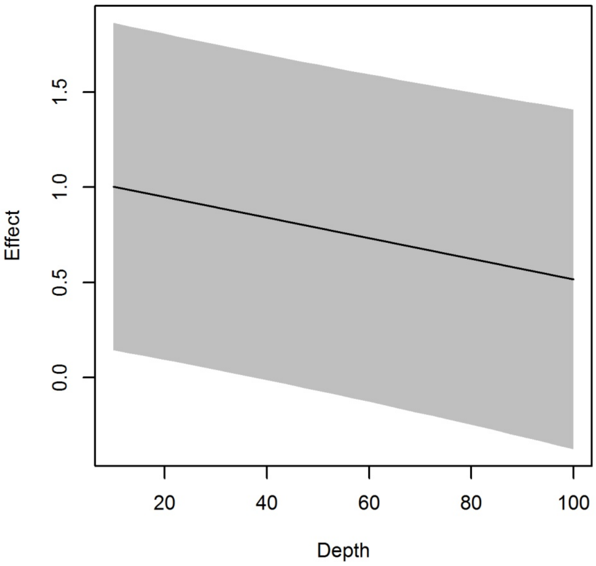




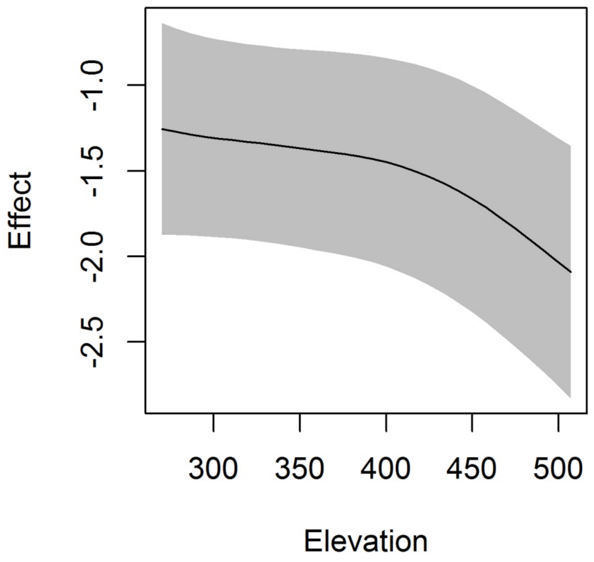


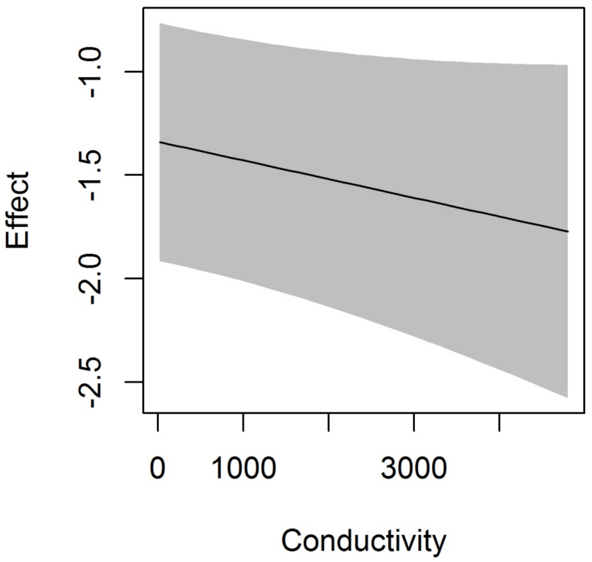




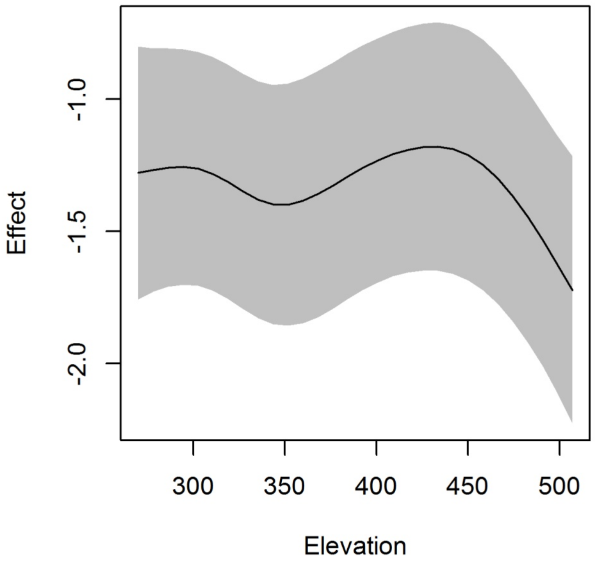


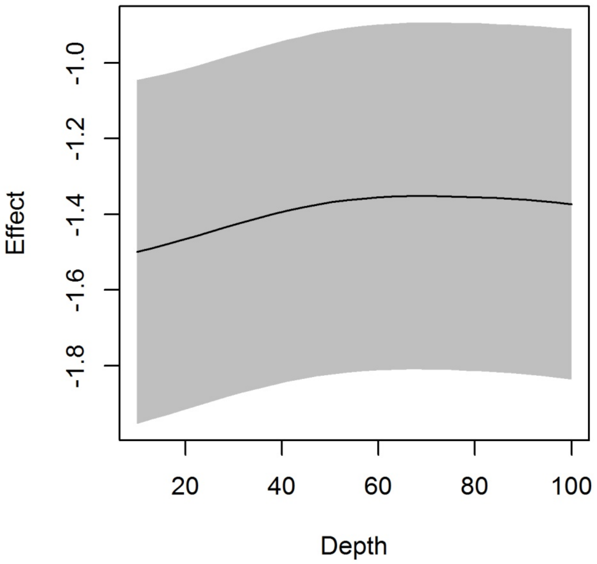
S2.3.2.2 Species richness:

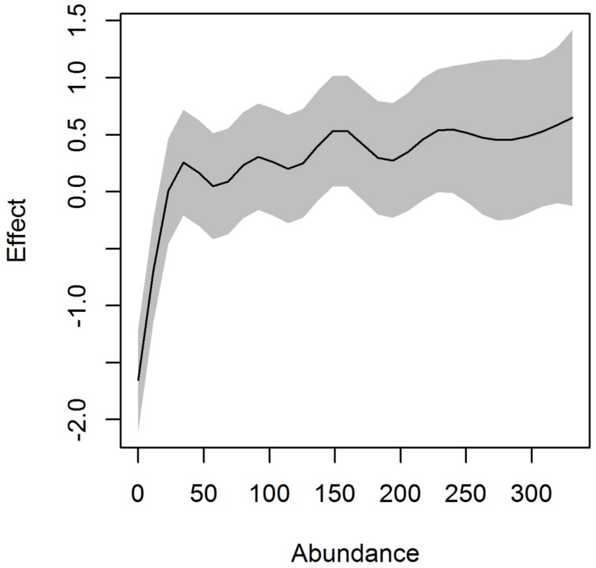




S2.3.2.3 Relative richness







S2.4: List of captured and analyzed beetle species per year. n water bodies specifies in how many waters it was found in the corresponding year. Individuals is the sum of total catches per year:

		1991		1993		1995		2007		2008		2017		2018	
		75 samplings						49 samplings				29 samplings			
Family	Species	n waters	individuals	n waters	individuals	n waters	individuals	n waters	individuals	n waters	individuals	n waters	individuals	n waters	individuals
Haliplidae	*Brychius elevatus*	0	0	0	0	0	0	0	0	0	0	1	2	0	0
	Haliplus flavicollis	4	29	2	8	0	0	2	5	0	0	0	0	0	0
	Haliplus fluviatilis	2	30	1	7	0	0	4	10	0	0	0	0	0	0
	Haliplus fulvus	2	10	2	11	0	0	2	4	0	0	2	108	0	0
	Haliplus heydeni	3	21	6	30	0	0	8	26	6	62	4	58	0	0
	Haliplus immaculatus	7	30	4	6	0	0	4	10	0	0	0	0	2	3
	Haliplus laminatus	2	14	4	7	0	0	1	6	0	0	0	0	0	0
	Haliplus lineatocollis	5	131	4	28	0	0	4	20	1	1	4	20	0	0
	Haliplus obliquus	1	77	1	4	0	0	1	6	0	0	2	4	0	0
	Haliplus ruficollis	13	305	10	209	0	0	14	344	8	202	7	55	2	11
	Haliplus sibiricus	1	20	0	0	0	0	0	0	0	0	0	0	0	0
	Peltodytes caesus	6	34	3	12	0	0	5	63	1	1	6	14	2	30
Dytiscidae	*Agabus affinis*	6	172	5	179	2	5	6	50	0	0	0	0	0	0
	Agabus bipustulatus	13	58	14	60	2	23	9	33	6	45	11	91	0	0
	Agabus congener	2	67	3	40	0	0	2	15	0	0	0	0	0	0
	Agabus didymus	1	3	1	1	0	0	0	0	0	0	0	0	0	0
	Agabus labiatus	1	1	0	0	0	0	0	0	0	0	0	0	0	0
	Agabus melanarius	3	14	3	7	0	0	0	0	0	0	0	0	0	0
	Agabus nebulosus	5	40	6	15	1	1	0	0	1	1	0	0	0	0
	Agabus sturmii	10	178	10	106	2	9	4	45	1	2	2	2	0	0
	Agabus uliginosus	2	3	0	0	1	1	1	3	1	52	0	0	0	0

	Agabus undulatus	0	0	0	0	0	0	0	0	0	0	3	14	0	0
	Agabus unguicularis	1	1	1	1	0	0	0	0	0	0	0	0	0	0
	Ilybius aenescens	2	2	1	2	1	1	0	0	0	0	0	0	0	0
	Ilybius ater	7	28	5	31	0	0	3	5	4	7	5	7	1	1
	Ilybius chalconatus	8	49	10	64	0	0	7	19	5	11	2	6	0	0
	Ilybius crassus	1	5	1	8	0	0	2	4	0	0	0	0	0	0
	Ilybius fenestratus	3	22	2	4	0	0	0	0	0	0	0	0	0	0
	Ilybius fuliginosus	11	84	10	55	1	3	8	27	4	4	3	19	1	1
	Ilybius guttiger	1	2	1	3	0	0	0	0	0	0	0	0	0	0
	Ilybius neglectus	1	24	1	19	0	0	2	25	0	0	2	2	0	0
	Ilybius quadriguttatus	4	14	2	4	1	1	2	2	2	4	1	1	0	0
	Ilybius subaeneus	2	5	1	3	0	0	0	0	0	0	0	0	0	0
	Ilybius subtilis	3	38	2	17	0	0	3	11	0	0	0	0	0	0
	Colymbetes fuscus	4	41	4	38	0	0	2	3	0	0	0	0	0	0
	Copelatus haemorrhoidalis	7	54	5	21	1	7	7	75	3	24	12	142	0	0
	Rhantus exsoletus	6	30	4	11	0	0	4	9	0	0	0	0	0	0
	Rhantus frontalis	1	5	2	2	1	1	0	0	0	0	0	0	0	0
	Rhantus grapii	3	10	1	1	0	0	1	1	0	0	1	1	0	0
	Rhantus latitans	1	11	0	0	0	0	0	0	1	1	0	0	0	0
	Rhantus suturalis	1	3	3	6	0	0	4	33	3	5	2	2	0	0
	Rhantus suturellus	0	0	1	1	0	0	0	0	0	0	0	0	0	0
	Acilius canaliculatus	1	2	0	0	0	0	0	0	0	0	1	2	0	0
	Acilius sulcatus	5	11	5	13	0	0	6	8	0	0	2	3	1	1
	Graphoderus cinereus	5	47	3	50	1	2	6	12	0	0	5	7	2	3
	Hydaticus seminiger	6	69	8	41	0	0	6	16	2	4	8	20	0	0
	Hydaticus transversalis	4	71	3	35	0	0	1	7	0	0	1	1	0	0
	Bidessus grossepunctatus	0	0	0	0	1	66	0	0	0	0	0	0	0	0
	Graptodytes bilineatus	1	31	0	0	0	0	0	0	0	0	1	1	0	0
	Graptodytes granularis	1	3	0	0	0	0	1	1	2	3	2	3	0	0
	Graptodytes pictus	11	375	8	89	0	0	5	8	3	11	3	3	0	0

	Hydroglyphus geminus	9	92	6	412	0	0	10	74	3	102	2	7	0	0
	Hydroporus angustatus	7	72	4	95	1	3	11	68	3	16	9	32	2	3
	Hydroporus discretus	1	1	1	1	0	0	1	1	0	0	0	0	0	0
	Hydroporus erythrocephalus	7	77	6	89	2	16	10	196	6	33	8	59	0	0
	Hydroporus gyllenhalii	5	185	5	162	0	0	7	151	0	0	0	0	0	0
	Hydroporus incognitus	7	469	6	367	0	0	11	228	1	4	3	56	0	0
	Hydroporus melanarius	3	19	1	3	0	0	1	4	0	0	0	0	0	0
	Hydroporus memnonius	7	93	5	30	0	0	6	79	2	3	2	10	0	0
	Hydroporus neglectus	5	125	5	120	0	0	5	298	0	0	2	25	0	0
	Hydroporus nigrita	1	1	0	0	0	0	0	0	0	0	1	1	0	0
	Hydroporus obscurus	1	12	3	97	0	0	2	5	0	0	0	0	0	0
	Hydroporus palustris	14	524	13	232	2	26	20	501	8	108	9	143	2	3
	Hydroporus planus	7	101	10	37	2	14	8	115	8	327	5	24	0	0
	Hydroporus striola	1	1	0	0	0	0	1	7	2	18	1	36	0	0
	Hydroporus tristis	5	173	6	193	1	5	9	77	2	2	6	18	0	0
	Hydroporus umbrosus	1	13	1	8	0	0	3	102	0	0	0	0	0	0
	Hydrovatus cuspidatus	0	0	0	0	0	0	0	0	0	0	0	0	2	5
	Hygrotus confluens	2	115	1	203	0	0	0	0	0	0	0	0	0	0
	Hygrotus decoratus	7	33	3	18	1	1	6	22	0	0	6	89	1	2
	Hygrotus impressopunctatus	1	1	3	11	0	0	5	24	3	19	3	6	0	0
	Hygrotus inaequalis	11	467	8	211	0	0	13	120	7	28	8	90	2	14
	Hygrotus versicolor	1	1	0	0	0	0	1	1	0	0	0	0	0	0
	Hyphydrus ovatus	11	136	5	244	0	0	10	40	3	6	7	10	3	5
	Nebrioporus canaliculatus	2	14	0	0	0	0	0	0	0	0	0	0	0	0
	Scarodytes halensis	3	55	3	209	0	0	0	0	1	1	0	0	0	0
	Stictotarsus duodecimpustulatus	1	2	0	0	0	0	0	0	0	0	0	0	0	0
	Laccophilus minutus	14	293	9	345	2	28	15	144	4	16	9	154	2	82
	Laccophilus poecilus	2	69	1	104	0	0	1	1	0	0	1	1	2	6
Noteridae	*Noterus clavicornis*	9	182	7	452	2	7	17	432	6	198	12	248	3	73
	Noterus crassicornis	6	239	4	390	0	0	10	654	2	168	12	280	2	32

S2.5: Spearman correlation matrix of measured water parameters

	Temperature	**pH**	**Conductivity**	**Total hardness**	**Carbonate Hardness**	**O2**	**NO2**	**Cl$^-$**
Temperature	1	0.5	0.15	0.17	0.21	0.35	-0.1	0.28
pH	0.5	1	0.56	0.42	0.63	0.42	0.16	0.59
Conductivity	0.15	0.56	1	0.65	0.8	0.21	0.4	0.81
Total hardness	0.17	0.42	0.65	1	0.81	0.02	0.1	0.6
Carbonate Hardness	0.21	0.63	0.8	0.81	1	0.13	0.23	0.72
O2	0.35	0.42	0.21	0.02	0.13	1	0.17	0.25
NO2	-0.1	0.16	0.4	0.1	0.23	0.17	1	0.33
Cl$^-$	0.28	0.59	0.81	0.6	0.72	0.25	0.33	1

S2.6: Canonical Correspondence Analysis (CCA) details

S2.6 Table 1: CCA eigenvalues and their contribution to the scaled Chi-square

	CCA1	**CCA2**	**CCA3**	**CCA4**	**CCA5**	**CCA6**	**CCA7**	**CCA8**	**CCA9**
Eigenvalue	0.6601	0.4393	0.2668	0.2236	0.21247	0.13115	0.09739	0.09234	0.05507
Proportion explained	0.303	0.2017	0.1225	0.1026	0.09755	0.06021	0.04471	0.04239	0.02528
Cumulative proportion	0.303	0.5047	0.6272	0.7299	0.8274	0.88761	0.93232	0.97472	1
	CA1	**CA2**	**CA3**	**CA4**	**CA5**	**CA6**	**CA7**	**CA8**	**CA9**
Eigenvalue	0.5993	0.56041	0.53941	0.51324	0.46909	0.43205	0.40396	0.36189	0.34231
Proportion explained	0.05189	0.04852	0.04671	0.04444	0.04062	0.03741	0.03498	0.03133	0.02964
Cumulative proportion	0.24048	0.28901	0.33571	0.38015	0.42076	0.45817	0.49315	0.52449	0.55412

S2.6 Table 2: Partitioning of scaled Chi-square

	Inertia	**Proportion**
Total	11.549	1
Constrained	2.178	0.1886
Unconstrained	9.371	0.8114

S2.6 Table 3: Variable selection results table

Df	**Nitrite**	**pH**	**Carbonate hardness**	**Oxygen saturation**	**Temperature**	**Year**	**Conductivity**	**Chloride**	**Total hardness**
F	8.0415	6.5583	3.0842	2.7437	2.2512	1.7681	3.5355	2.7339	1.7719
Significance	***	***	***	***	**	*	*	*	*

Chapter 3: Host specificity and species colouration mediate the regional decline of nocturnal moths in central European forests

This Chapter is submitted to Ecography (minor revision) as: Roth, N., Hacker, H. H., Heidrich, L., Friess, N., Garcia-Barros, E., Habel, J. C., Thorn, S., Müller, J. Host specificity and species colouration mediate the regional decline of nocturnal moths in central European forests

3.1 Summary

The high diversity of insects has limited the volume of long-term community data with a high taxonomic resolution and considerable geographic replications, especially in forests. Therefore, trends and causes of changes are poorly understood. Here we analyse trends in species richness, abundance and biomass of nocturnal macro moths in three quantitative data sets collected over four decades in forests in southern Germany. Two local data sets, one from coppiced oak forests and one from high oak forests included 125K and 48K specimens from 559 and 532 species, respectively. A third regional data set, representing all forest types in the temperate zone of Central Europe comprised 735K specimens from 848 species. Generalized additive mixed models revealed temporal declines in species richness (-36 %), abundance (-53 %) and biomass (-57 %) at the regional scale. These were more pronounced in plant host specialists and in dark coloured species. In contrast, the local coppiced oak forests showed an increase, in species richness (+60 %), while the high oak forests showed no clear trends. Left and right censoring as well as cross validation confirmed the robustness of the analyses, which led to four conclusions. First, the decline in insects appears in hyper diverse insect groups in forests and affects species richness, abundance and biomass. Second, the pronounced decline in host specialists suggests habitat loss as an important driver of the observed decline. Third, the more severe decline in dark species might be an indication of global warming as a potential driver. Fourth, the trends in coppiced oak forests indicate that maintaining complex and diverse forest ecosystems through active management may be a promising conservation strategy in order to counteract negative trends in biodiversity, alongside rewilding approaches.

3.2 Introduction

Recent studies have raised concerns about ‘insect decline’ as a worldwide phenomenon (Cardoso et al., 2020; Harvey et al., 2020; Samways et al., 2020). Insects have been shown to decrease in terms of species richness (Thomas et al., 2004a), abundance (Conrad et al., 2006), and biomass (Hallmann et al., 2017). There are indications of diversity loss in Hymenoptera (Biesmeijer et al., 2006; Potts et al., 2010), Hemiptera (Schuch, Bock, Krause, Wesche, &

Schaefer, 2011; Schuch, Wesche, & Schaefer, 2012), Coleoptera (Desender et al., 2010; Brooks et al., 2012), Diptera (Gatter et al., 2020) and Lepidoptera (Conrad et al., 2006; Habel et al., 2016b). Although many studies show that 'insect decline' is occurring, a recent review by Sánchez-Bayo & Wyckhuys (2019) predicting the extinction of 40% of the world's insect species over the next few decades raised criticism, as their approach is considered biased towards studies reporting declines and thus accused of drawing 'too alarmist' conclusions (Komonen et al., 2019). This criticism is supported by several studies showing no trends, increasing trends in insect biodiversity or positive trends for a considerable number of species (Fox et al., 2014; Boyes et al., 2019; Macgregor et al., 2019; Crossley et al., 2020). The trends of insect populations are complex and depend on the habitat types, the taxonomic group and the study sites (Shortall et al., 2009; Hallmann et al., 2018; Van Klink et al., 2020). In addition, long time-series featuring a high taxonomical resolution and a high number of replicates are lacking or neglect management gradients or certain habitats. Uncertainties about the trends in insect biodiversity have increased calls for more robust temporal data on insects, covering time spans that are relevant when investigating effects of climate change and replicated at large geographical scales (Habel et al., 2019a; Kunin, 2019; Thomas et al., 2019). Additionally, there is rising concern about the accurate analysis of time series data and monitoring schemes in general (Didham et al., 2020). Shifting or false baseline effects may lead to non-robust conclusions, especially when time series do not feature at least 10-15 individually sampled years (Fournier et al., 2019; White, 2019). Furthermore, the meta analyses of insect declines come with drawbacks such as non-standardized sampling by various entomologists and pooling of samplings at different scales. This makes the generalisability of the conclusions doubtful in certain instances (Welti et al., 2020).

Forest dwelling insect species are often thought to be less endangered, especially in Europe (Juslén et al., 2016a; Potocký et al., 2018), as forest use intensity has not changed dramatically over recent decades in central Europe compared to agriculture, with its marked increase in pesticides and fertilizers (Reif et al., 2006). Previous studies have shown stable temporal trends in woodlands for moths and other insects (Brooks et al., 2012; Hunter et al., 2014) and increasing species richness has been observed at individual locations (Thomsen et al., 2015 but see Seibold et al., 2019). Moreover, modern forestry often promotes continuous forest cover (uneven-even aged forest management), creating a stable and homogenous habitat (Schall et al., 2017). However, this homogenization of forests might come with costs in terms of habitat heterogeneity and the related biodiversity (Merckx et al., 2012a; Thorn et al., 2015), as the forest stages with the highest canopy cover are usually quite species poor (Hilmers et al., 2018). Furthermore, threats like diverging trends in phenology between hosts and pollinators or herbivores (Asch & Visser, 2007; Memmott et al., 2007), have reduced the nutritive value of the host plants due to rising CO2 levels (Lincoln et al., 1986; Cornelissen, 2011). Also, general nitrogen input and the accompanying homogenization in plants (Gilliam, 2006) are likely to affect forests in a similar fashion to open habitats (Seibold et al., 2019). Although forests are a major habitat type in Europe, general trends in the diversity of forest insects are largely unknown. So far, most quantitative long term studies on insects have been conducted in open habitats, focused on mainly open-habitat groups such as butterflies, have been based on monitoring schemes which are not habitat specific, or featured temporal extents smaller than four decades (e.g. Conrad et al., 2006; Groenendijk & Ellis, 2011; Hallmann et al., 2017, 2019; Hunter et al., 2014).

Furthermore, species traits can influence trends in insect populations, and may also lead to diverging patterns within taxa, especially if they are taxonomically rich (Stefanescu et al., 2011b; Habel et al., 2019b). Traits like large wingspans, nocturnal activity and preference for woody or herbaceous food sources have been associated with species declines in moths (Coulthard et al., 2019). More generally, species with a higher degree of feeding specialization have been shown to be more negatively affected by habitat degradation and loss because of the higher flexibility generalists show regarding their diets (Habel et al., 2016b; Coulthard et al., 2019; Wölfling et al., 2019). This makes generalists potentially more resilient to deterioration of habitat quality. Another trait which may be associated with differentiated decline/increase is colour (Zeuss et al., 2014). The variability in colour pattern is associated with niche breadth and feeding specialization (Forsman et al., 2020), whereas the colour lightness of insects exhibits patterns along thermal gradients. Thus colour lightness decreases with latitude (Zeuss et al., 2014; Pinkert et al., 2017; Heidrich et al., 2018), elevation (Xing et al., 2018; Wu et al., 2019) and from open to shaded habitats (Xing et al., 2016). Although mechanisms driving these relationships are not fully understood, the incidence suggests that lighter colouration will be favoured under climate warming (Zeuss et al., 2014).

In order to address the issue of forest insect diversity we analysed a lifework moth data set with high taxonomic resolution collected by HHH over four decades, featuring plots located in all forest types typical for Central Europe. Nocturnal moths make up 86 % of Lepidoptera in Germany (Steiner et al., 2014) and constitute a model group of insects covering a large trait space and exhibiting varying life histories. Thus, they are suitable for identifying overall, functional or lineage specific response differences. Their taxonomy is largely understood in Central Europe (Timmermans et al., 2014; Mitter et al., 2017) and there is substantial knowledge about their ecology (Potocký et al., 2018). However, while macro-moth diversity has been shown to decrease because of land use intensification, habitat loss, light pollution and climate change (Conrad et al., 2006; Merckx et al., 2012b; Fox, 2013; Mangels et al., 2017; Boyes et al., 2020), trends in forests are still unclear. We distinguished between two local scale data sets and one regional scale data set from light trapping samples, in order to analyse the temporal trends of species richness, abundance and biomass. We used left and right censoring as well as cross validation to check the robustness of the results. In addition to overall trends of species richness, abundances and biomass of macro moths, we analysed the three most abundant macro-moth families (Geometridae, Noctuidae & Erebidae) to test if (1) species richness, abundance and biomass have declined during the last four decades and whether these responses apply to all main subtaxa. Furthermore, we split the dataset into opposite halves of trait spectra (light/dark – and generalist/specialist species) to test if, (2) dark and light species and (3) feeding specialists and generalists differ in their trends.

3.3 Material and methods

3.3.1 Study area

The study area is split into three. Two core areas were sampled regularly within the study period, as well as a regional data set featuring plots across the whole German federal state of Bavaria (70,550 km²). The first core area is an oak forest characterized by a continuous coppice-with-standards management (coppicing wood-management method with several trees, which are allowed to grow bigger; subsequently named coppiced forest) and was sampled in 23 years from 1979 to 2018 (see also Fig. 3.1). Within an area of approximately 1 km radius, eight plots were sampled on a total of 283 plot dates. The minimum number of resamplings per plot was nine, the maximum was 80 resamplings. The second core area is an oak high forest (subsequently named high forest), which was sampled in 18 years from 1979 to 2018. Within an area of approximately 200 m radius, nine plots were sampled on 118 plot dates. The minimum number of resamplings per plot was 7, the maximum was 36. At the regional scale, all forest types typical for Central Europe (for details on forest types see Hacker & Müller, 2006; Hacker & Müller, 2009; Müller, 2005) were sampled on 531 plots in 41 years spanning 1978 to 2018 and an elevational range from 210 to 1740 m a.s.l. Ninety-eight of the plots were sampled only once, 50 twice. The maximum number of resamplings on one plot was 62. In total we analysed 2806 sample dates at the regional scale.

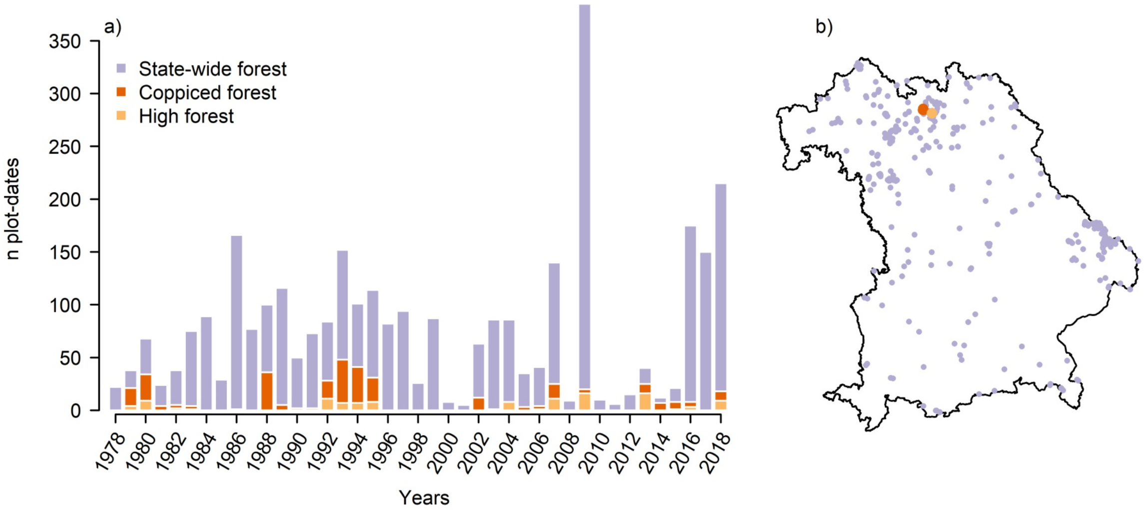


Fig. 3.1: Sum of trapping nights per plot and year split according to the three analysed data sets (a), and plot locations within the federal state of Bavaria, Germany (b).

3.3.2 Moth sampling and classification

Moths were collected using light traps equipped with super-actinic ultraviolet light tubes mounted above plastic funnels for one full night per sampling. The attracted moths were collected in plastic containers at the bottom of the traps and killed with chloroform (Müller et al., 2012). All moth specimens were counted and identified by HHH, if necessary by examining genital preparations, following the higher-rank taxonomy by Zahiri et al. (2013) for the Noctuoidea. We used only data on macro moths for this study, for which all families were completely determined in all years. We analysed the data across all species (overall), and for Geometridae, Noctuidae, and Erebidae (including Acrtiinae and Lymantriinae) separately, as these were the most abundant families. We separated all the species into different subsets (light coloured or dark coloured and dietary specialist or generalist) to create groups for which species richness trends could be compared. We grouped all species into two classes of food specialisation with monophagous and oligophagous species (feeding on one or a few plant species) as a proxy for host specialists and polyphagous species as a proxy for host generalists, based on the classification by Hacker & Müller (2006). Information about host specificity was available for 785 of the 861 species sampled. We excluded species without information on host specificity from the respective analyses. We assessed species colour lightness by analysing photos extracted from Segerer & Hausmann (2011) with an Epson Perfection V33 scanner (48 bits depth of colour). We removed the background and converted the images to eight-bit grey values (mean of the red green and blue values) following the protocol of Zeuss et al. (2014), and scaled colour lightness from zero (completely black) to one (completely white) using the software package ‘png’ (Urbanek, 2013). We used the full dorsal surface area of the body and wings to calculate the colour lightness of species (see Heidrich et al., 2018). We then separated species into light and dark according to the grey values, to estimate if trends in species richness are affected by colour lightness. Species above the median were categorized as “light” species and species below as “dark” species. We chose this dichotomous approach to be able to analyse this trait in the same way as host specialization. Information about colour lightness was available for 853 of the total 861 sampled species. We excluded species without information on colour lightness from the respective analyses.

3.3.3 Statistical methods

We excluded 34 plot-dates on which only one species was sampled (numbers above refer to cleaned data). All statistical analyses were performed using R (version 3.5.2). We predicted the biomass of each sample using a model based on data published by García-Barros (2015). We modelled the dry weight as a function of the total area (mm^2) of the moth species reported by García-Barros (2015), using the ‘lm’ function from the ‘stats’ package (R Core Team, 2018). Based on this model, we then predicted the biomass of each species in our data set using the ‘predict’ function from the ‘stats’ package (see Supporting Information S3.1 for details). For each sample, we added up the biomass of all species, multiplied by its respective number of individuals.

In order to account for nonlinear predictors (e.g. season and space), we used generalized additive mixed models (GAMMs; Wood, 2004) to model species richness (e.g. the raw species number, negative binomial error-term), abundance (negative binomial error-term), and biomass (gaussian error-term), per plot and trapping night as dependent variables. We used the 'gam' function in the package 'mgcv' (Wood, 2017) to model the dependent variables as a function of the year (as a numerical variable for all groups and additionally as a factor for overall species richness, abundance, and biomass), season (calendar day) and elevation as well as latitude and longitude for the regional dataset. Latitude and longitude, and the season were included as smoothed variables (basis functions: splines on the sphere for latitude and longitude and cubic regression splines for the season; dimensions were set to default); plot id was included in the models as a random factor to account for replicated measurements on the same plot. We excluded latitude, longitude and elevation from the local models due to limited variation.

We predicted species richness, abundance and biomass using the 'predict.gam' function in the 'mgcv' package for each year between 1978 and 2018, in order to illustrate the results (Wood, 2017). Latitude, longitude and elevation (regional data set only) as well as day of the year and the plot-id were set to null in the predictions in order to generate species richness, abundance and biomass trends independent of these variables. In order to test for robustness of the models we conducted left and right censoring as well as a cross validation of the models (Didham et al., 2020). For the left censoring models were recalculated by progressively removing the early time points from the data set until the year 2008 (Fournier et al., 2019). For the right censoring the latest years were progressively removed until the year 1988. For cross-validation models were calculated with only odd or even years, respectively. After prediction of species richness, abundance, and biomass for the odd and even years, respectively, we calculated Pearson correlations between predicted and observed values.

We determined species richness, abundance (total number of specimens) and biomass per plot-date for light/dark and specialist/generalist species (subsequently called groups) and subsequently calculated GAMMs as described above with the group as an additional factor and an interaction term between group and years. We identified the group specific effects of the year and tested for significant interactions between groups.

3.4 Results

At the local scale, 125,078 specimens (mean 441.9 per sample, range 10–10,599) belonging to 559 macro-moth species (mean 49.6 per sample, range 6–164) in the coppiced forest and 58,270 specimens (mean 493.8 per sample, range 30–2,932) belonging to 532 macro-moth species (average 61.8 per sample, range 12–133) in the high forest, were recorded. At the regional scale 735,483 (average 262.1 per sample, range 2–7,321) belonging to 848 macro-moth species (average 37.9 per sample, range 2–176) were sampled in the state-wide forests, over the whole sampling period. Nine macro-moth families (Geometridae and Noctuidae being richest in specimens and species) were collected; 43,261 specimens from 260 species and 40,867 from 204 species, for Geometridae and Noctuidae, respectively were collected in the coppiced forest; 20,937 specimens from 212 species and 27,014 from 201 species, for Geometridae and Noctuidae, respectively in the high forest. At the regional scale 329,592 Geometridae specimens from 338 species and 200,506 Noctuidae specimens from 334 species were sampled in state-wide forests at the regional scale. The Erebidae family was the third group, which we analysed separately. 26,117/5,321/130,833 specimens from 54/49/79 species were obtained from the coppiced, high, and state-wide forests, respectively.

We found that the season (day of the year, Fig. 3.2b), and space (latitude/longitude) were significantly correlated with species richness, abundance and biomass at the regional scale and at the local scale (season only) (Fig. 3.2 & Table 3.1) except for Noctuidae biomass in the high forest (Supporting Information S3.2 and S3.3). In state-wide forests we found elevation to have a significant negative effect on overall species richness (Table 3.1), and on Geometridae, Erebidae and Erebidae abundance and biomass (Supporting Information S3.3).

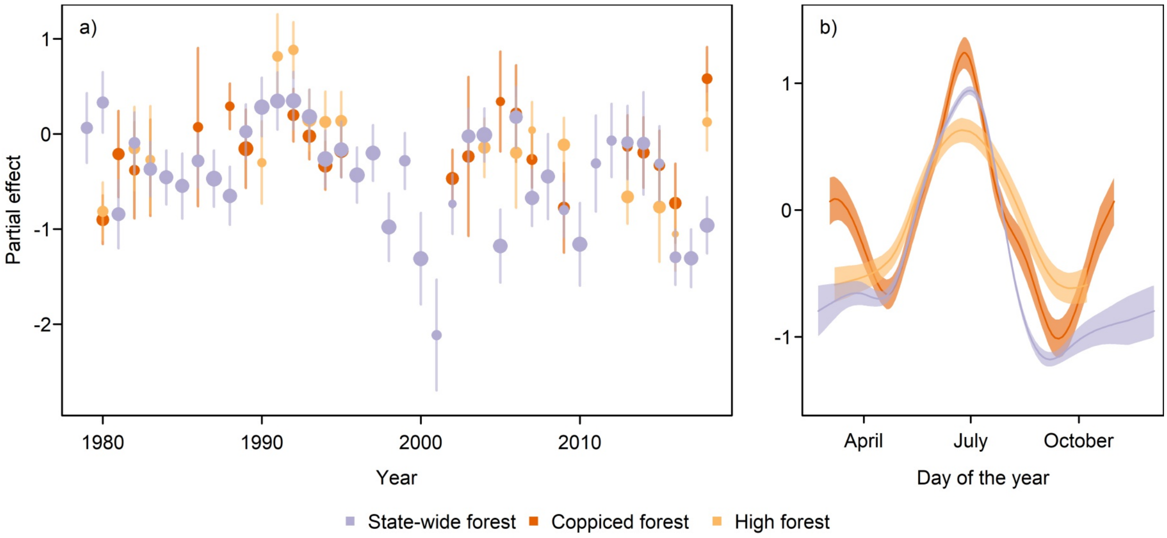


Fig. 3.2: Partial effects the variable year scaled as a factor (a) and the season (b, day of the year as continuous variable) on the biomass. Colours indicate the three data sets. See Supporting Information S3.4 for raw data.

3.4.1 Long-term trend of macro moth diversity and biomass

We found pronounced temporal fluctuation (not the overall temporal trend) in species richness, abundance and biomass (Fig. 3.2a, Supporting Information S3.4). This fluctuation was consistent throughout the three datasets. Time as a linear predictor had a significant negative effect on the overall number of macro-moth species in the state-wide forests at the regional scale. We detected an overall decrease in species richness of 0.9 % per year (predicted values decreased by 36 % from 1978 to 2018, see Supporting Information S5) and abundance and biomass decreases of 1.3% and 1.4% per year, respectively (53% and 57% decrease over four decades, respectively Fig. 3.3b&c & Table 3.1). The decline in species richness, abundances and biomass in the state-wide forests affected Noctuidae the most followed by Geometridae. Erebidae showed a positive, significant temporal trend for all three biodiversity measures (Supporting Information S3.3).

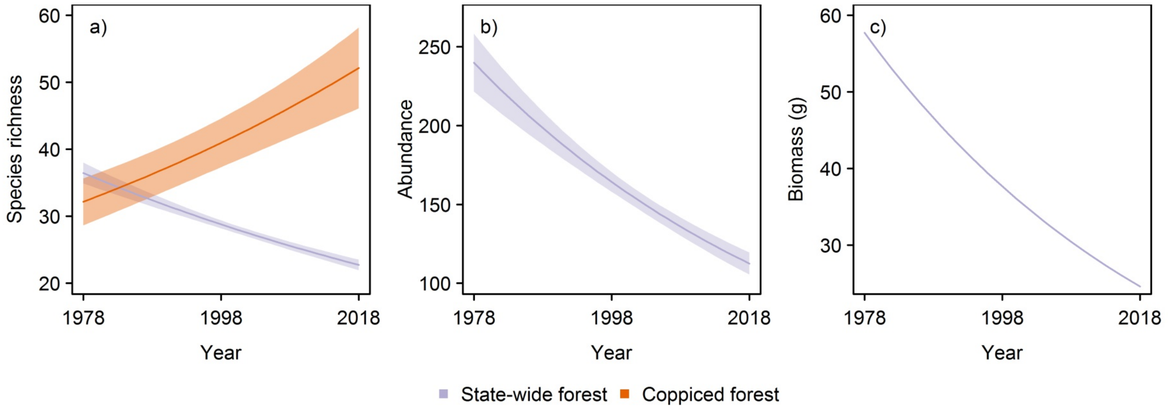


Fig. 3.3: Trends of species richness (a), abundance (b) and biomass (c) between 1978 and 2018 at the local (coppiced forest) and regional scale (state-wide forest). The lines are based on predictions of the original models. Only significant trends are shown.

Table 3.1: Effect sizes of parametric and smoothed terms of GAMs for the state-wide (left), the coppiced (middle) and the high forest (right). Significances are indicated with * = <0.05, ** = <0.005, *** = <0.001; not significant where not indicated.

State-wide forest				**Coppiced forest**			**High forest**			
Species richness										
	Estimate	z/F value		Estimate	z/F value		Estimate	z/F value		
Intercept	27.22	8.35	***	-20.41	-2.98	***	-0.48	-0.06		
Year	-0.01	-7.24	***	0.01	3.52	***	0	0.56		Parametric
Elevation	0	-4.04	***							Parametric
Season	7.29	4308.46	***	5.84	791.08	***	5.53	382.87	***	Smoothed
lat/lon	18.93	1593.56	***							Smoothed
Abundance										
	Estimate	z/F value		Estimate	t/F value		Estimate	z/F value		
Intercept	43.05	7.34	***	3.99	0.31		39.75	1.63		
Year	-0.02	-6.47	***	0	0.14		-0.02	-1.38		Parametric
Elevation	0	-0.96								Parametric
Season	7.4	2160.57	***	7.17	274.48	***	4.56	132.41	***	Smoothed
lat/lon	22.12	2259.99	***							Smoothed
Biomass										
	Estimate	t/F value		Estimate	t/F value		Estimate	t/F value		
Intercept	51.11	7.89	***	4.59	0.33		35.07	1.47		
Year	-0.02	-6.6	***	0	0.31		-0.01	-1.08		Parametric
Elevation	0	-1.78								Parametric
Season	7.34	224.88	***	6.68	26.39	***	4.07	12.68	***	Smoothed
lat/lon	22.62	26.96	***							Smoothed

At the local scale we detected an increase in species richness of 1.5% per year (60 % increase over four decades) on coppiced plots from 1978 – 2018 (Fig. 3.3a & Table 3.1). The species richness of all families (Geometridae, Noctuidae, Erebidae) increased significantly over time on coppiced forest plots, while only Erebidae increased in species richness and biomass in the high forest (Supporting Information S3.3).

Left censoring showed the robustness of these results as the trends were constant in the state-wide forests for species richness (Fig. 3.4). Increases in species richness in coppiced forest were apparent until the removal of the sampling years up to the 1990s. In the high forest negative trends of abundance and biomass became apparent on removing the first three sampling years. Also, within the separately analysed families the trends were generally robust (Supporting Information S3.6). However, left censoring indicated that the positive trends in Erebidae species richness, abundance and biomass, in the high forest, and species richness of Geometridae in the coppiced forest, were due to the first decade in the data set. (Supporting Information S3.6). Major deviations from the reported overall pattern were detected when excluding sampling years before 2003 (Fig. 3.4 light grey line). Right censoring showed that leaving out the years after 2005 would lead to non-significant trends or less pronounced trends (Supporting Information S3.6). When all recent years until 1995 were removed, it resulted in the same patterns as with complete time-series data. Cross-validation showed that the predicted values correlate well with the measured ones especially at the regional scale at the order level (Supporting Information S3.6). Species richness was predicted most accurately, while the strength of the correlations was partly weak (e.g. biomass and abundance predictions for single families at the regional level).

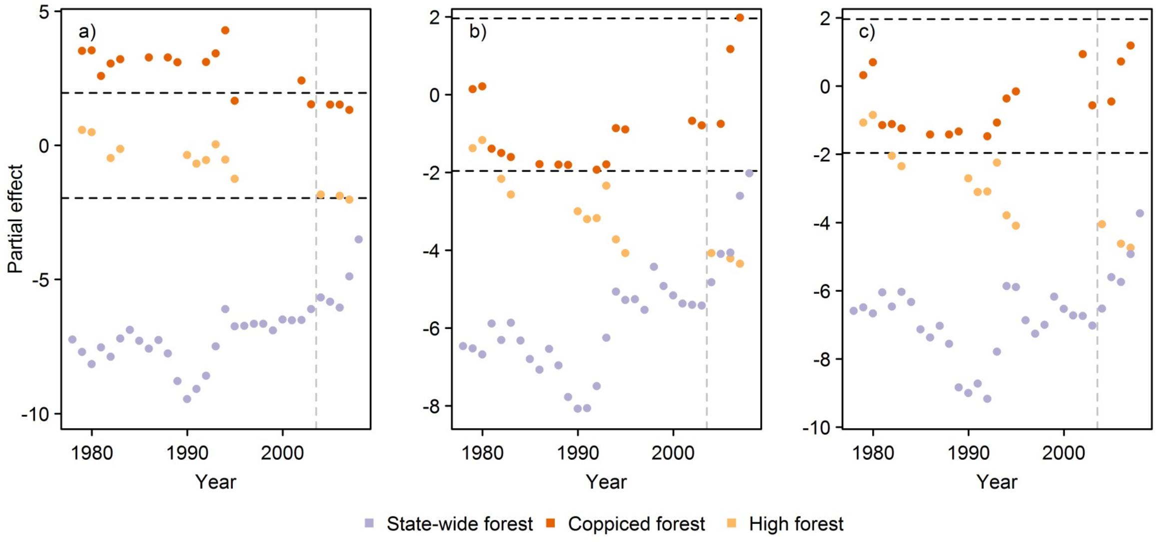


Fig. 3.4: Left censoring of overall data (subsequent removal of the oldest year in the data set, and recalculation of the model), species richness (a), abundance (b) and biomass (c). Dashed black lines indicate significance threshold. The dashed grey line indicates subsets spanning less than 15 years, which may reduce the reliability of trend.

3.4.2 Association between species colouration, host specialisation and long-term trend

In the state-wide forests at the regional scale overall species richness, abundance and biomass decreased for dark and light species (Table 3.2). However, the species richness, abundance, and biomass of dark moths decreased significantly more than those of light moths. In the coppiced forest, we found increases in species richness in both light and dark groups, with no significant differences between the two functional groups (Table 3.2). In the high forest only the abundance of dark species decreased significantly.

In the state-wide forests at the regional scale, species richness, abundance and biomass of specialist species declined significantly, but not those of generalist species (Table 3.2). In the coppiced forest, species richness of generalists and specialists increased with no significant difference between the two groups (Table 3.2). In high forest only the abundance of specialists decreased significantly.

Table 3.2: Partial effects of interaction terms of between dark/light and generalist/specialist species richness (negative binomial error distribution), abundance (negative binomial error distribution), biomass (gaussian error distribution) and the year, of GAMs calculated with the state-wide forest data set. Significances are indicated with * = <0.05, ** = <0.005, *** = <0.0001. Significant differences between the groups dark/light and generalists/specialists are indicated in grey.

	State-wide forest				**Coppiced forest**				**High forest**		
Color											
Species richness											
Interaction	Estimate	z/F value			Estimate	z/F value			Estimate	z/F value	
dark	-0.01	-7.89	***	dark	0.01	3.62	***	dark	0	0.1	
light	-0.01	-3.56	***	light	0.01	3.73	***	light	0	0.83	
Abundance											
Interaction	Estimate	z/F value			Estimate	z/F value			Estimate	z/F value	
dark	-0.02	-8.31	***	dark	0	0.65		dark	-0.03	-2.04	*
light	-0.01	-4.15	***	light	-0.01	-0.88		light	-0.02	-1.54	
Biomass											
Interaction	Estimate	t/F value			Estimate	t/F value			Estimate	t/F value	
dark	-0.02	-7.67	***	dark	0.01	0.96		dark	-0.02	-1.27	
light	-0.01	-4.61	***	light	0	0.36		light	-0.01	-0.73	
Feeding guild											
Species richness											
Interaction	Estimate	z/F value			Estimate	z/F value			Estimate	z/F value	
generalists	0	-0.99		generalists	0.01	3.75	***	generalists	0	1.09	
specialists	-0.01	-8.07	***	specialists	0.01	3.44	***	specialists	0	0.33	
Abundance											
Interaction	Estimate	z/F value			Estimate	z/F value			Estimate	z/F value	
generalists	0	0.69		generalists	0	0.04		generalists	-0.02	-1.09	
specialists	-0.03	-8.64	***	specialists	-0.01	-1.35		specialists	-0.03	-2.19	*
Biomass											
Interaction	Estimate	t/F value			Estimate	t/F value			Estimate	t/F value	

3.5 Discussion

We found temporal fluctuation in species richness, abundance and biomass comparable to the fluctuations found in other insect biomass studies in Europe (Fig. 3.2a, Supporting Information S3.2) (Hallmann et al., 2017; Macgregor et al., 2019). The decline in insect biomass in northern Germany from the mid-nineties to the year 2000 and the peaks after the year 2000 (2005/2006, 2011/2013) (Hallmann et al., 2017) match the patterns we found particularly closely. Similarly, the decline in biomass from the late 1970s to present (Fig. 3.2) matches the gradual decline observed in moth biomass in Great Britain forests (Macgregor et al., 2019). Fluctuations and tipping points of trends were also reflected in left and right censoring. There was a peak in species richness, abundance and biomass around 1990 at the regional scale as subsets excluding the sampling years before showed the steepest decline across the left-censoring (Fig. 3.4). Left-censoring also indicates that the increase in species richness in the coppiced forest happened before the year 2000. The non-significant trends of abundance and biomass in the high forest become negative on removing the early sampling years from the analyses. This suggests an increase until the early eighties followed by a decrease (see also Macgregor et al. 2019) and possibly a trend which is more strongly negative than the overall analyses suggests. However, we also found that the annual linear decline in moth biomass, of 1.3% within the sampled forests, did not occur in such drastic rates as those noted for Malaise traps sampled in open habitats (i.e. 6.1% in Hallmann et al. 2017) but was more pronounced than in moth biomass in forested habitat in Great Britain (i.e. 0.4 % from 9 plots in Macgregor et al., 2019). However, Macgregor et al. (2019) found biomass to decrease more steeply in grasslands than in woodlands. This might be due to the fact that nocturnal moths in general did not show such a drastic decline as Diptera or Hymenoptera sampled predominantly with Malaise traps. This is supported by Macgregor et al. (2019) who found only a gradual decline with phases of net gains in moth biomass over the past 50 years (Macgregor et al., 2019). This may also be linked to a higher resilience of forests in comparison to open lands where intensification including inputs of pesticides, mowing, and fertilizers are higher (Simon-Delso et al., 2017), and to the fact that forest may moderate responses to climate warming due to a microclimate buffered significantly by the canopy cover (Frenne et al., 2013). In a direct comparison, Seibold et al (2019) also observed a steeper decline in insects in grasslands than in forests over one decade.

As species richness, abundance and biomass decreased at comparable magnitudes at the regional scale, this is an indication that the reported declines in biomass (Hallmann et al., 2017; Macgregor et al., 2019) might also mirror declines in species richness of insects (see also Seibold et al., 2019). In the forests at the regional scale we found a decline in moth richness in line with previous studies (Conrad et al., 2006; Groenendijk & Ellis, 2011; Van Langevelde et al., 2018). The possible reasons for biodiversity declines are manifold, including climate change, light pollution, habitat loss and combinations of both (Fox, 2013; Boyes et al., 2020). Rising

CO2 levels and changing air quality can lead to reduced nutritive value in leaves and thus negatively influence herbivore diversity (Lincoln et al., 1986; Cornelissen, 2011; Pescott et al., 2015) through a higher mortality rate (Fajer, 1989; Stiling et al., 2003). Also, differing changes in phenology between host and herbivores might result in a biodiversity decrease (Asch & Visser, 2007; Memmott et al., 2007). In woodlands, the degradation of the structural complexity and the preference for closed canopy in silviculture (Vilén et al., 2012, see below) have been discussed as possible factors driving population and species losses of Lepidoptera (Jeffries et al., 2006; Hilmers et al., 2018). However, there is an increasing number of studies showing constant diversity across recent decades (Crossley et al., 2020; Van Klink et al., 2020). Note that in contrast to numerous case studies, it is often meta-analyses, which report constant or increasing trends in insect communities. However, these studies tend to assemble data on a multitude of taxa, sampled on different scales, with inconsistent sampling of the different habitats (Welti et al., 2020). This might be a reason for undirected trends and conclusions which might not apply generally. In this study we cannot rule out that the different results at the regional and the local scales are partly due to the difference in sampling intensity per plot (Weiser et al., 2019; Wainwright et al., 2020). However, we analysed data from one taxon sampled only in forested habitats over a long time span. This should assure a certain degree of reliability of the trends we report. Different results at the regional and the local scales can also be due to the scale itself, as regional species richness is not only a product of α-diversity, but also of β-diversity (Chase et al. 2019).

3.5.1 Effects of habitat structure and silvicultural practices on moth communities

We observed stable moth diversity in oak high forest plots and increasing species richness in coppice with standards plots. The latter forest management type has already been shown to be beneficial to common but declining species (Merckx et al., 2012a). It implies the regular creation of gaps which undergo succession until trees are cut down again after 20 – 30 years. This is in contrast to most other forests in our study region that are kept in an optimum phase with continuous forest cover and thus feature less dynamics (Villén et al 2012). This lack of dynamics in forests may be one reason why these forest types cannot compensate for habitat alteration leading to subsequent species losses through, for example, nitrogen input (De Schrijver et al., 2011) and/or insecticides. The observed increase in insect biodiversity in coppice with standards may be connected to the expansion of range sizes of species from lower latitudes (Pateman et al., 2012). However, it is most likely a combination of temperature rise, which enables warm adapted and non-forest species to colonize the area, and the positive effects of the successional mosaic, which outweigh regional, negative effects in our coppice with standards plots. In order to corroborate these indications, broader scale analyses of differences in diversity trends with different management techniques would be necessary.

We also found the Erebidae to thrive at a regional scale in the regional data set with the present forestry practice. This may be due to the Lymantriinae (Erebidae) subfamily, which harbours several pest species (e.g. *L. dispar*, *L. monacha*), some of which have increased significantly in population over recent decades (Klapwijk et al., 2013). This is in line with other pest species which are increasing as a consequence of global warming (Klapwijk et al., 2013; Seidl et al., 2014; Seidl & Rammer, 2017; Thompson et al., 2017). Our finding on Erebidae found broad support in the long-term data from different habitats in Great Britain (Macgregor et al., 2019). In Macgregor et al (2019), Erebidae were the only group increasing in biomass since the 1980ies. This might be an indication of a general pattern in Erebidae in Europe, although further analyses would be needed in order to confirm this.

3.5.2 Association between host specialisation and long-term trend

Habitat loss and degradation have negative effects on Lepidoptera diversity, especially on species dependent on a restricted number of host species (Stefanescu et al., 2011a). The general declines found in our data are most pronounced in specialist species which is in line with other recent studies on Lepidoptera (Stefanescu et al., 2011a; Habel et al., 2016b, 2019c; Wölfling et al., 2019). Beyond the faster decline of specialists, we found that generalists typically increased in diversity, abundance, and biomass. This will lead to a major shift in community composition, as shown by Habel et al., (2016, 2019b) at one site over 200 years for butterflies and three decades for moths, in addition to the stated loss of macro-moth diversity. This tendency is possibly caused by a homogenization of forest vegetation (Keith et al., 2009; Dirnböck et al., 2014) which is partly due to nitrogen input (De Schrijver et al., 2011) and increasingly homogenous canopy densities resulting from increasing growing stock (Schelhaas et al., 2003). In our study, however, the local data indicated either no change for specialists or generalists (oak high forest), or an increase in both groups on coppice with standards plots. Thus, there seem to be certain forest types where specialists survive or increase. Nonetheless, note that forest specialists remain vulnerable especially because of intense forest fragmentation (Slade et al., 2013).

3.5.3 Association between colour lightness and long-term trend

Climate change may impact species population dynamics and survival if ambient temperatures approach thermal thresholds of species' climate niches. We found dark species to decline faster than light ones, which is in line with ecological findings that the expected climate change favours light coloured insects (Zeuss et al., 2014). Furthermore, this matches the colour distribution of insects at broader elevational and geographical scales (Bässler et al., 2013; Pinkert et al., 2017; Heidrich et al., 2018; Wu et al., 2019), though the mechanisms remain unclear for nocturnal insects. Thus, we hypothesize that light colouration is beneficial for forest dwelling moths under the current development of the climate, although factors other than temperature may have a bearing on driving colour trends. These might include passive defence against visual predators (e.g. background matching, Kettlewell, 1959; Wilson et al., 2001) and unexpected consequences due to pleiotropism in the induction of pigment production

(Dubovskiy et al., 2013; Roulin, 2014). However, we detected differences between the richness of light and dark species in the state-wide forests predominantly at the regional scale, which means the differences in these trait trends seem to be detectable only at a broad scale.

3.5.4 Implications for conservation and prospects

The diversity responses of hyperdiverse taxa over time and to changes in the environment are complex, habitat dependent and scale dependent. Our data set indicates that insect decline also occurs in these insect groups in forests, supporting the recent findings by Seibold et al. (2019) over the last decade for other insects. A more pronounced loss of habitat specialists and dark species indicates that, similarly to open land, habitat loss and temperature effects due to global warming are potentially the main drivers of loss in forests. However, we would like to stress that in practice these drivers act differently in forest than in open land. While open land is especially affected by direct effects of pesticides and intensification (Simon-Delso et al., 2017), habitat loss in the forest is most probably mediated by indirect effects of, for example, nitrogen input and changes in microclimates (De Schrijver et al., 2011). The same applies to global warming (see above).

The increasing biodiversity in coppice with standards forests shows that forest landscapes with a high diversity of tree species and succession stages are still able to buffer negative trends. This is especially interesting in the light of increasing disturbance intensities (Seidl et al., 2014), which create heterogeneous patterns in landscapes, which in turn increase biodiversity (Beudert et al., 2015) Coppicing might be a way to emulate natural disturbance in order to maintain diversities. Note that rewilding and the abandonment of management may be alternative or complementary approaches to create structural heterogeneity in forests for insect conservation (Müller et al., 2010; Merckx & Pereira, 2015; Dantas de Miranda et al., 2019).

We finally note that all our data are observational data collected over long periods. Although we have accounted for the season and the geographic location, the whole study area was not sampled constantly throughout the sampling years. Cross validation also showed that predictions for the odd and the even years was generally good but not always as accurate as desirable ($R^2 << 0.5$, Supporting Information S3.6). This is possibly due to the fluctuating nature of the samplings, i.e. samplings did not follow a regular sampling scheme on all plots. However, left-censoring (Didham et al., 2020) showed that the trends are nevertheless quite robust when some sampling years were removed subsequently starting with the oldest (Fig. 3.4). Right-censoring showed the importance of the latest three to five sampling years identifying the significant trends we report. We conclude that although the sampling design has its flaws, the analyses and the reported results are robust. However, in order to develop evidence-based conservation strategies in forests under a changing climate, we need more evidence from spatially and temporally replicated silviculture-biodiversity experiments.

3.6 Appendix

Supporting Information Appendix S3.1:

Based on data of 375 macro-moth species provided by EGB we calculated the total area of the moths by multiplication of abdomen length with abdomen width and thorax length with thorax width. We added both of these measures to twice the forewing area and twice the hind wing area. We subsequently modelled the area as a function of the dry-weight of the moths as a linear model (see Table and Figure below).

Table S3.1-1: Moth area as a function of dry-weight model output. Adjusted R^2 was 0.91

Term	Estimate	Std.error	Statistic	p-value
Intercept	-5.075	0.137	-37.036	<0.001
log(AREA)	1.386	0.025	56.233	<0.001

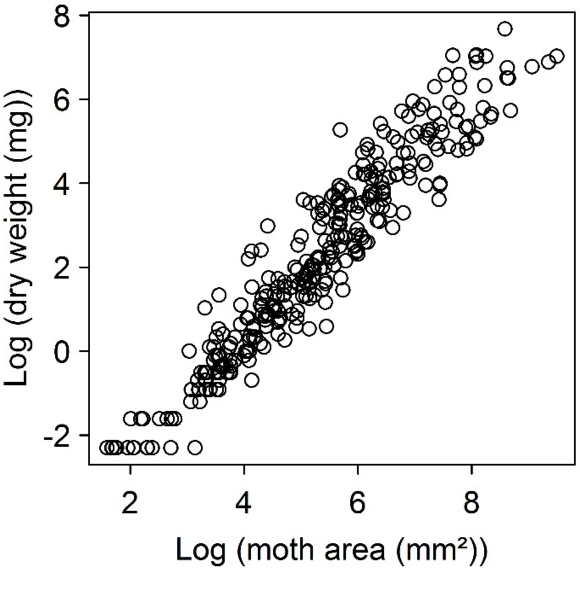


Figure S3.1-1: Logarithms of Moth dry-weight plotted against area

We calculated the area of the moths in our data set based on pixels, using the scanned images (see main manuscript for details). We then predicted moth biomass based on the linear model above, using the areas of the species we used in our data set. We used the 'predict' function from the 'stats' package.

Supporting Information Appendix S3.2:

Interaction terms output for gams including subgroups, light and dark species, and specialists and generalists. Table S3.2-1 shows the output for the dark and light species, table S3.2-2 for the generalists and specialists. We used the following formulas for the locals data sets:

Species richness ~ smoothed(day) + group + group:year + random factor(plot id)

Abundance ~ smoothed(day) + group + group:year + random factor(plot id)

Biomass ~ smoothed(day) + group + group:year + random factor(plot id)

We used the following formulas for the regional data set:

Species richness ~ smoothed(day) + elevation + smoothed(Lon/Lat) + group + group:year + random factor(plot id)

Abundance ~ smoothed(day) + elevation + smoothed(Lon/Lat) + group + group:year + random factor(plot id)

Biomass ~ smoothed(day) + elevation + smoothed(Lon/Lat) + group + group:year + random factor(plot id)

Method was "REML" family negative binomial for species richness and abundance and gaussian for biomass. If there was significant results in one of the groups we calculated an additional model with a "*" interaction to check where there was a significant difference between the groups. Marked in grey below.

Table S3.2-1: Model outputs for dark and light colored species.

State-wide forest

	Species richness				**Abundance**				**Biomass**			
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	28.04	3.19	8.8	<0.001	51.74	5.71	9.06	<0.001	56.86	6.41	8.87	<0.001
Elevation	0	0	-3.36	<0.001	0	0	-0.81	0.42	0	0	-1.78	0.08
Guild [light]	-13.86	2.29	-6.05	<0.001	-23.62	4.07	-5.81	<0.001	-19.94	4.78	-4.17	<0.001
Guild [dark] : year	-0.01	0	-7.89	<0.001	-0.02	0	-8.31	<0.001	-0.02	0	-7.67	<0.001
Guild [light] : year	-0.01	0	-3.56	<0.001	-0.01	0	-4.15	<0.001	-0.01	0	-4.61	<0.001
	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	F	p-value
Day	7.48	8	8534.4	<0.001	7.57	8	3955.76	<0.001	7.52	8	460.76	<0.001
Lon/Lat	20.07	49	7303.36	<0.001	20.25	49	6590.86	<0.001	19.68	49	83.73	<0.001
Plot ID	366.65	529	1810.67	<0.001	366.22	529	2031.04	<0.001	343.79	529	3.05	<0.001

Coppiced forest

	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	-20.71	6.56	-3.16	<0.001	-3.16	12.74	-0.25	0.8	-5.18	13.97	-0.37	0.71
Guild [light]	-0.58	6.8	-0.09	0.93	19.21	13.03	1.47	0.14	8.17	14.62	0.56	0.58
Guild [dark] : year	0.01	0	3.62	<0.001	0	0.01	0.65	0.52	0.01	0.01	0.96	0.34
Guild [light] : year	0.01	0	3.73	<0.001	-0.01	0.01	-0.88	0.38	0	0.01	0.36	0.72

	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	F	p-value
Day	6.56	8	1444.29	<0.001	7.47	8	485.84	<0.001	7.12	8	46.39	<0.001
Plot ID	6.42	7	103.12	<0.001	6.46	7	77.7	<0.001	6.12	7	7.82	<0.001
High forest												
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	2.5	8.58	0.29	0.77	59.37	26.47	2.24	0.02	40.12	24.86	1.61	0.11
Guild [light]	-6.39	7.31	-0.87	0.38	-13.11	13.44	-0.98	0.33	-13.52	15.09	-0.9	0.37
Guild [dark] : year	0	0	0.1	0.92	-0.03	0.01	-2.04	0.04	-0.02	0.01	-1.27	0.21
Guild [light] : year	0	0	0.83	0.41	-0.02	0.01	-1.54	0.12	-0.01	0.01	-0.73	0.47
	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	F	p-value
Day	6.1	8	554.88	<0.001	6.1	8	554.88	<0.001	4.73	8	20.25	<0.001
Plot ID	4.94	8	22.32	<0.001	4.94	8	22.32	<0.001	6.21	8	8.52	<0.001

Table S3.2-2: Model outputs for specialist and generalist species.

	Species richness				Abundance				Biomass			
State-wide forest												
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	5.39	3.27	1.65	0.1	-0.14	5.94	-0.02	0.98	14.26	6.41	2.23	0.03
Elevation	0	0	-3.81	<0.001	0	0	-1.39	0.17	0	0	-1.41	0.16
Guild [specialists]	23.11	2.37	9.73	<0.001	56.15	4.22	13.31	<0.001	55.22	4.86	11.35	<0.001
Guild [generalists] : year	0	0	-0.99	0.32	0	0	0.69	0.49	0	0	-1.13	0.26
Guild [specialists] : year	-0.01	0	-8.07	<0.001	-0.03	0	-8.64	<0.001	-0.03	0	-9.62	<0.001
	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	F	p-value
Day	7.57	8	8041.78	<0.001	7.57	8	8041.78	<0.001	7.64	8	430.92	<0.001
Lon/Lat	20.56	49	5370.47	<0.001	20.56	49	5370.47	<0.001	22.95	49	61.86	<0.001
Plot ID	356.87	529	1634.93	<0.001	356.87	529	1634.93	<0.001	324.67	529	2.52	<0.001
Coppiced forest												
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	-23.99	6.96	-3.45	<0.001	3.71	13.2	0.28	0.78	-14.55	15.11	-0.96	0.34
Guild [specialists]	5.85	7	0.84	0.4	19.53	13.54	1.44	0.15	29.54	15.79	1.87	0.06

Guild [generalists] : year	0.01	0	3.75	<0.001	0	0.01	0.04	0.97	0.01	0.01	1.44	0.15
Guild [specialists] : year	0.01	0	3.44	<0.001	-0.01	0.01	-1.35	0.18	0	0.01	-0.42	0.67
	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	F	p-value
Day	6.54	8	1253.9	<0.001	7.51	8	650.15	<0.001	6.9	8	49.17	<0.001
Plot ID	6.34	7	88.38	<0.001	6.5	7	76.23	<0.001	6.26	7	8.66	<0.001
High forest												
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	-7.12	8.78	-0.81	0.42	35.58	28.5	1.25	0.21	29.72	26.98	1.1	0.27
Guild [specialists]	8.3	7.6	1.09	0.27	32.72	13.32	2.46	0.01	24.66	15.09	1.63	0.1
Guild [generalists] : year	0	0	1.09	0.28	-0.02	0.01	-1.09	0.28	-0.01	0.01	-0.81	0.42
Guild [specialists] : year	0	0	0.33	0.74	-0.03	0.01	-2.19	0.03	-0.02	0.01	-1.68	0.09
	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	F	p-value
Day	5.83	8	490.29	<0.001	5.93	8	267.01	<0.001	5.28	8	23.01	<0.001
Plot ID	4.7	8	19.27	<0.001	6.76	8	116.25	<0.001	6.4	8	9.42	<0.001

Supporting Information Appendix S3.3:

Complete results of GAMMs where we set the year as a numeric variable. Figure S3.3-1 shows the partial effect of the year on biomass, abundance and Species richness. Effect sizes of parametric and smoothed terms are shown in tables S3.3 1-3. We used the following formulas for the locals data sets:

Species richness ~ smoothed(day) + year + random factor(plot id)

Abundance ~ smoothed(day) + year + random factor(plot id)

Biomass ~ smoothed(day) + year + random factor(plot id)

We used the following formulas for the regional data set:

Species richness ~ smoothed(day) + elevation + smoothed(Lon/Lat) + year + random factor(plot id)

Abundance ~ smoothed(day) + elevation + smoothed(Lon/Lat) + year + random factor(plot id)

Biomass ~ smoothed(day) + elevation + smoothed(Lon/Lat) + year + random factor(plot id)

Method was “REML” family negative binomial for species richness and abundance and gaussian for biomass

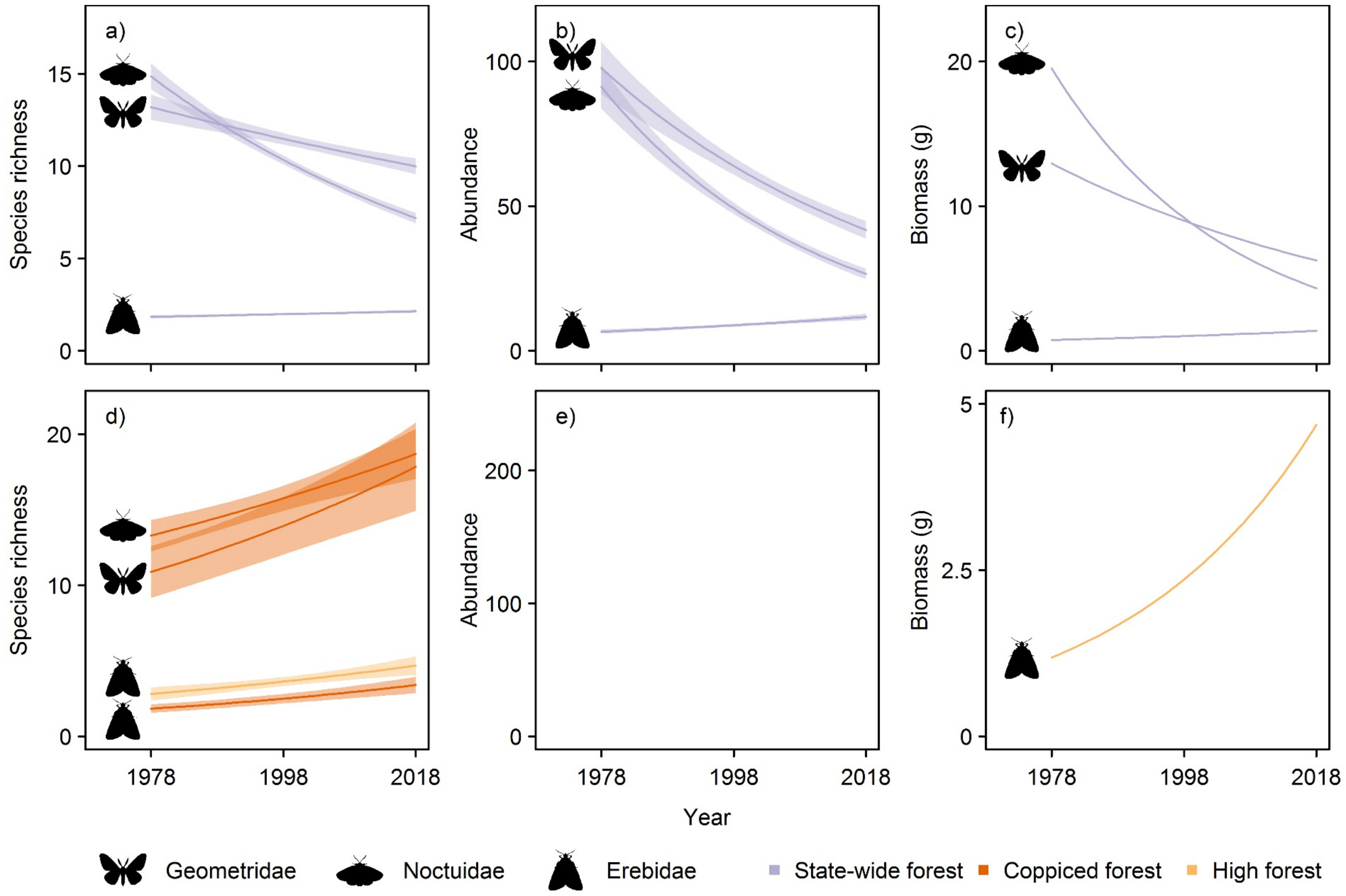


Figure S3.3-2: Development of species richness (a,d) abundances (b,e) and biomass (c,f) per family for regional (a-c) and local (d-f) data sets.

Table S3.3-1: Effect sizes and significances of parametric and smoothed terms of GAMMs for the state-wide forests.

		Geometridae				**Noctuidae**				**Erebidae**			
Species richness		Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
	(Intercept)	16.61	3.95	4.21	<0.001	38.62	3.66	10.54	<0.001	-5.8	3.62	-1.6	0.11
	Year	-0.01	0	-3.53	<0.001	-0.02	0	-9.93	<0.001	0	0	2.13	0.03
	Elevation	0	0	-2.98	<0.001	0	0	0.16	0.8	0	0	-12.99	<0.001
		edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
	Season	7.31	8	4235.62	<0.001	7.74	8	2064.28	<0.001	7.22	8	2989.16	<0.001
	Lon/Lat	18.91	49	2938.24	<0.001	21.08	49	1237.96	<0.001	20.93	49	1004.11	<0.001
	Plot ID	322.95	529	1129.78	<0.001	249.66	529	710.59	<0.001	231.37	529	553.19	<0.001
Abundance													
		Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
	(Intercept)	46.68	6.92	6.75	<0.001	65.29	6.42	10.16	<0.001	-24.64	8.53	-2.89	<0.001
	Year	-0.02	0	-6.16	<0.001	-0.03	0	-9.63	<0.001	0.01	0	3.39	<0.001
	Elevation	0	0	-0.15	0.88	0	0	1.74	0.08	0	0	-9.19	<0.001
		edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
	Season	7.53	8	2353.06	<0.001	7.79	8	918.42	<0.001	7.43	8	2991.11	<0.001
	Lon/Lat	13.03	49	2456.16	<0.001	28.83	49	1439.15	<0.001	29.43	49	1307.29	<0.001
	Plot ID	330.68	529	1361.14	<0.001	239.78	529	672.44	<0.001	261.69	529	760.48	<0.001

Biomass

	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	43.6	10.13	4.3	<0.001	81.82	7.93	10.32	<0.001	-24.64	8.53	-2.89	<0.001
Year	-0.02	0.01	-3.61	<0.001	-0.04	0	-9.52	<0.001	0.01	0	3.39	<0.001
Elevation	0	0	-1.45	0.15	0	0	1.45	0.15	0	0	-9.19	<0.001
	edf	Ref.df	F	p-value	edf	Ref.df	F	p-value	edf	Ref.df	Chi.sq	p-value
Season	7.31	8	209.85	<0.001	7.73	8	82.77	<0.001	7.43	8	2991.11	<0.001
Lon/Lat	21.28	49	33.75	<0.001	17.48	49	8.05	<0.001	29.43	49	1307.29	<0.001
Plot ID	286.82	529	1.74	<0.001	199.23	529	0.85	<0.001	261.69	529	760.48	<0.001

Table S3.3-2: Effect sizes and significances of parametric and smoothed terms of GAMMs for the coppiced forest.

		Geometridae				**Noctuidae**				**Erebidae**			
Species richness		Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
	(Intercept)	-22.08	8.39	-2.63	0.01	-14.32	6.45	-2.22	0.03	-30.02	9.31	-3.22	<0.001
	Year	0.01	0	2.94	<0.001	0.01	0	2.65	0.01	0.02	0	3.32	<0.001
		edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
	Season	6.46	8	795.63	<0.001	7.14	8	306.46	<0.001	6.1	8	550.71	<0.001
	Plot ID	6.4	7	90.84	<0.001	4.46	7	15.54	<0.001	5.88	7	39.03	<0.001
Abundance													
		Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
	(Intercept)	4.52	15.57	0.29	0.77	-8.3	12.96	-0.64	0.52	-20.04	22.4	-0.89	0.37
	Year	0	0.01	0	1	0.01	0.01	1	0.32	0.01	0.01	1.03	0.3
		edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
	Season	7.19	8	257.71	<0.001	7.6	8	232.78	<0.001	7.56	8	862.94	<0.001
	Plot ID	6.03	7	62.3	<0.001	4.94	7	17.7	<0.001	6.08	7	34.32	<0.001

Biomass

	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	z value	p-value
(Intercept)	-7.39	18.5	-0.4	0.69	3.72	16.51	0.23	0.82	-20.04	22.4	-0.89	0.37
Year	0.01	0.01	0.8	0.43	0	0.01	0.23	0.81	0.01	0.01	1.03	0.3
	edf	Ref.df	F	p-value	edf	Ref.df	F	p-value	edf	Ref.df	Chi.sq	p-value
Season	7.19	8	30.55	<0.001	7.08	8	16.55	<0.001	7.56	8	862.94	<0.001
Plot ID	5.73	7	6.02	<0.001	4.74	7	2.43	<0.001	6.08	7	34.32	<0.001

Table S3.3-3: Effect sizes and significances of parametric and smoothed terms of GAMMs for the high forest.

		Geometridae				Noctuidae				Erebidae			
Species richness		Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
	(Intercept)	-2.87	9.96	-0.29	0.77	4.97	8.46	0.59	0.56	-24.22	11.81	-2.05	0.04
	Year	0	0	0.6	0.55	0	0	-0.22	0.82	0.01	0.01	2.16	0.03
		edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
	Season	6.01	8	326.07	0	4.5	8	137.88	0	5.45	8	200.78	0
	Plot ID	3.83	8	11.51	0	3.75	8	8.87	0.02	3.52	8	10.74	0
Abundance													
		Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
	(Intercept)	35.74	29.79	1.2	0.23	30.52	21.65	1.41	0.16	-48.06	30.26	-1.59	0.11
	Year	-0.02	0.01	-1.03	0.3	-0.01	0.01	-1.17	0.24	0.03	0.02	1.68	0.09
		edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
	Season	6.29	8	307.04	0	3.84	8	20.74	0	6.06	8	254.95	0
	Plot ID	6.05	8	58.25	0	4.96	8	22.49	0	4.79	8	20.76	0

Biomass

	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	z value	p-value
(Intercept)	44.23	33.86	1.31	0.19	27.64	19.28	1.43	0.15	-48.06	30.26	-1.59	0.11
Year	-0.02	0.02	-1.07	0.29	-0.01	0.01	-1.01	0.32	0.03	0.02	1.68	0.09

	edf	Ref.df	F	p-value	edf	Ref.df	F	p-value	edf	Ref.df	Chi.sq	p-value
Season	4.53	8	10.69	0	1.74	8	0.54	0.07	6.06	8	254.95	0
Plot ID	4.96	8	2.9	0	0.84	8	0.13	0.29	4.79	8	20.76	0

Supporting Information Appendix S3.4: Raw data plots and complete results of GAMMs with year as a factor

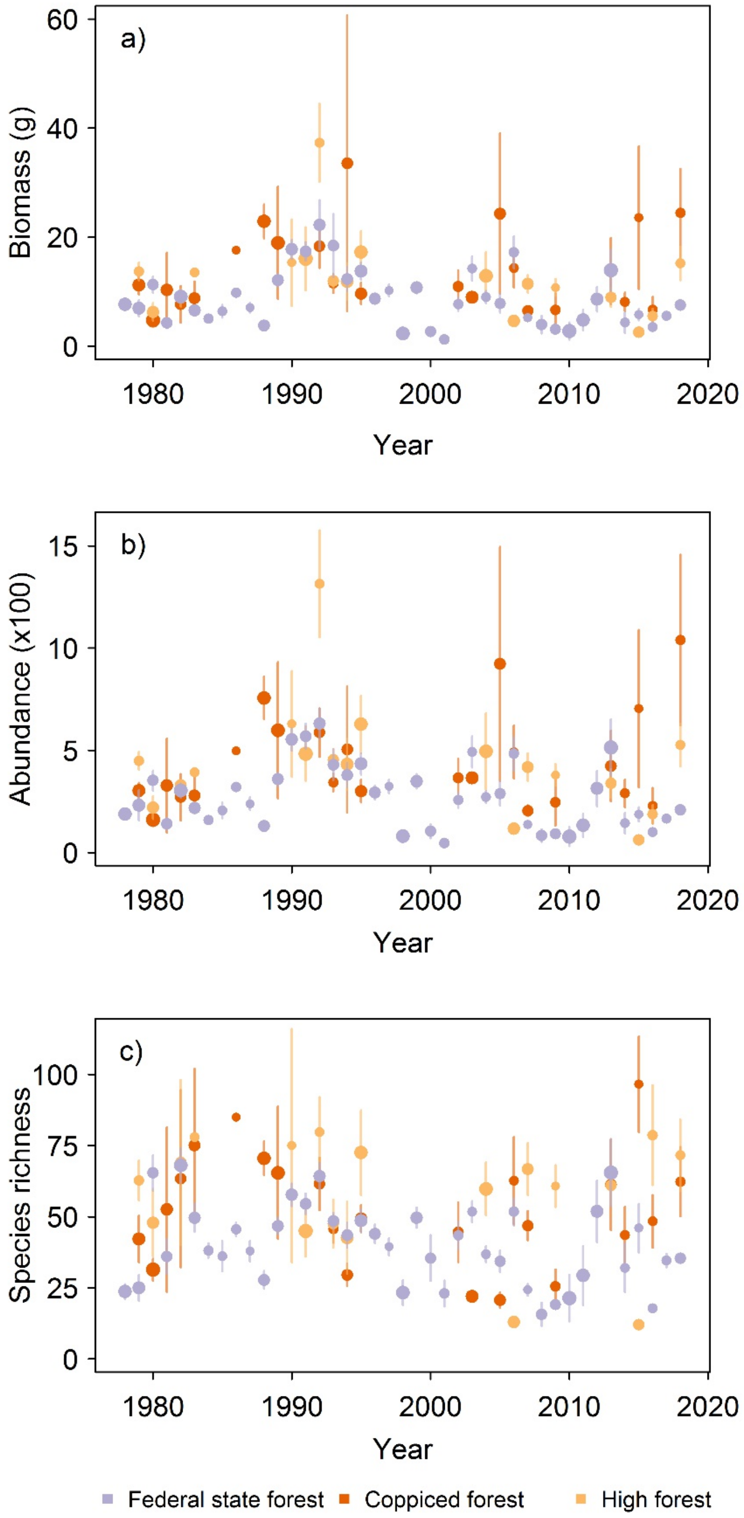


Figure S3.2-1: Raw values of biomass (a), abundance (b) and species richness per plot and year with standard errors.

Complete results of GAMMs where we set the year as a factor. Figure S3.2-1 shows the partial effect of the year as a factor on species richness, abundance and biomass. Effect sizes of parametric and smoothed terms are shown in tables S3.2 1-3. We used the following formulas for the locals data sets:

Species richness ~ smoothed(day) + year + random factor(plot id)

Abundance ~ smoothed(day) + year + random factor(plot id)

Biomass ~ smoothed(day) + year + random factor(plot id)

We used the following formulas for the regional data set:

Species richness ~ smoothed(day) + elevation + smoothed(Lon/Lat) + year + random factor(plot id)

Abundance ~ smoothed(day) + elevation + smoothed(Lon/Lat) + year + random factor(plot id)

Biomass ~ smoothed(day) + elevation + smoothed(Lon/Lat) + year + random factor(plot id)

Method was "REML" family negative binomial for species richness and abundance and gaussian for biomass.

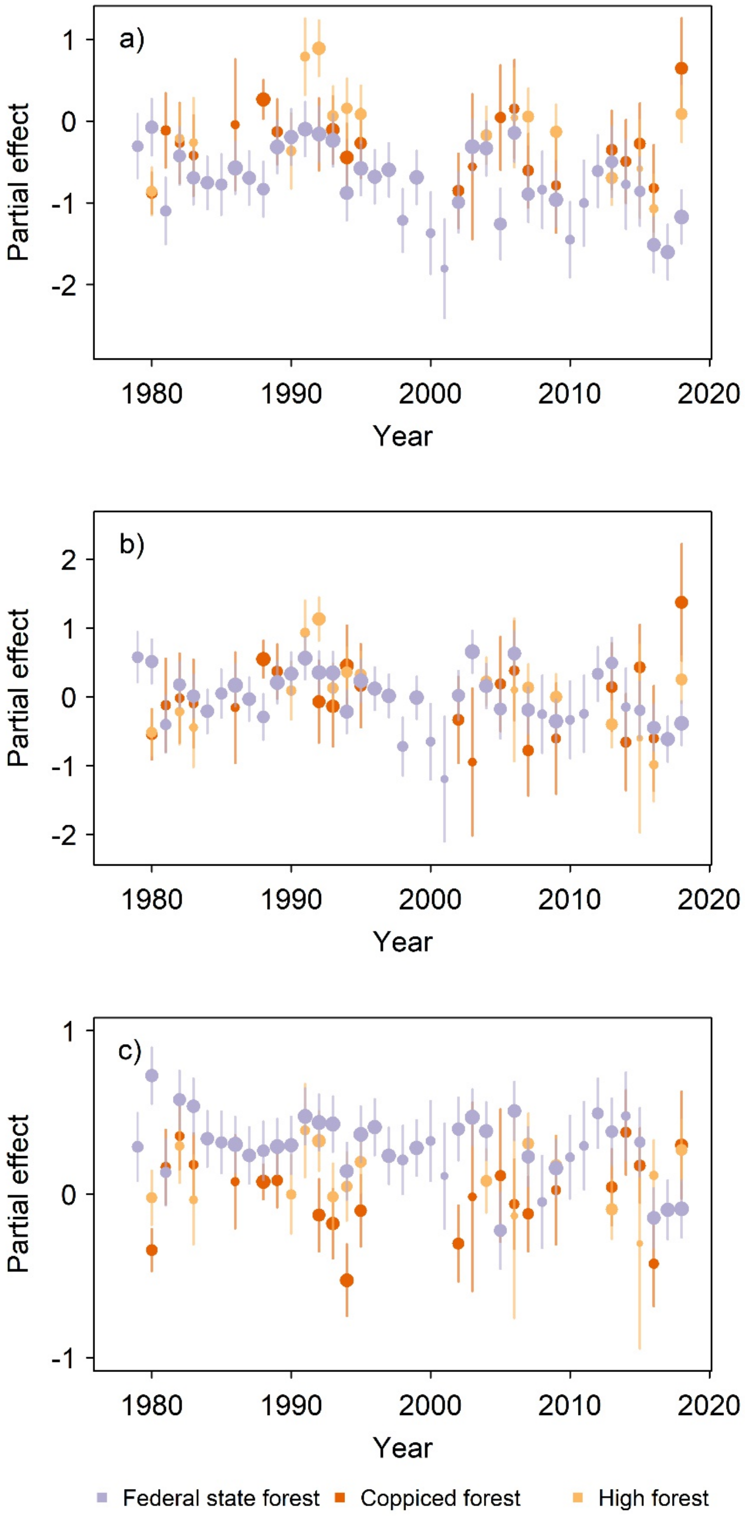


Figure S3.2-3: Partial effect of the year as a factor for biomass (a) abundance (b) and species richness (c)

Table S3.2-1: Effect sizes and significances of parametric and smoothed terms of biomass GAMMs for the coppiced, the high forest and the state-wide forest.

	State-wide forest				**Coppiced forest**				**High forest**			
	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value	Estimate	Std. Error	t value	p-value
(Intercept)	8.96	0.29	30.77	<0.001	9.29	0.2	45.94	<0.001	9.3	0.26	36.27	<0.001
Year 1979	0.06	0.37	0.17	0.87								
Year 1980	0.33	0.32	1.04	0.3	-0.9	0.26	-3.52	<0.001	-0.81	0.3	-2.69	0.01
Year 1981	-0.84	0.36	-2.35	0.02	-0.21	0.45	-0.47	0.64				
Year 1982	-0.09	0.32	-0.3	0.77	-0.38	0.51	-0.76	0.45	-0.15	0.44	-0.35	0.72
Year 1983	-0.37	0.29	-1.29	0.2	-0.36	0.51	-0.7	0.48	-0.27	0.56	-0.48	0.63
Year 1984	-0.46	0.28	-1.61	0.11								
Year 1985	-0.55	0.34	-1.6	0.11								
Year 1986	-0.28	0.28	-1	0.32	0.07	0.83	0.09	0.93				
Year 1987	-0.47	0.3	-1.59	0.11								
Year 1988	-0.65	0.3	-2.14	0.03	0.29	0.24	1.2	0.23				
Year 1989	0.02	0.29	0.08	0.94	-0.16	0.41	-0.38	0.7				
Year 1990	0.28	0.31	0.92	0.36					-0.3	0.43	-0.7	0.49
Year 1991	0.35	0.3	1.15	0.25					0.81	0.44	1.84	0.07
Year 1992	0.35	0.3	1.15	0.25	0.2	0.28	0.7	0.48	0.88	0.29	3	<0.001
Year 1993	0.18	0.29	0.63	0.53	-0.03	0.24	-0.11	0.91	0.15	0.32	0.46	0.65
Year 1994	-0.26	0.3	-0.89	0.37	-0.34	0.25	-1.33	0.18	0.12	0.32	0.39	0.7

Year 1995	-0.17	0.29	-0.56	0.57	-0.18	0.28	-0.65	0.52	0.13	0.31	0.44	0.66
Year 1996	-0.43	0.29	-1.49	0.14								
Year 1997	-0.2	0.29	-0.68	0.49								
Year 1998	-0.98	0.36	-2.75	0.01								
Year 1999	-0.28	0.29	-0.97	0.33								
Year 2000	-1.31	0.48	-2.73	0.01								
Year 2001	-2.12	0.58	-3.63	<0.001								
Year 2002	-0.74	0.31	-2.36	0.02	-0.47	0.3	-1.55	0.12				
Year 2003	-0.02	0.29	-0.08	0.93	-0.24	0.84	-0.28	0.78				
Year 2004	-0.01	0.28	-0.04	0.97					-0.15	0.31	-0.48	0.64
Year 2005	-1.18	0.38	-3.08	<0.001	0.34	0.53	0.65	0.52				
Year 2006	0.17	0.32	0.54	0.59	0.21	0.51	0.42	0.67	-0.2	0.58	-0.34	0.73
Year 2007	-0.67	0.3	-2.27	0.02	-0.27	0.29	-0.92	0.36	0.04	0.3	0.13	0.9
Year 2008	-0.45	0.45	-1	0.32								
Year 2009	-0.8	0.29	-2.8	0.01	-0.78	0.47	-1.65	0.1	-0.12	0.28	-0.41	0.69
Year 2010	-1.16	0.43	-2.68	0.01								
Year 2011	-0.31	0.51	-0.62	0.54								
Year 2012	-0.07	0.39	-0.18	0.86								
Year 2013	-0.09	0.39	-0.24	0.81	-0.14	0.33	-0.41	0.68	-0.66	0.28	-2.34	0.02
Year 2014	-0.1	0.54	-0.19	0.85	-0.2	0.37	-0.53	0.6				
Year 2015	-0.31	0.39	-0.79	0.43	-0.33	0.37	-0.91	0.37	-0.77	0.58	-1.34	0.18

Year 2016	-1.3	0.29	-4.45	<0.001	-0.73	0.42	-1.75	0.08	-1.05	0.39	-2.73	0.01
Year 2017	-1.31	0.3	-4.3	<0.001								
Year 2018	-0.96	0.3	-3.24	<0.001	0.58	0.33	1.74	0.08	0.13	0.3	0.42	0.68
Elevation	0	0	-2.26	0.02								
	edf	Ref.df	F	p-value	edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
Season	7.19	8	146.62	<0.001	6.65	8	18.24	<0.001	4.47	8	12.68	<0.001
Lon/Lat	38.32	49	5.37	<0.001								
Plot ID	0	1	0	0.53	0.86	1	6.03	0.01	0	0	Inf	1

Table S3.2-2: Effect sizes and significances of parametric and smoothed terms of abundance GAMMs for the coppiced, the high forest and the state-wide forest.

	State-wide forest				**Coppiced forest**				**High forest**			
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
(Intercept)	5.49	0.25	21.96	<0.001	5.96	0.18	32.54	<0.001	5.94	0.26	22.6	<0.001
Year 1979	0.63	0.31	2	0.05								
Year 1980	0.62	0.27	2.26	0.02	-0.68	0.23	-2.95	<0.001	-0.59	0.3	-1.98	0.05
Year 1981	-0.16	0.31	-0.53	0.59	-0.37	0.41	-0.89	0.37				
Year 1982	-0.03	0.27	-0.13	0.9	-0.22	0.46	-0.48	0.63	-0.05	0.43	-0.1	0.92
Year 1983	-0.19	0.25	-0.78	0.44	-0.27	0.46	-0.58	0.56	-0.43	0.56	-0.77	0.44
Year 1984	-0.22	0.24	-0.89	0.37								
Year 1985	-0.24	0.29	-0.82	0.41								
Year 1986	0	0.24	-0.02	0.99	-0.16	0.75	-0.21	0.83				
Year 1987	-0.16	0.25	-0.63	0.53								
Year 1988	-0.33	0.26	-1.28	0.2	0.43	0.22	1.97	0.05				
Year 1989	0.21	0.25	0.86	0.39	0.07	0.37	0.19	0.85				
Year 1990	0.45	0.26	1.7	0.09					0	0.43	0.01	0.99
Year 1991	0.64	0.26	2.51	0.01					0.87	0.44	1.99	0.05
Year 1992	0.51	0.26	1.96	0.05	0.42	0.25	1.69	0.09	1	0.29	3.46	<0.001
Year 1993	0.42	0.24	1.7	0.09	0.17	0.22	0.78	0.44	0.38	0.31	1.2	0.23
Year 1994	-0.03	0.25	-0.13	0.9	0.01	0.23	0.04	0.97	0.27	0.32	0.84	0.4

Year 1995	0.33	0.25	1.3	0.19	0.1	0.25	0.4	0.69	0.22	0.3	0.74	0.46
Year 1996	0	0.25	0.01	0.99								
Year 1997	0.1	0.25	0.41	0.68								
Year 1998	-0.79	0.31	-2.57	0.01								
Year 1999	-0.01	0.25	-0.04	0.97								
Year 2000	-0.75	0.41	-1.82	0.07								
Year 2001	-1.63	0.5	-3.26	<0.001								
Year 2002	-0.35	0.27	-1.31	0.19	0.1	0.27	0.35	0.73				
Year 2003	0.57	0.25	2.29	0.02	-0.33	0.75	-0.44	0.66				
Year 2004	0.16	0.24	0.66	0.51					0.05	0.3	0.17	0.87
Year 2005	-0.64	0.33	-1.92	0.05	0.68	0.47	1.44	0.15				
Year 2006	0.47	0.27	1.73	0.08	0.43	0.46	0.94	0.34	-0.41	0.58	-0.72	0.47
Year 2007	-0.41	0.25	-1.6	0.11	-0.27	0.27	-1.03	0.3	0.08	0.29	0.28	0.78
Year 2008	-0.51	0.38	-1.33	0.18								
Year 2009	-0.56	0.24	-2.31	0.02	-0.6	0.43	-1.4	0.16	-0.04	0.28	-0.15	0.88
Year 2010	-1.01	0.37	-2.7	0.01								
Year 2011	0.14	0.43	0.32	0.75								
Year 2012	0.21	0.33	0.63	0.53								
Year 2013	0.37	0.33	1.12	0.26	0.09	0.3	0.28	0.78	-0.5	0.28	-1.79	0.07
Year 2014	-0.12	0.46	-0.27	0.79	0.06	0.33	0.18	0.86	-1	0.58	-1.72	0.09
Year 2015	-0.15	0.34	-0.44	0.66	-0.01	0.33	-0.04	0.97	-1.04	0.38	-2.73	0.01

Year 2016	-0.71	0.25	-2.83	<0.001	-0.68	0.38	-1.82	0.07				
Year 2017	-1.05	0.26	-4.01	<0.001								
Year 2018	-0.75	0.25	-2.94	<0.001	0.92	0.3	3.05	<0.001	0.24	0.3	0.81	0.42
Elevation	0	0	-1.11	0.27								
	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
Season	7.29	8	1371.99	<0.001	7.28	8	203.52	<0.001	4.94	8	111.64	<0.001
Lon/Lat	40.1	49	304.26	<0.001								
Plot ID	0	1	0	0.77	0.92	1	11.45	<0.001	0	1	0	0.59

Table S3.2-3: Effect sizes and significances of parametric and smoothed terms of species richness GAMs for the coppiced, the high forest and the state-wide forest.

	State-wide forest				**Coppiced forest**				**High forest**			
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
(Intercept)	3.5	0.15	23.73	<0.001	3.8	0.1	37.9	<0.001	3.88	0.16	23.91	<0.001
Year 1979	0.44	0.19	2.34	0.02								
Year 1980	0.86	0.16	5.39	<0.001	-0.22	0.13	-1.75	0.08	-0.09	0.17	-0.51	0.61
Year 1981	0.24	0.18	1.31	0.19	0.16	0.22	0.72	0.47				
Year 1982	0.59	0.16	3.69	<0.001	0.28	0.24	1.14	0.25	0.33	0.24	1.34	0.18
Year 1983	0.44	0.15	3.01	<0.001	0.21	0.24	0.87	0.38	-0.05	0.3	-0.18	0.86
Year 1984	0.34	0.14	2.34	0.02								
Year 1985	0.28	0.17	1.6	0.11								
Year 1986	0.24	0.14	1.7	0.09	0.18	0.38	0.46	0.65				
Year 1987	0.2	0.15	1.31	0.19								
Year 1988	0.17	0.15	1.12	0.26	0.13	0.12	1.12	0.26				
Year 1989	0.35	0.15	2.41	0.02	0.04	0.2	0.2	0.84				
Year 1990	0.44	0.15	2.85	<0.001					-0.07	0.24	-0.28	0.78
Year 1991	0.54	0.15	3.55	<0.001					0.41	0.25	1.63	0.1
Year 1992	0.49	0.15	3.19	<0.001	0.1	0.14	0.74	0.46	0.27	0.16	1.68	0.09
Year 1993	0.47	0.14	3.22	<0.001	0.03	0.12	0.22	0.83	0.04	0.18	0.24	0.81
Year 1994	0.22	0.15	1.43	0.15	-0.36	0.13	-2.81	<0.001	0	0.18	0.01	0.99

Year 1995	0.39	0.15	2.65	0.01	0.11	0.13	0.8	0.43	0.15	0.17	0.87	0.38
Year 1996	0.33	0.15	2.27	0.02								
Year 1997	0.25	0.15	1.7	0.09								
Year 1998	0.02	0.18	0.11	0.91								
Year 1999	0.35	0.15	2.33	0.02								
Year 2000	0.16	0.24	0.66	0.51								
Year 2001	-0.11	0.3	-0.36	0.72								
Year 2002	0.17	0.16	1.08	0.28	-0.01	0.15	-0.1	0.92				
Year 2003	0.46	0.15	3.14	<0.001	0.22	0.43	0.52	0.61				
Year 2004	0.35	0.14	2.48	0.01					0.07	0.17	0.39	0.7
Year 2005	-0.39	0.19	-2.05	0.04	0.26	0.27	0.98	0.33				
Year 2006	0.52	0.16	3.23	<0.001	0.14	0.24	0.57	0.57	-0.26	0.41	-0.63	0.53
Year 2007	0.09	0.15	0.62	0.54	0.23	0.14	1.6	0.11	0.36	0.16	2.17	0.03
Year 2008	-0.07	0.24	-0.31	0.76								
Year 2009	0.01	0.15	0.09	0.93	0.17	0.24	0.73	0.47	0.18	0.16	1.15	0.25
Year 2010	-0.03	0.23	-0.13	0.89								
Year 2011	0.5	0.26	1.95	0.05								
Year 2012	0.61	0.19	3.14	<0.001								
Year 2013	0.51	0.19	2.64	0.01	0.27	0.16	1.66	0.1	-0.12	0.16	-0.77	0.44
Year 2014	0.65	0.27	2.4	0.02	0.57	0.18	3.12	<0.001				
Year 2015	0.53	0.2	2.69	0.01	0.26	0.17	1.52	0.13	-0.36	0.41	-0.88	0.38

Year 2016	-0.3	0.15	-2.05	0.04	-0.27	0.2	-1.33	0.18	0.08	0.21	0.4	0.69
Year 2017	-0.22	0.15	-1.46	0.15								
Year 2018	-0.07	0.15	-0.47	0.64	0.39	0.16	2.4	0.02	0.24	0.17	1.47	0.14
Elevation	0	0	-5.31	<0.001								
	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
Season	7.18	8	2905.59	<0.001	5.79	8	504.69	<0.001	5.35	8	334.49	<0.001
Lon/Lat	36.2	49	234.91	<0.001	0.9	1	8.54	<0.001	0	1	0	0.11
Plot ID	0	1	0	0.77								

Supporting Information Appendix S3.5: Predicted values

Predicted values of species richness, abundance and biomass gained using the ‘predict.gam’ function for each year between 1978 and 2018. Predictions were based on the model described in the methods section, but with latitude, longitude and elevation (regional data set only) as well as day of the year and the plot-id set to null.

Table S3.5-1: Predicted values for the regional data set (stade-wide forests).

	Species richness			**Abundance**			**Biomass [g]**		
Year	**Value**	**±**	**SE**	**Value**	**±**	**SE**	**Value**	**±**	**SE**
1978	36.45	±	1.54	239.86	±	18.33	8.66	±	0.08
1979	36.02	±	1.47	235.36	±	17.39	8.64	±	0.08
1980	35.60	±	1.41	230.95	±	16.48	8.62	±	0.08
1981	35.18	±	1.34	226.62	±	15.61	8.60	±	0.08
1982	34.77	±	1.28	222.37	±	14.77	8.58	±	0.07
1983	34.36	±	1.22	218.21	±	13.97	8.55	±	0.07
1984	33.96	±	1.16	214.12	±	13.20	8.53	±	0.07
1985	33.56	±	1.10	210.10	±	12.47	8.51	±	0.06
1986	33.17	±	1.05	206.16	±	11.77	8.49	±	0.06
1987	32.78	±	0.99	202.30	±	11.10	8.47	±	0.06
1988	32.40	±	0.94	198.51	±	10.47	8.45	±	0.06
1989	32.02	±	0.90	194.79	±	9.88	8.43	±	0.05
1990	31.64	±	0.85	191.13	±	9.32	8.40	±	0.05
1991	31.27	±	0.81	187.55	±	8.80	8.38	±	0.05
1992	30.90	±	0.77	184.04	±	8.31	8.36	±	0.05
1993	30.54	±	0.73	180.59	±	7.86	8.34	±	0.05
1994	30.18	±	0.70	177.20	±	7.46	8.32	±	0.05
1995	29.83	±	0.67	173.88	±	7.09	8.30	±	0.04
1996	29.48	±	0.64	170.62	±	6.76	8.28	±	0.04
1997	29.13	±	0.62	167.42	±	6.47	8.26	±	0.04
1998	28.79	±	0.60	164.28	±	6.23	8.23	±	0.04
1999	28.46	±	0.58	161.20	±	6.02	8.21	±	0.04
2000	28.12	±	0.57	158.18	±	5.86	8.19	±	0.04
2001	27.79	±	0.56	155.22	±	5.74	8.17	±	0.04
2002	27.47	±	0.56	152.31	±	5.65	8.15	±	0.04
2003	27.15	±	0.56	149.45	±	5.60	8.13	±	0.04
2004	26.83	±	0.56	146.65	±	5.58	8.11	±	0.04
2005	26.51	±	0.57	143.90	±	5.60	8.08	±	0.04
2006	26.20	±	0.57	141.21	±	5.63	8.06	±	0.04
2007	25.90	±	0.59	138.56	±	5.69	8.04	±	0.04
2008	25.59	±	0.60	135.96	±	5.77	8.02	±	0.05
2009	25.29	±	0.61	133.41	±	5.86	8.00	±	0.05
2010	25.00	±	0.63	130.91	±	5.97	7.98	±	0.05
2011	24.70	±	0.65	128.46	±	6.09	7.96	±	0.05
2012	24.41	±	0.66	126.05	±	6.21	7.94	±	0.05
2013	24.13	±	0.68	123.69	±	6.34	7.91	±	0.06
2014	23.85	±	0.70	121.37	±	6.47	7.89	±	0.06
2015	23.57	±	0.72	119.09	±	6.60	7.87	±	0.06
2016	23.29	±	0.74	116.86	±	6.74	7.85	±	0.06
2017	23.02	±	0.76	114.67	±	6.87	7.83	±	0.07
2018	22.75	±	0.78	112.52	±	7.01	7.81	±	0.07

Table S3.5-2: Predicted values for the local data set (coppiced forest).

	Species richness			**Abundance**			**Biomass [g]**		
Year	**Value**	**±**	**SE**	**Value**	**±**	**SE**	**Value**	**±**	**SE**
1978	32.16	±	3.50	314.84	±	66.62	8.88	±	0.20
1979	32.55	±	3.48	315.13	±	65.55	8.88	±	0.20
1980	32.95	±	3.46	315.41	±	64.52	8.88	±	0.19
1981	33.35	±	3.44	315.69	±	63.54	8.89	±	0.19
1982	33.75	±	3.42	315.97	±	62.60	8.89	±	0.19
1983	34.16	±	3.41	316.25	±	61.72	8.89	±	0.18
1984	34.58	±	3.40	316.53	±	60.89	8.89	±	0.18
1985	35.00	±	3.39	316.82	±	60.12	8.90	±	0.18
1986	35.43	±	3.38	317.10	±	59.41	8.90	±	0.17
1987	35.86	±	3.38	317.38	±	58.75	8.90	±	0.17
1988	36.29	±	3.38	317.67	±	58.16	8.90	±	0.17
1989	36.73	±	3.38	317.95	±	57.64	8.90	±	0.17
1990	37.18	±	3.39	318.23	±	57.19	8.91	±	0.16
1991	37.63	±	3.41	318.52	±	56.80	8.91	±	0.16
1992	38.09	±	3.42	318.80	±	56.49	8.91	±	0.16
1993	38.55	±	3.45	319.09	±	56.25	8.91	±	0.16
1994	39.02	±	3.47	319.37	±	56.09	8.91	±	0.16
1995	39.49	±	3.50	319.66	±	56.00	8.92	±	0.16
1996	39.97	±	3.54	319.94	±	55.99	8.92	±	0.16
1997	40.46	±	3.59	320.23	±	56.05	8.92	±	0.16
1998	40.95	±	3.64	320.51	±	56.20	8.92	±	0.16
1999	41.45	±	3.69	320.80	±	56.42	8.93	±	0.16
2000	41.95	±	3.75	321.08	±	56.72	8.93	±	0.16
2001	42.46	±	3.82	321.37	±	57.09	8.93	±	0.16
2002	42.97	±	3.90	321.66	±	57.54	8.93	±	0.16
2003	43.50	±	3.98	321.94	±	58.06	8.93	±	0.16
2004	44.02	±	4.07	322.23	±	58.65	8.94	±	0.17
2005	44.56	±	4.16	322.52	±	59.32	8.94	±	0.17
2006	45.10	±	4.27	322.81	±	60.05	8.94	±	0.17
2007	45.65	±	4.38	323.10	±	60.85	8.94	±	0.17
2008	46.20	±	4.49	323.38	±	61.72	8.95	±	0.18
2009	46.76	±	4.61	323.67	±	62.64	8.95	±	0.18
2010	47.33	±	4.74	323.96	±	63.62	8.95	±	0.18
2011	47.91	±	4.88	324.25	±	64.67	8.95	±	0.19
2012	48.49	±	5.02	324.54	±	65.76	8.95	±	0.19
2013	49.08	±	5.17	324.83	±	66.91	8.96	±	0.20
2014	49.67	±	5.33	325.12	±	68.11	8.96	±	0.20
2015	50.28	±	5.50	325.41	±	69.36	8.96	±	0.20
2016	50.89	±	5.67	325.70	±	70.65	8.96	±	0.21
2017	51.51	±	5.84	325.99	±	71.99	8.96	±	0.21
2018	52.13	±	6.03	326.28	±	73.37	8.97	±	0.22

Table S3.5-3: Predicted values for the local data set (high forest).

	Species richness			**Abundance**			**Biomass [g]**		
Year	**Value**	**±**	**SE**	**Value**	**±**	**SE**	**Value**	**±**	**SE**
1978	52.58	±	5.14	637.67	±	191.24	9.59	±	0.29
1979	52.69	±	4.97	627.03	±	181.39	9.58	±	0.28
1980	52.81	±	4.80	616.57	±	171.91	9.56	±	0.27
1981	52.93	±	4.63	606.28	±	162.77	9.55	±	0.26
1982	53.05	±	4.46	596.16	±	153.99	9.54	±	0.25
1983	53.17	±	4.30	586.21	±	145.57	9.52	±	0.24
1984	53.29	±	4.14	576.43	±	137.51	9.51	±	0.23
1985	53.41	±	3.98	566.81	±	129.80	9.50	±	0.22
1986	53.53	±	3.82	557.35	±	122.47	9.48	±	0.21
1987	53.65	±	3.67	548.05	±	115.50	9.47	±	0.21
1988	53.77	±	3.53	538.90	±	108.92	9.46	±	0.20
1989	53.89	±	3.39	529.91	±	102.72	9.45	±	0.19
1990	54.01	±	3.25	521.06	±	96.94	9.43	±	0.18
1991	54.13	±	3.13	512.37	±	91.56	9.42	±	0.17
1992	54.25	±	3.01	503.82	±	86.62	9.41	±	0.17
1993	54.38	±	2.90	495.41	±	82.13	9.39	±	0.16
1994	54.50	±	2.81	487.14	±	78.11	9.38	±	0.16
1995	54.62	±	2.73	479.01	±	74.56	9.37	±	0.15
1996	54.74	±	2.66	471.02	±	71.51	9.36	±	0.15
1997	54.87	±	2.61	463.16	±	68.95	9.34	±	0.14
1998	54.99	±	2.58	455.43	±	66.90	9.33	±	0.14
1999	55.11	±	2.56	447.83	±	65.35	9.32	±	0.14
2000	55.24	±	2.56	440.35	±	64.28	9.30	±	0.14
2001	55.36	±	2.58	433.00	±	63.66	9.29	±	0.14
2002	55.49	±	2.62	425.78	±	63.47	9.28	±	0.14
2003	55.61	±	2.68	418.67	±	63.67	9.27	±	0.15
2004	55.73	±	2.76	411.69	±	64.22	9.25	±	0.15
2005	55.86	±	2.85	404.82	±	65.07	9.24	±	0.16
2006	55.99	±	2.96	398.06	±	66.18	9.23	±	0.16
2007	56.11	±	3.08	391.42	±	67.50	9.21	±	0.17
2008	56.24	±	3.21	384.88	±	69.00	9.20	±	0.17
2009	56.36	±	3.35	378.46	±	70.63	9.19	±	0.18
2010	56.49	±	3.50	372.15	±	72.38	9.18	±	0.19
2011	56.62	±	3.66	365.93	±	74.20	9.16	±	0.20
2012	56.74	±	3.83	359.83	±	76.08	9.15	±	0.21
2013	56.87	±	4.01	353.82	±	78.00	9.14	±	0.22
2014	57.00	±	4.19	347.92	±	79.93	9.12	±	0.22
2015	57.13	±	4.38	342.11	±	81.87	9.11	±	0.23
2016	57.26	±	4.57	336.40	±	83.80	9.10	±	0.24
2017	57.39	±	4.77	330.79	±	85.71	9.09	±	0.25
2018	57.51	±	4.97	325.27	±	87.59	9.07	±	0.26

Chapter 4: Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity

This Chapter is published as: Roth, N., Doerfler, I., Bässler, C., Blaschke, M., Bussler, H., Gossner, M. M., Heideroth, A., Thorn, S., Weisser, W. W. & Müller, J. (2019). Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity. Diversity and Distributions, 25(3), 430-441.

4.1 Summary

European temperate forests have lost dead wood and the associated biodiversity owing to intensive management over centuries. Nowadays, some of these forests are being restored by enrichment with dead wood, but mostly only at stand scales. Here, we investigated effects of a seminal dead-wood enrichment strategy on saproxylic organisms at the landscape scale. In a before–after control–impact design, we compared assemblages and gamma diversities of saproxylic organisms in strictly protected old-growth forest areas (reserves) and historically moderately and intensively managed forest areas before and a decade after starting a landscape-wide strategy of dead-wood enrichment. Before enrichment with dead wood, the gamma diversity of saproxylic organisms in historically intensively managed forest stands was significantly lower than in reserves and historically moderately managed forest stands; this difference disappeared after 10 years of dead-wood enrichment. The species composition of beetles in forest stands of the three historical management intensities differed before the enrichment strategy, but a decade thereafter, the species compositions of previously intensively logged and forest reserve plots were similar. However, the differences in fungal species composition between historical management categories before and after 10 years of enrichment persisted. Our results demonstrate that intentional enrichment of dead wood at the landscape scale is a powerful tool for rapidly restoring saproxylic beetle communities and for restoring wood-inhabiting fungal communities, which need longer than a decade for complete restoration. We propose that a strategy of area-wide active restoration combined with some permanent strict refuges is a promising means of promoting the biodiversity of age-long intensively managed Central European beech forests.

4.2 Introduction

Central European forests have been exploited for centuries, which has resulted in a loss of old-growth forest structures (Hannah et al., 1995; Parviainen, 2005). Human activities have markedly reduced the amount and quality of dead wood in forests (Lassauce et al. 2011), which has greatly affected population sizes of many species and the composition of forest communities. Between 20 and 25% of all forest-dwelling species are saproxylic, i.e., dependent on dead wood or on wood-inhabiting fungi, for at least a part of their lifespan (Speight, 1989; Schmidl & Bußler, 2004; Stokland et al., 2012). Beetles and fungi are the most diverse saproxylic taxa and comprise multiple habitat guilds (Stokland et al., 2012) with distinct requirements for the amount and quality of dead wood in space and time (Lassauce et al., 2011; Sverdrup-Thygeson et al., 2014). Saproxylic species that depend on old-growth structures (e.g., tree hollows, and dead wood of large diameter and in late decay stages) suffer most from the loss of habitats and can thus be considered as 'old-growth specialists' (Müller et al., 2008; Blaschke et al., 2009).

Due to differing management, e.g. royal hunting grounds and wood-production forests, the amount of dead wood varied considerably at the landscape scale historically, which led to both refuges for species that depend on old-growth structures and forests depauperated of species (Bußler & Müller, 2006). Currently, high amounts of dead wood at the landscape scale in beech forests are almost exclusively restricted to forest reserves in Eastern Europe (Christensen et al., 2005), while managed beech forests lack large old trees and dead wood in Europe in general (Gossner et al., 2013b). As >95% of the forest area in Europe is unprotected and economically exploited (e.g. for timber production) (Morales-Hidalgo et al., 2015), debates on the effectiveness of land sparing vs. land sharing concepts (Fischer et al., 2008; Grau et al., 2013) are important, and conservation strategies need to be assessed for their efficacy. It has been shown that land sharing, i.e. integrative conservation approaches in European forests, can locally promote saproxylic organisms, depending on the time scale and taxon, by restoring or retaining dead wood and old-growth elements (Brunet & Isacsson, 2009; Komonen et al., 2014; Pasanen et al., 2014; Vandekerkhove & Thomaes, 2015). However, most of these approaches are restricted to the stand scale, and landscape-wide applications of dead-wood enrichment and their evaluation with respect to biodiversity are rare. Dead-wood enrichment at landscape scales might not be homogenous and thus biodiversity assessments should not restrict to local alpha diversity, when dead-wood enrichment is evaluated. To assess the total effect of landscape-wide deadwood enrichment, an approach that compares the gamma diversities in areas of different management intensities prior to the implementation of dead wood enrichment strategies is needed.

In a before–after control–impact design, we compared saproxylic beetle and fungal communities in beech forest stands historically intensively or moderately managed, before and after 10 years of intentional enrichment with dead wood at the landscape scale. As a control, we compared the communities in the managed forests with those in strictly protected forest reserves, which have age and dead-wood characteristics similar to those of primeval beech forests (Müller et al., 2007b). Only the managed parts of the forests were actively enriched with dead wood. Enrichment began in 2004 (officially approved in 2006) (Doerfler et al., 2017) to compensate for strong differences in the gamma diversity and composition of saproxylic organisms, including guild patterns, among forest stands of the three management intensities (Müller et al., 2007a, 2008; Bässler et al., 2014; Gossner et al., 2014).

We hypothesized that after a decade of dead-wood enrichment at the landscape scale, the lower diversity found in 2004 in the intensively managed part of the study area would no longer be apparent and the differences in gamma diversity and community composition of the former management categories would diminish. We also analysed guild-specific responses. As dead-wood enrichment in the study area is an ongoing process that was implemented 10 years before the resurvey, more dead wood of all decay stages was present on the plots (Doerfler et al., 2017). We therefore expected that diversities of all analysed guilds would have caught up with those of the forest reserves.

4.3 Methods

4.3.1 Study area

The study was carried out in the Steigerwald forest in southern Germany (49°N 10°E), which covers 1,115.2 km² and spans an elevation of 350 to 500 m a.s.l. The mean annual temperature is 7–8 °C. The annual rainfall is 850 mm (Lischeid, 2001). The study plots are located in the forest district Ebrach, where European Beech (*Fagus sylvatica*) is the dominating tree species (~40%), followed by oaks (*Quercus sp.*) (~20%) (Müller et al., 2007a). The study area covers 17,000 ha, 92% of which is managed by a state company.

4.3.2 Study design

Within the study area, 69 circular plots were established in beech forests. Each plot was 0.1 ha in size and classified to one of the three historical management categories (according to Müller et al. 2007a, 2008) (Fig. 4.1): intensively managed (intensive logging) (24 plots), moderately managed (moderate logging with conservation goals) (24 plots), and unmanaged, forest reserves (no logging) (21 plots; as a control). In the intensively managed forest stands, timber was extensively extracted, especially after World War II, at rates of 11 m^3 ha−1 year−1, which led to almost complete loss of habitat trees and dead wood. Moderately managed forest stands have been moderately thinned and logged since 1972, with a focus on the preservation of cavity trees. This management has led to more habitat trees and dead wood retained than in intensively managed areas (for a detailed description of historical management intensities, see Appendix S4.1 in Zytynska et al., 2018). The strictly protected forest reserves have had no human influence since at least 1978 (16 plots) or 1995 (5 plots) and contain dead wood and veteran tree structures similar to those found in primeval forests in Eastern Europe and therefore could serve as a control (Müller et al., 2007b). The management of all managed parts of the study area, but not of the protected parts, changed officially in 2006 (unofficially in 2004) and follows an ongoing integrative conservation concept in which dead wood is enriched to promote the diversity of saproxylic organisms. Remnants, e.g., crowns and the bottom meter of rotten or crooked trunks, are actively enriched during harvesting, and naturally developed dead wood, e.g. snags and storm-felled trees, is retained. The mean volume of dead wood in the production forest increased from 18.9 ± 1.1 m^3 ha−1 before dead-wood enrichment to 49.1 ± 3.8 m^3 ha−1 ten years after the strategy started (for details, see Doerfler et al. 2017), thus resulting in a before–after control–impact design. Plot features, e.g., dead-wood volume (see Appendix S4.7), were recorded on all 69 plots in 2004 and 2014 (Müller et al., 2007b; Doerfler et al., 2017).

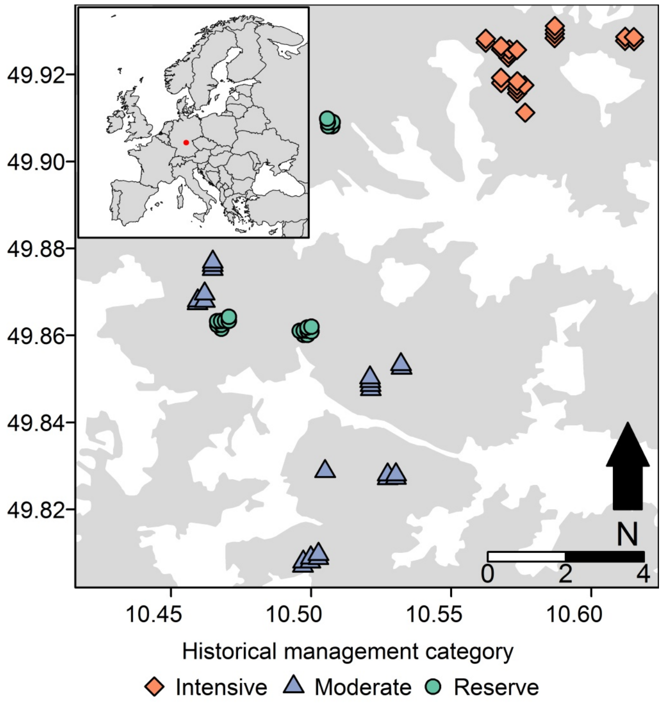


Fig. 4.1: Study area in Steigerwald (Germany) with 69 plots in three different categories of previous management: intensive, intensively managed with extensive logging; moderate, conservation-oriented moderately managed since the 1970s; reserve, strictly protected with no logging since the 1970s. Scale bar indicates kilometres. Inset: location in Central Europe.

4.3.3 Saproxylic beetle sampling

We sampled beetles from April to October in 2004 (before enrichment of dead wood) and in 2014 (after 10 years of enrichment) with flight-interception traps (Müller et al., 2008). Traps consisted of two crossed plastic shields (40 cm × 60 cm) with a funnel (40 cm diameter) attached at the bottom. The funnel fed into a 750-ml container filled with 1.5% copper sulphate solution and a small amount of odourless detergent. Copper sulphate efficiently kills and conserves insects without attracting them (Stoeckle et al., 2010). In addition, an experienced entomologist (HB) directly searched each 0.1 ha plot for 45 min in spring, summer, and autumn of both sampling years for beetle fragments, larvae, larval structures, and flightless species. In the direct search, woody objects, wood-inhabiting fungi, tree cavities, and brood chambers were examined. We pooled data from both sampling methods for statistical analyses. Beetles were classified as saproxylic following Schmidl & Bußler (2004). We defined a subset of species that contained saproxylic beetle species dependent on old-growth forest structures, e.g., dead wood of large diameter and tree cavities, based on data specific for our study area provided by HB (see Müller, 2005). These species are referred to as ‘old-growth specialists’. Some ‘old-growth specialists’ are even more demanding in their habitat choice and are referred to as ‘extreme old-growth specialists’ (see Appendix S4.3) (Müller, 2005). The study region is generally depauperated in terms of diversity. Hence, only seven species are found in the list of primeval forest relict species (Eckelt et al., 2018); therefore, we summed records per plot for this species subset (Appendix S4.3). Beetle species were also classified into habitat guilds (fresh dead wood, old dead wood, or on fungi in dead wood) (Schmidl & Bußler, 2004).

4.3.4 Wood-inhabiting fungi sampling

Macroscopic fruiting bodies (macromycetes) of wood-inhabiting fungi were recorded on all woody objects over 45 min on each 0.1 ha plot in spring, summer, and autumn in the same years as the beetle samplings by experienced mycologists before dead-wood enrichment (Heinz Engel) and after enrichment (MB). Critical species were later examined with a microscope. MB followed the same protocol as HE. Fungal species were classified into habitat guilds (dwelling in fresh dead wood or in old dead wood) according to a list compiled by MB, which is based on the mean decay stage of dead wood on which each species was found in previous studies. 'Old-growth specialists', which are demanding in their habitat requirements, were classified following Blaschke et al. (2009).

4.3.5 Statistical methods

Insect populations (Martikainen & Kaila, 2004) and fungal populations (Halme & Kotiaho, 2012) vary considerably between years, and thus analyses between years might reflect fluctuations in population densities rather than an effect of the forest management strategy (see Appendix S4.1). Therefore, we analysed each sampling year separately and compared patterns of the communities between the sampling years. As the fungi were sampled by two different people and the beetle data set contained data from both hand sampling and flight-interception traps, we used presence/absence data on each plot in our analyses of both saproxylic groups to avoid biased results. However, we additionally used abundance data to corroborate our results concerning community compositions (Appendix S4.8). All analyses were performed using R (version 3.3.1, R Core Team, 2016).

To analyse landscape scale effects of dead-wood enrichment, we compared gamma diversities of all species, old-growth specialists, and species within habitat guilds, between management categories before and after dead-wood enrichment. We chose the gamma diversity approach because we were interested in the total effect of a landscape-wide enrichment on a forest area of specific history (Doerfler et al., 2017). To estimate gamma diversity for each category and guild, we used the framework of Chao et al. (2014a), which is implemented in the R package 'iNEXT' (Hsieh et al., 2016). This framework unifies interpolation and extrapolation approaches (Chao et al., 2014a) with Hill numbers (Hill, 1973), which allows analysis of the effects on rare (low frequency) and dominant species (high frequency) within a common framework. Furthermore, this framework allows estimation of sample completeness (Chao & Jost, 2012) and uses bootstrapping to construct confidence intervals around the Hill numbers (Colwell et al., 2012). This simplifies comparison of multiple assemblages. We calculated gamma diversity for species richness ($q = 0$), typical species ($q = 1$), and dominant species ($q = 2$) (Chao et al., 2014b), with a sample size of 24 (maximum number of plots per category) for all categories. Differences between analysed groups were considered significant when confidence intervals did not overlap (Schenker & Gentleman, 2001). Furthermore, we analysed sample completeness for each diversity estimation.

We calculated association of species with the three management categories using the 'multipatt' function of the 'indicspecies' package in R (Cáceres & Legendre, 2009) in which indicator values of each species are calculated for the respective category. Species that were significantly associated to one category are referred to as indicator species in the following. We analysed whether guild compositions (number of species dwelling in fresh dead wood, old dead wood, or wood fungi) of the calculated indicator species varied between the three historical management categories.

For analyses of community composition, we used nonmetric multidimensional scaling (NMDS), which is among the most robust unconstrained ordination methods in community ecology (Minchin, 1987). We used the 'metaMDS' function within the 'vegan' package in R (Oksanen et al., 2018). The number of dimensions was set to four to reduce stress below 0.2 (Clarke & Warwick, 2001). Differences in community assemblages between management categories were tested by permutational multivariate analysis of variance using distance matrices with the 'adonis' function within the 'vegan' package with 999 permutations (Anderson 2001) . We included plot coordinates in this analysis to control for potential spatial effects. As the number of occurrences markedly varied between sampling years, we artificially reduced the data set that contained more occurrences to the size of the other data set. We repeated this procedure 1,000 times and compared centroids of NMDS ordinations and results of permutational multivariate analysis of variance. The results were not substantially influenced by different occurrences (Fig. S4.6.7 and Fig. S4.6.8).

4.4 Results

In the two sampling years, we recorded 14,759 specimens (average 107 per plot, range 6–1,712) of 341 saproxylic beetle species (average 24 per plot, range 5–50) on all plots together. Abundances were lower after 10 years of dead-wood enrichment (5,493; average 134 per plot, range 16–1,712) than before enrichment (9,266; average 80 per plot, range 6–769). We also recorded 7,230 occurrences (sum of woody objects per species and plot; average 52.4 per plot, range 2–137) of 218 species of wood-inhabiting fungi (average 25.3 per plot, range 2–47). We recorded 2,361 occurrences (average 34.2 per plot, range 2–91) of 174 species before enrichment and 4,869 occurrences (average 70.6 per plot, range 29–137) of 162 species after enrichment.

4.4.1 Diversity of saproxylic beetles and wood-inhabiting fungi

We found no overall significant difference in gamma diversity between the management categories in overall saproxylic beetle species richness, before and after dead-wood enrichment ($q = 0$) (Fig. 4.2a and Table 4.1). The diversity of typical ($q = 1$) and abundant species ($q = 2$) in intensively managed forest stands was significantly lower than in moderately managed stands and forest reserves (indicated by non-overlapping confidence intervals, Table 4.1 and Appendix Fig. S4.2.2 and S4.2.3). After 10 years of enrichment, the beetle diversity (q = 1 and 2) of previously intensively managed forest stands equalled that of forest reserves. Sample coverage did not vary significantly between the plot categories (before enrichment: 0.857–0.927; after enrichment: 0.823–0.931) (Fig. 4.2c).

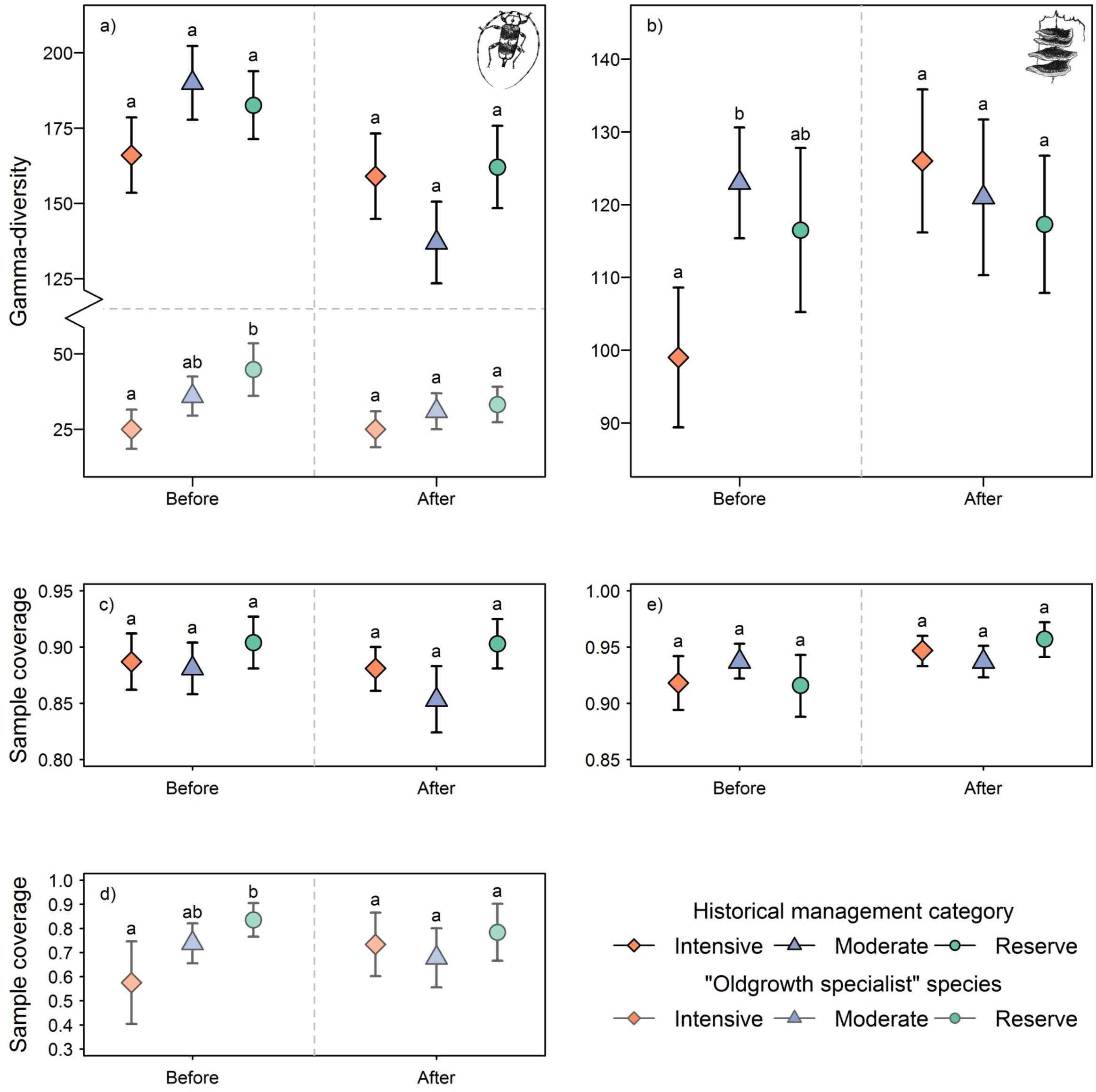


Fig. 4.2: Gamma diversity (q = 0) of (a) saproxylic beetles (including 'old-growth' specialists in lighter colors) and (b) wood-dwelling fungi of each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected) before and after 10 years of dead-wood enrichment. Gamma diversity is shown for a sample size of 24 plots (24 intensively managed plots, 24 moderately managed plots, 21 strictly protected plots). Sample coverage is shown for each diversity estimation; 95% confidence intervals were obtained by bootstrapping with 200 replications. Differences between the categories reach significance when 95% confidence intervalls do not overlap. Sample coverage is shown for (c) saproxylic beetles, (d) 'old-growth' specialists, and (e) wood-dwelling fungi.

Table 4.1: Summary of significant differences in gamma diversity (non-overlapping 95% confidence intervals) between historical management categories intensive (I), moderate (M), and strictly protected forest reserves (R), before and 10 years after the dead-wood enrichment started. Both the overall diversity of beetles (Overall) and the diversity of old-growth specialist beetles (Specialists) were considered. '< >', diversity of the indicated categories differs significantly.

	Before enrichment			**After enrichment**		
	Beetles		**Fungi**	**Beetles**		**Fungi**
Hill number	Overall	Old-growth specialists		Overall	Old-growth specialists	
q = 0		I<>R	I<>M			
q = 1 &	I<>M		I<>M	M<>I		
q = 2	I<>R		I<>R	M<>R		

Before dead-wood enrichment, the gamma diversity of wood-inhabiting fungi was significantly lowest in intensively managed forest stands, for all three orders of Hill numbers (Fig. 4.2b, Table 4.1, and Appendix S4.2). After 10 years of dead-wood enrichment, the species richness in forest stands of the previous management categories did not significantly differ, independent of the weighting of rare and dominant species (Fig. 4.2b, Table 4.1, and Appendix S4.2). Sample coverage was constant within each sampling year and varied between 0.894 and 0.955 in 2004, and 0.921 and 0.974 in 2014 (Fig. 4.2e).

4.4.2 Diversity of 'old-growth specialists'

In the two sampling years together, 81 saproxylic beetle 'old-growth specialist' species (1–13 per plot) were captured. The number of species and abundances were lower before dead-wood enrichment (2 species and 5 individuals per plot) than after 10 years of enrichment (3 species and 9 individuals per plot). In 2004, species richness was significantly higher in forest reserves than in intensively managed forest stands (indicated by non-overlapping confidence intervals, Fig. 2a bottom and Table 1). After 10 years of enrichment, the species richness in forest stands of the different historical management categories did not significantly differ. Note that sample coverage increased with decreasing historical management intensity before dead-wood enrichment (intensively managed: 0.399–0.751; moderately managed: 0.646–0.829; reserves: 0.758–0.914; Fig. 2d). However, the records of 'extreme old-growth specialists' and primeval forest relict species per plot was very low on previously intensively managed plots (Fig. S3.4).

Only 11 species of wood-inhabiting fungi recorded in both years are classified as 'old-growth specialists'. Owing to this low number of species, we restricted our analyses of the historical management intensities to comparisons of total number of records per plot. Before enrichment with dead wood, the number of records reflected the historical management intensity (low number of records on intensively managed plots, and high number of records on reserve plots). Ten years after enrichment, this pattern was much less discernible (Fig. S4.5).

4.4.3 Diversity in different habitat guilds

Before dead-wood enrichment, the species richness (q = 0) of fungi-dwelling beetles was significantly lower in intensively managed forest stands (0–8 species per plot) than in forest reserves (2–15 species per plot). After 10 years of enrichment, no difference between any management category was found (0–11 species per plot) (Fig. 4.3a, c indicated by overlapping confidence intervals). Before enrichment, the richness of beetle species dwelling on old dead wood was significantly lower in intensively managed forest stands (3–20 species per plot) than in moderately managed forest stands (4–29 species per plot), but the richness of species

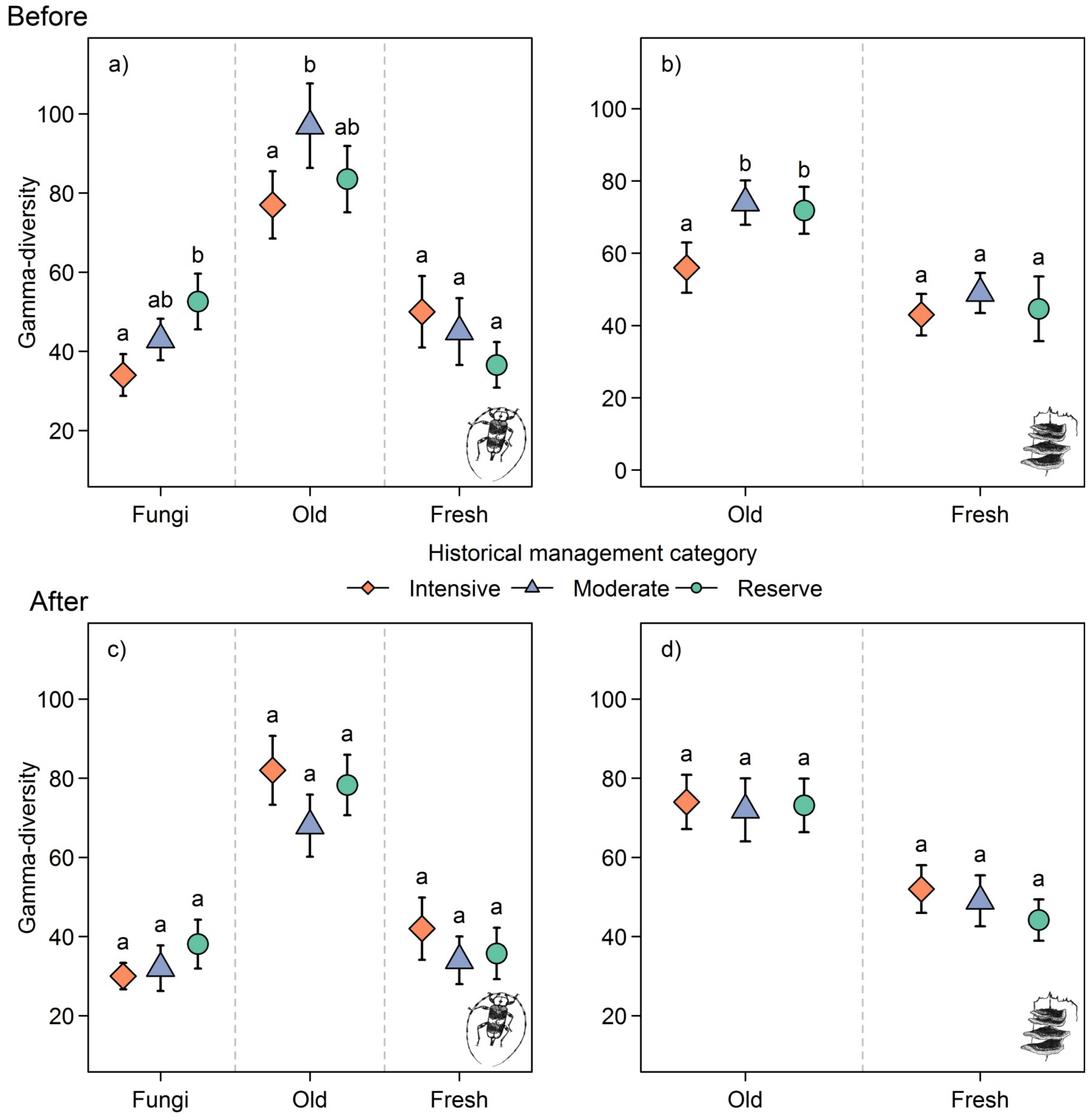


Fig. 4.3: Gamma diversity (q = 0) of habitat guilds of (a, c) saproxylic beetles and (b, d) wood-dwelling fungi (a, b) before and (c, d) after 10 years of dead-wood enrichment for each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected). Habitat guilds of beetles: fungi, dwelling on fungi in dead wood; old, dwelling in old dead wood; fresh, dwelling in fresh dead wood. Habitat guilds of fungi: old, dwelling in old dead wood; fresh, dwelling in fresh dead wood. Gamma diversity is shown for a sample size of 24 plots (24 intensively managed plots, 24 moderately managed plots, 21 strictly protected plots); 95% confidence intervals were obtained by bootstrapping with 200 replications. Differences between the categories reach significance when 95% confidence intervalls do not overlap.

dwelling on fresh dead wood did not differ between any management category (3–14 species per plot). After 10 years of enrichment, the richness of beetle species dwelling on fresh (0–14 species per plot) or old (3–28 species per plot) dead wood did not differ between any management category. The sample coverage did not significantly differ among the management categories before (0.805–0.975) and after 10 years of dead-wood enrichment (0.778–0.965), except between fungi-dwelling beetle species on intensively managed plots (0.878–0.963) and moderately managed plots (0.527–0.794) (Fig. S4.5.6).

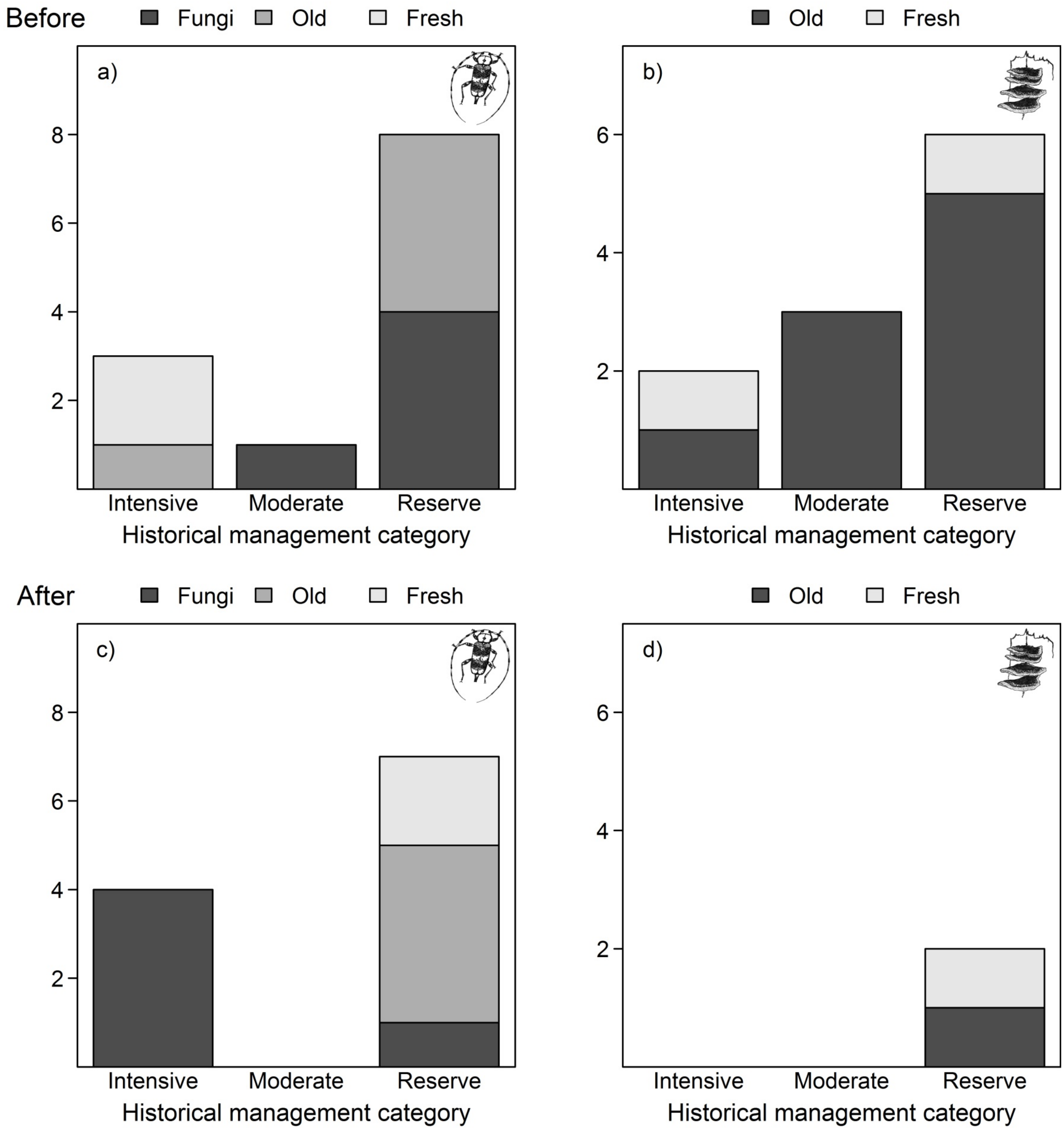


Fig. 4.4: Calculated number of (a, c) beetle and (b, d) fungal indicator species for each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected) (a, b) before and (c, d) after 10 years of dead-wood enrichment and the proportion of each habitat guild. Habitat guilds of beetles: fungi, dwelling on fungi in dead wood; old, dwelling in old dead wood; fresh, dwelling in fresh dead wood. Habitat guilds of fungi: old, dwelling in old dead wood; fresh, dwelling in fresh dead wood.

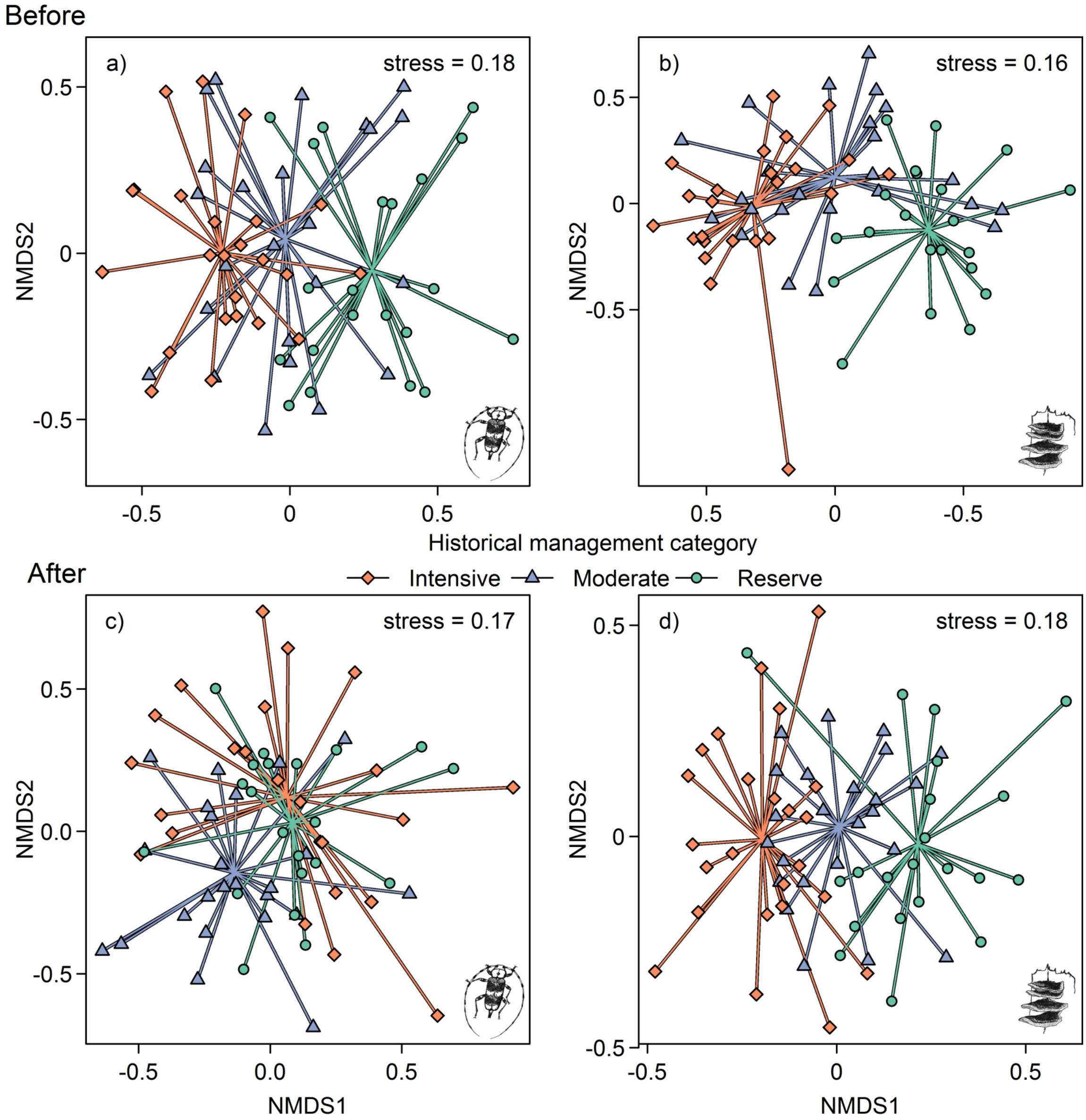


Fig. 4.5: NMDS ordinations of (a, c) saproxylic beetle and (b, d) fungal communities (a, b) before and (c, d) after 10 years of dead-wood enrichment. All NMDSs were calculated with four dimensions. Note that each spiderplot shows the centroid of the respective management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected).

Before dead-wood enrichment, the species richness of fungi dwelling on old dead wood (q = 0) was significantly lower in intensively managed forest stands (1–21 species per plot) than in moderately managed and forest reserves (4–31 species per plot) (Fig. 4.3b). After 10 years of dead-wood enrichment, we found no significant differences among management categories (5–26 species per plot) (Fig. 4.3d). We detected no significant differences in sample coverage within each guild before (0.817–0.972) and after (0.906–0.993) enrichment with dead wood (Fig. S4.5.6).

4.4.4 Management intensity indicator species

Before dead-wood enrichment, more beetle indicator species, which colonized old dead wood (4) and fungi (4), were identified in strictly preserved forests reserves (8) than in intensively managed forest stands (3), where most (2) colonized fresh dead wood (Fig. 4.4a). After 10 years of enrichment, this pattern changed; the beetle indicator species in reserves colonized fresh and old dead wood and fungi, and those in previously intensively managed forest stands now colonized fungi (Fig. 4.4c).

Before dead-wood enrichment, the number of fungal indicator species was higher in reserves (6) than in moderately (4) and intensively managed forest stands (2) (Fig. 4.4b). After 10 years of enrichment, only two species were identified, both in forest reserves (Fig. 4.4d).

Table 4.2: Permutational multivariate analysis of variance using distance matrices with 999 permutations for overall beetle and fungal communities before and after 10 years of dead-wood enrichment. Category, previous management intensity category; lat, latitude; lon, longitude.

	Variable	**p**	**R^2**	**F**
Saproxylic beetles				
Before enrichment	Category	0.001	0.071	2.591
	Lat	0.002	0.032	2.301
	Lon	0.168	0.017	1.231
After enrichment	Category	0.003	0.046	1.618
	Lat	0.001	0.043	3.015
	Lon	0.783	0.011	0.771
Wood-inhabiting fungi				
Before enrichment	Category	0.001	0.128	5.007
	Lat	0.003	0.035	2.610
	Lon	0.132	0.018	1.421
After enrichment	Category	0.001	0.090	3.384
	Lat	0.001	0.034	2.548
	Lon	0.014	0.024	1.789

4.4.5 Community composition

Before enrichment with dead wood, the centroids of the NMDS ordinations of saproxylic beetle communities were ordered according to decreasing management intensity (Fig. 4.5a). After 10 years of enrichment, the formerly intensively managed plots were more similar to forest reserve plots than to moderately managed plots (Fig. 4.5c). Similar patterns appeared when we considered abundance data (Appendix S4.8). Multivariate analysis of variance showed significant differences between the previous management categories before and after 10 years of enrichment with dead wood (Table 4.2). However, the effect of latitude became more pronounced after enrichment, which suggests a weakening influence of historical management intensity.

The centroids of the NMDS ordinations of wood-inhabiting fungal communities were ordered according to decreasing management intensity both before and after 10 years of dead-wood enrichment (Fig. 4.5b, d). Similar to that of beetle communities, multivariate analysis of variance showed significant differences between the previous management categories before and after 10 years of enrichment (Table 4.2). Latitude and longitude became more important for the fungal community composition after 10 years of enrichment than before. However, the previous management intensity category remained clearly more important than latitude and longitude for the community composition.

4.5 Discussion

The enrichment of dead wood at the landscape scale had significant effects on saproxylic beetle and fungal communities, after only 10 years following its implementation. This is in line with findings of well-designed experiments at the stand scale that suggest short-term positive effects of dead-wood accumulation for saproxylic organisms (Hyvärinen et al., 2006; Komonen et al., 2014; Pasanen et al., 2014; Seibold et al., 2015a). Historically intensively managed, and hence species poorer forest stands, aligned with forest reserves after 10 years of dead-wood enrichment in terms of gamma diversity and community composition. The underlying mechanism is most likely an increase in niche availability caused by the increase in the volume of dead wood, which positively affects saproxylic communities (see also Seibold et al. 2017). The ongoing dead-wood enrichment in managed forest stands since 2005, mitigates the differences in dead-wood amount and diversity between managed and unmanaged forest stands (Doerfler et al., 2017). Habitat restoration through dead-wood enrichment therefore positively affects saproxylic species not only on the plot level (Seibold et al., 2015a) but also at the landscape scale.

4.5.1 Community composition after dead-wood enrichment

The number of indicator species of the management categories, especially of wood-inhabiting fungi, was lower after 10 years of dead-wood enrichment. This decrease indicates a general homogenization of communities across plots of the three previous management intensities. Furthermore, the community compositions changed, as demonstrated by the changes in guilds of indicator species. Before dead-wood enrichment, beetle and fungal indicator species on intensively managed plots belonged to the old and fresh dead-wood guilds. Such a promotion of some selected saproxylic species in managed forests has been described by Grove (2002). After 10 years of enrichment, only indicator beetle species living on fungi and no fungal indicator species were found on the previously intensively managed plots. Therefore, we conclude that dead-wood enrichment with retention of naturally damaged trees results in successful restoration of fungi as hosts for beetles on intensively managed plots. These plots were not only poor in dead wood but also poor in key species, such as tinder fungus (Fomes fomentarius) (Thunes, 1994). This species, which was driven to local extinction in this area, sporadically began to recolonize before enrichment with dead wood, and is now very common (Zytynska et al., 2018).

The community composition of beetles changed more than that of fungi after enrichment with dead wood. This was especially the case for the community composition of beetles on intensively managed plots, which, after 10 years of enrichment, resembled that of forest reserves plots. Dispersal limitations should not play a large role at the scale of our study (20–30 km), as the majority of saproxylic beetles and wood-inhabiting fungi are good dispersers (Komonen & Müller, 2018). It is known that saproxylic beetle communities are mainly shaped by habitat filtering and dead-wood amounts (Klepzig et al., 2012; Bouget et al., 2013; Gossner et al., 2013a; Heikkala et al., 2016b). Therefore, within a decade, dead-wood enrichment contributed directly to the change in community composition (see also Thorn et al. 2016). The community composition of wood-inhabiting fungi, on the other hand, still showed the same order on the management-category plots after 10 years of dead-wood enrichment. This lack of change might be because wood-inhabiting fungi tend to 'defend' dead wood against other fungal species (Boddy, 2001), which leads to strong competition among fungi in a log and fructification of only a few species (Heilmann-Clausen & Christensen, 2004; Fukami et al., 2010), and this is often reflected by over-dispersed assembly patterns (Bässler et al., 2014). However, we expect that the fungal communities will change in the future as diversity peaks at more advance stages of decay of dead wood (Heilmann-Clausen & Christensen 2003, 2005; beech: 5–15 years after death, Müller-Using & Bartsch 2009), and this change might need more time to occur throughout the landscape.

4.5.2 Assessment of conservation goals

In Germany, forests harbour a mean of 20.6 m3 dead wood per hectare (Deutscher Holzwirtschaftsrat, 2017), which accounts for about 27% of the mean dead-wood volume found in European beech forest reserves (Christensen et al., 2005). This large difference between average forests and reserves explains why managed forests differ from protected areas in species richness and assemblages (Martikainen et al., 2000; Paillet et al., 2010). With the active enrichment of dead wood at the landscape scale in our study, the state forest management intended to promote saproxylic species diversity. The mean volume of dead wood rose from approximately 25 to 68 m^3/ha (Doerfler et al., 2017), and the strategy decreased the previous differences in beetle and fungal communities caused by earlier management. This land-sharing approach therefore promotes the diversity of saproxylic organisms and confirms the findings that the total amount of dead wood is of utmost importance for saproxylic organisms (Seibold et al., 2017). The positive developments showed that this integrative strategy is efficient and should therefore be implemented at even larger scales. This is regardless of the previous management intensity, as we found the greatest change in gamma diversity and community composition in forest stands with historically intensive management. Nevertheless, the application of this strategy requires the forest company to sacrifice 60–80 €/ha in sales per year (1–1.4 m^3 dead wood created per ha per year) throughout the entire study area (local state forest manager, personal communication). In addition, we would like to stress the following limitations of the applied strategy. Many saproxylic species have specific demands regarding tree species, size of dead-wood debris, decay stage, and type (snag or log) of dead wood (Stokland et al., 2012). As dead wood in the study area is enriched mostly during harvesting (Doerfler et al., 2017), it cannot be ensured that the creation of dead wood follows specific patterns needed to enhance specific, especially endangered, species (Pasanen et al., 2018). By applying the same management regime in the entire study area, plots tend to become more and more similar, which could possibly reduce overall diversity as a result of decreasing beta diversity. This issue should be addressed in further studies. Creation of canopy gaps during harvesting might be a way to counteract homogeneity, as canopy openness is important for a number of saproxylic organisms, also in beech forests (Bouget et al., 2013; Kraut et al., 2016). Moreover, a passive or even active (by thinning and induction of premature senescence, Speight 1989) increase in large veteran trees might add additional microhabitats for endangered saproxylic organisms, particularly those living in dead wood of large dimensions and in hollow trees (Schauer et al., 2017).

4.6 Appendix

S4.1 Study Limitations

We analyzed data from two sampling campaigns, which were separated by ten years. Therefore, differences between years can be correlated to the respective sampling year. Insufficient temporal replication is a known problem in ecological studies (see Harborne et al., 2008), with the exception of locally restricted studies (Martikainen & Kaila, 2004; Habel et al., 2016). It affects especially taxa which are highly variable in abundance and species richness from one year to another (Scott & Anderson, 2003; Martikainen & Kaila, 2004). Similarly to our findings, an independent study on saproxylic beetles in hollow trees in our study area found significantly less individuals in 2014 with standardized sampling as in 2015 (Schauer et al., 2017), which supports the view of an unfavorable deadwood insect year in 2014. The higher species number and beetle abundance in 2004 is therefore probably a result of the exceptional dry and warm summer in 2003 (Fig. S4.1.1) providing excellent development conditions for saproxylic beetles, in contrast to unfavorable conditions in 2013, where precipitation was higher and temperature lower, than the according mean values. We circumvented this problem by analyzing gradients inside each sampling year and comparing the differences in the gradient structures of the three plot categories. Furthermore, we tested consistency of the results with artificially reduced data sets (S4.7 & S4.8). We are thus convinced that our main results are not affected by the fluctuation in population densities between the two study years.

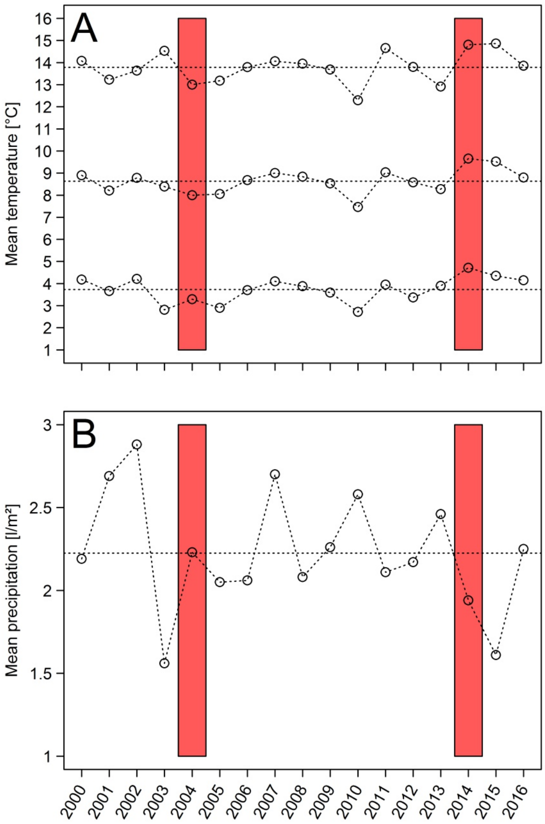


Fig. S4.1.1: Mean temperature [°C] (A) and mean precipitation [l/m²] (B) for Ebrach (within the study area) between 2000 and 2016. Red bars highlight sampling years 2004 (before treatment) and 2014 (after treatment). Data was recorded by the German Meteorological Service (DWD) and provided by http://skilma.de.

Supporting Information S4.2 Gamma diversity q = 1

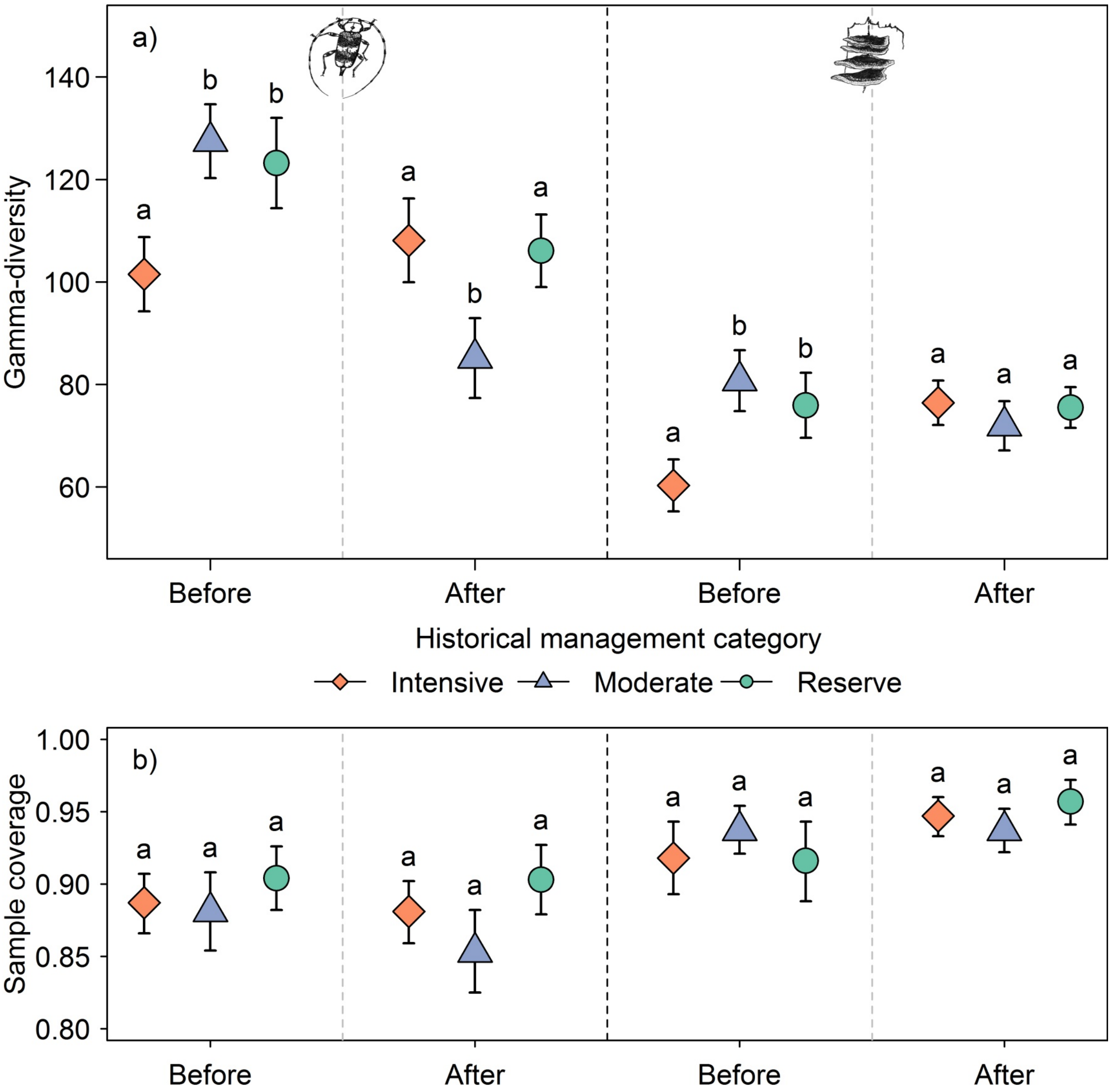


Fig. S4.2.2: Gamma diversity (q=1) of saproxylic beetles and wood dwelling fungi for each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected) before and after 10 years of dead-wood enrichment. (a). Gamma diversity is shown for sample size = 24 (24 intensive, 24 moderate, 21 reserve). Sample coverage (b) is shown for each diversity estimation. 95% confidence intervals obtained by bootstrapping with 200 replications. Differences between the categories reach significance when 95% confidence intervalls do not overlap.

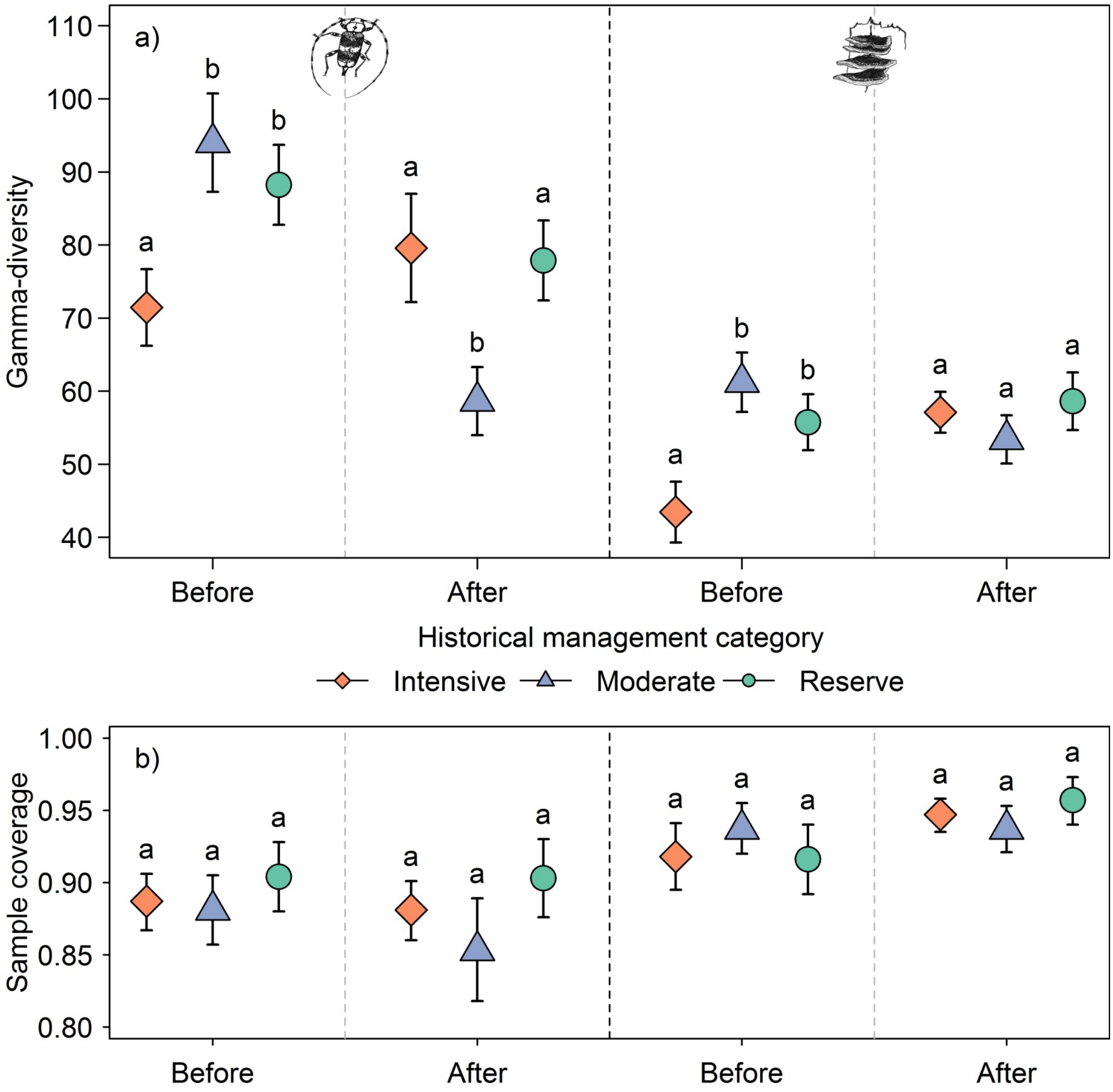


Fig. S4.2.3: Gamma diversity (q=2) of saproxylic beetles and wood dwelling fungi for each management (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected) before and after 10 years of dead-wood enrichment (a). Gamma diversity is shown for sample size = 24 (24 intensive, 24 moderate, 21 reserve). Sample coverage (b) is shown for each diversity estimation. 95% confidence intervals obtained by bootstrapping with 200 replications. Differences between the categories reach significance when 95% confidence intervalls do not overlap.

S4.3 Extreme old growth specialists

Fig S4.3.4: Occurrences (sum of records per plots) of "extreme old-growth specialist" beetle species and primeval forest relict beetle species before and after treatment These very exigent species are part of the "old-growth specialists" in the main manuscript. However, due to their demands to their habitat they can be seen as good indicators for a near to nature state of a forest.

Table S4.3.1: Occurrences of each saproxylic beetle "extreme old-growth specialist" per category and sampling year.

	Before			After		
	intensive	**moderate**	**reserve**	**intensive**	**moderate**	**reserve**
Allecula rhenana	0	0	1	0	0	1
Cerophytum elaterolides	0	0	0	0	0	2
Crepidophorus mutilatus	0	0	0	0	0	1
Dorcus parallelipipedus	0	1	12	0	1	3
Euthiconus conicicollis	0	1	2	0	0	0
Hesperus rufipennis	1	0	0	0	1	0
Ipidia binotata	0	0	0	0	0	1
Laemophloeus kraussi	0	0	0	1	1	1
Mycetophagus fulvicollis	0	0	1	0	0	4
Ptenidium gressneri	9	2	21	0	0	0
Rhyncolus reflexus	0	0	0	0	1	0
Scaphisoma boreale	0	0	1	0	0	0
Stictoleptura scutellata	2	1	3	2	0	0
Triplax lepida	1	2	44	0	0	0
Triplax rufipes	0	0	0	2	1	18

S4.4 Wood-inhabiting fungi, old growth specialists

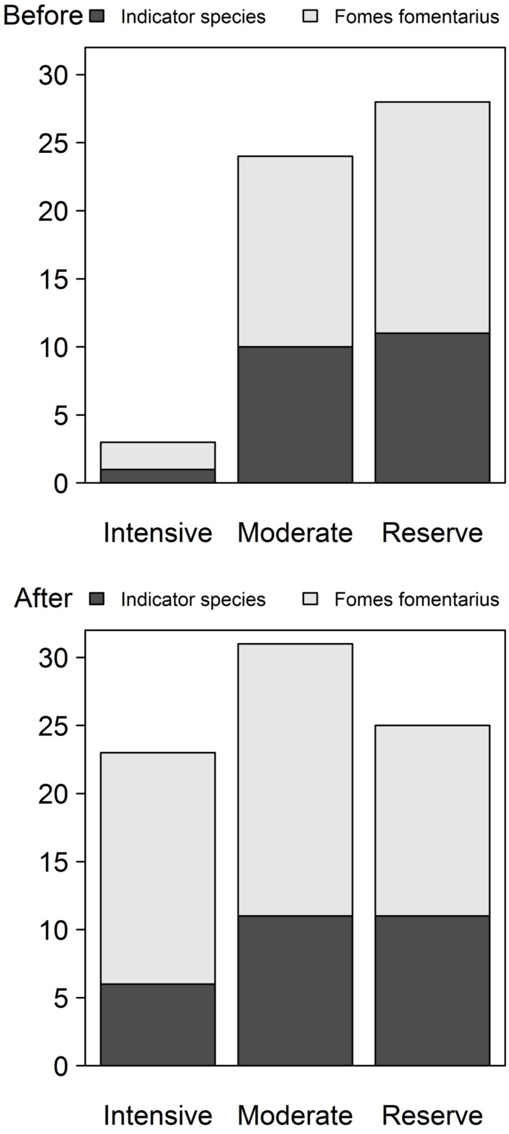


Fig. S4.4.5: Occurrences (sum of records per plots) of “old-growth specialist” fungi species before and after treatment. The tinder fungus (Fomes fometarius) is shown separately.

Table S4.4.2: Occurrences of each wood-inhabiting fungi “old-growth specialist” per category and sampling year.

		Before			**After**	
	intensive	**moderate**	**reserve**	**intensive**	**moderate**	**reserve**
Botryobasidium aureum	0	0	0	0	4	2
Ceriporiopsis pannocincta	0	2	1	0	0	0
Fomes fomentarius	2	14	17	17	20	14
Hericium coralloides	0	0	0	0	0	2
Ischnoderma resinosum	0	0	0	3	1	2
Lentinellus ursinus	0	1	0	0	0	1
Mycoacia nothofagi	0	0	0	0	2	1
Pluteus umbrosus	0	1	1	0	1	0
Polyporus badius	1	4	9	3	3	3
Spongipellis pachyodon	0	1	0	0	0	0
Tyromyces fissilis	0	1	0	0	0	0

S4.5 Sample coverage, guild analyses

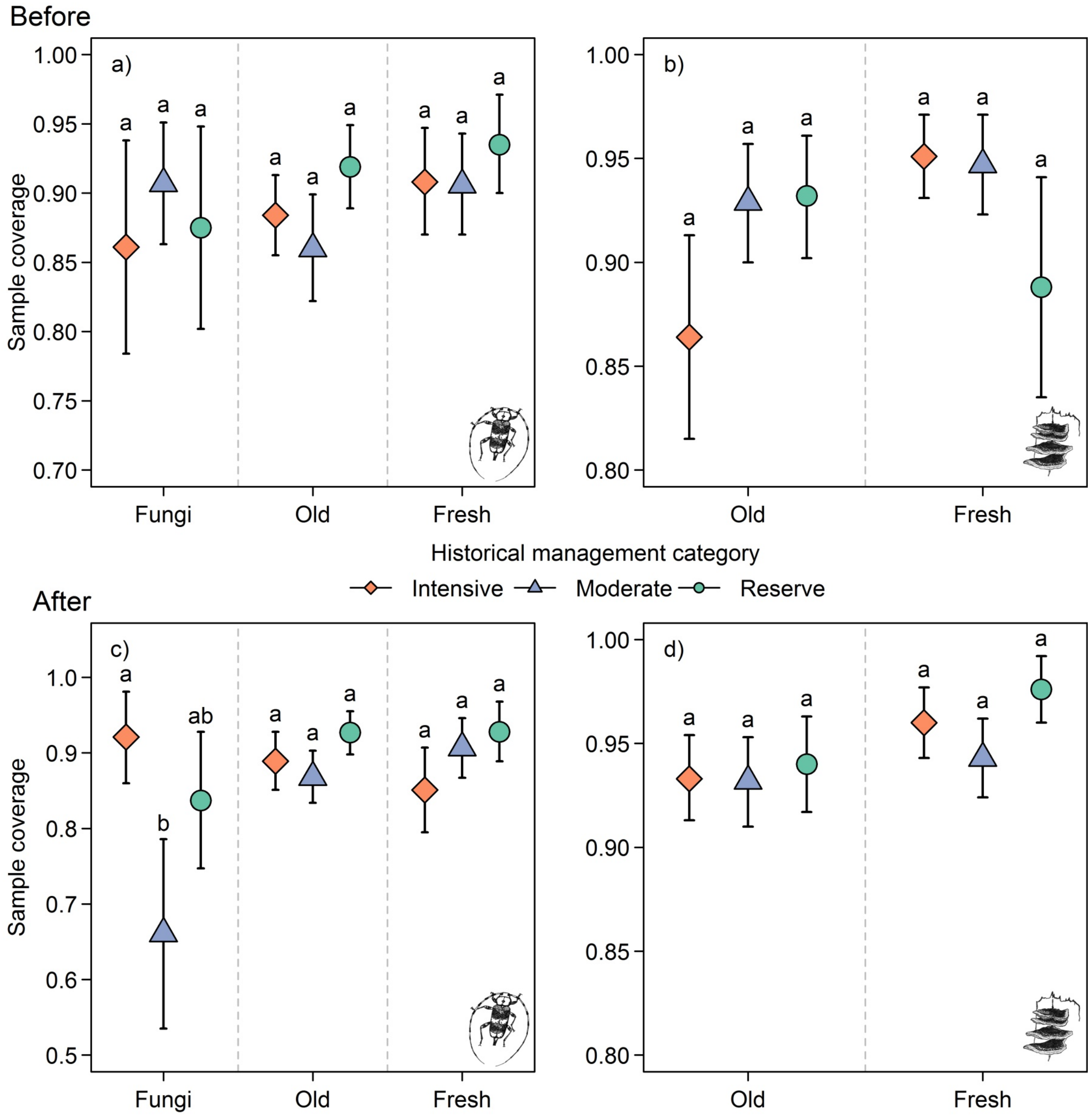


Fig. S4.5.6: Sample coverage of saproxylic beetles (a,c) and wood dwelling fungi (b,d) by guilds for each management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected) before (a,b) and after (c,d)10 years of dead-wood enrichment. Gamma diversity is shown for sample size = 24 (24 intensive, 24 moderate, 21 reserve). Sample coverage is shown for each diversity estimation. 95% confidence intervals obtained by bootstrapping with 200 replications. Differences between the categories reach significance when 95% confidence intervalls do not overlap.

S4.6 Reduced data sets Saproxylic beetles (2004) and wood-inhabiting fungi (2014)

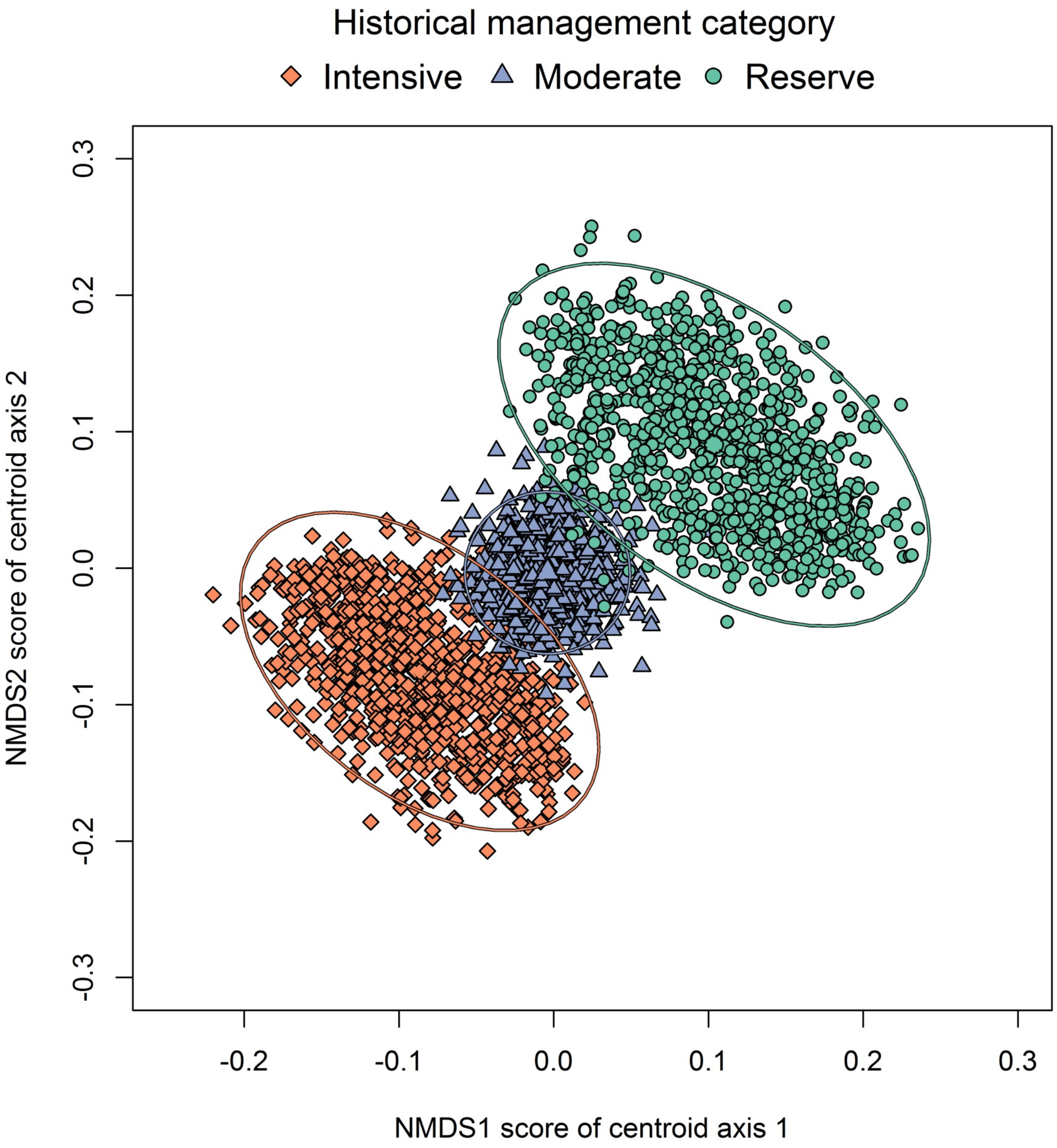


Fig. S4.6.7: NMDS scores of management category centroids for randomly reduced (1000 randomizations) saproxylic beetle data set in 2004 (before dead wood enrichment). The number of occurrences was reduced to occurrences of 2014 (1496 – 1860 original occurrences). Confidence limits for ellipses are 0.95. Differences between categories in 2004 remained significant after reducing the dataset to the occurrences of 2014 ($F \geq 1.44$, $p < 0.05$, $R^2 \geq 0.04$)

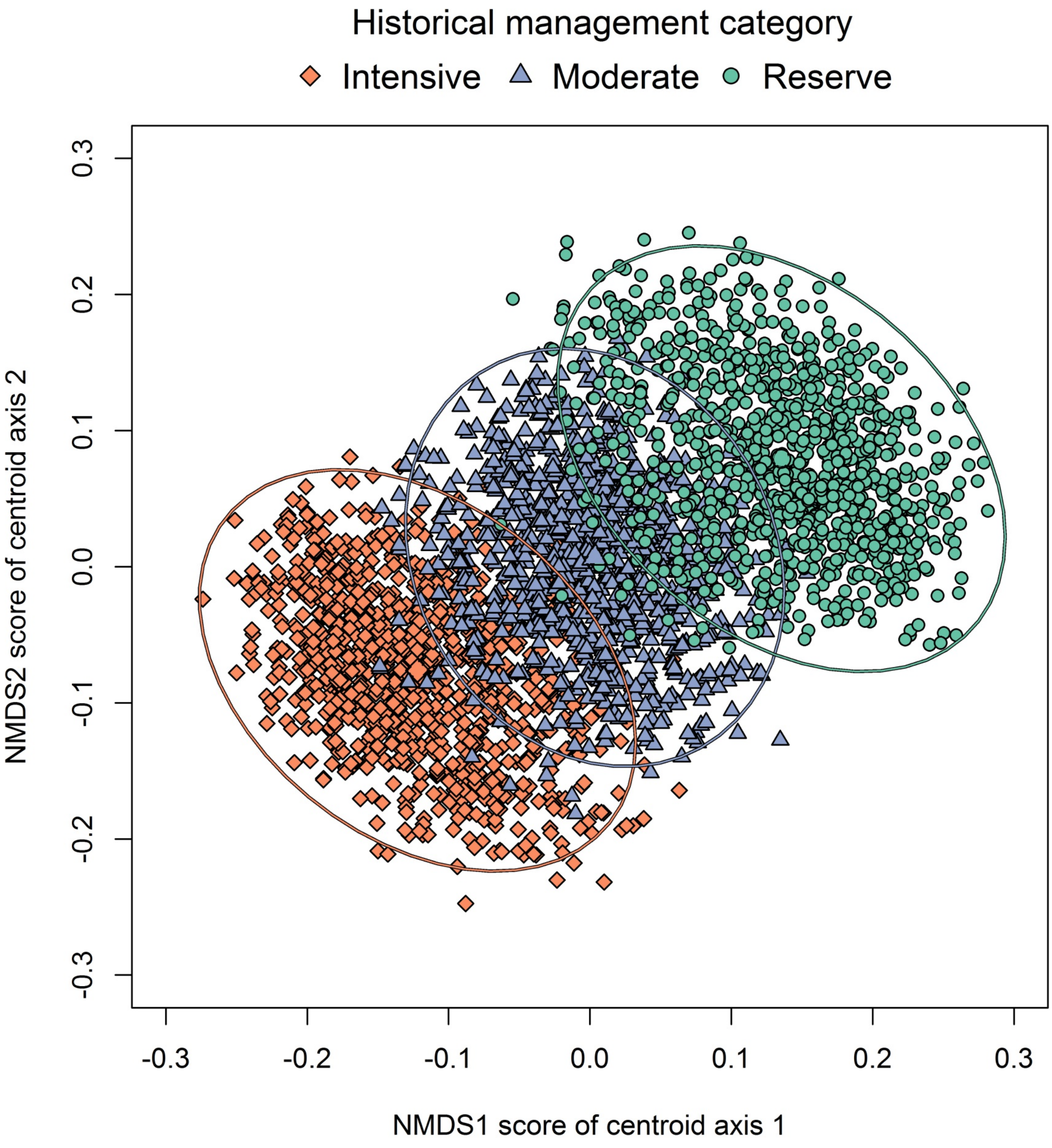


Fig. S4.6.8: NMDS scores of management category centroids for randomly reduced (1000 randomizations) wood-inhabiting fungi data set in 2014 (after deadwood enrichment). The number of occurrences was reduced to occurrences of 2004 (before treatment, 1456 – 2032 original occurrences). Confidence limits for ellipses are 0.95. Differences between categories remained significant after reducing the 2014 dataset to the occurrences of 2004 (F ≥ 1.56, p < 0 .01, $R^2 \geq 0.05$)

S4.7 – Dead-wood amounts in historical management categories per sampling year

Table S4.7.1: Table of absolute and relative dead-wood volume sums (m^2) in the three historical management categories intensive, moderate and reserve before (2004) and after ten years of dead-wood enrichment (2014). Relative volumes were calculated in relation to the dead-wood volume in the reserves in the according sampling year.

	Before		**After**	
	Absolute Volume	Relative Volume	Absolute Volume	RelativeVolume
Intensive	384.99	0.22	1209.96	0.22
Moderate	639.78	0.37	1455.6	0.26
Reserve	1733.61	1	5627.92	1

S4.8 – NMDS calculated with abundance data.

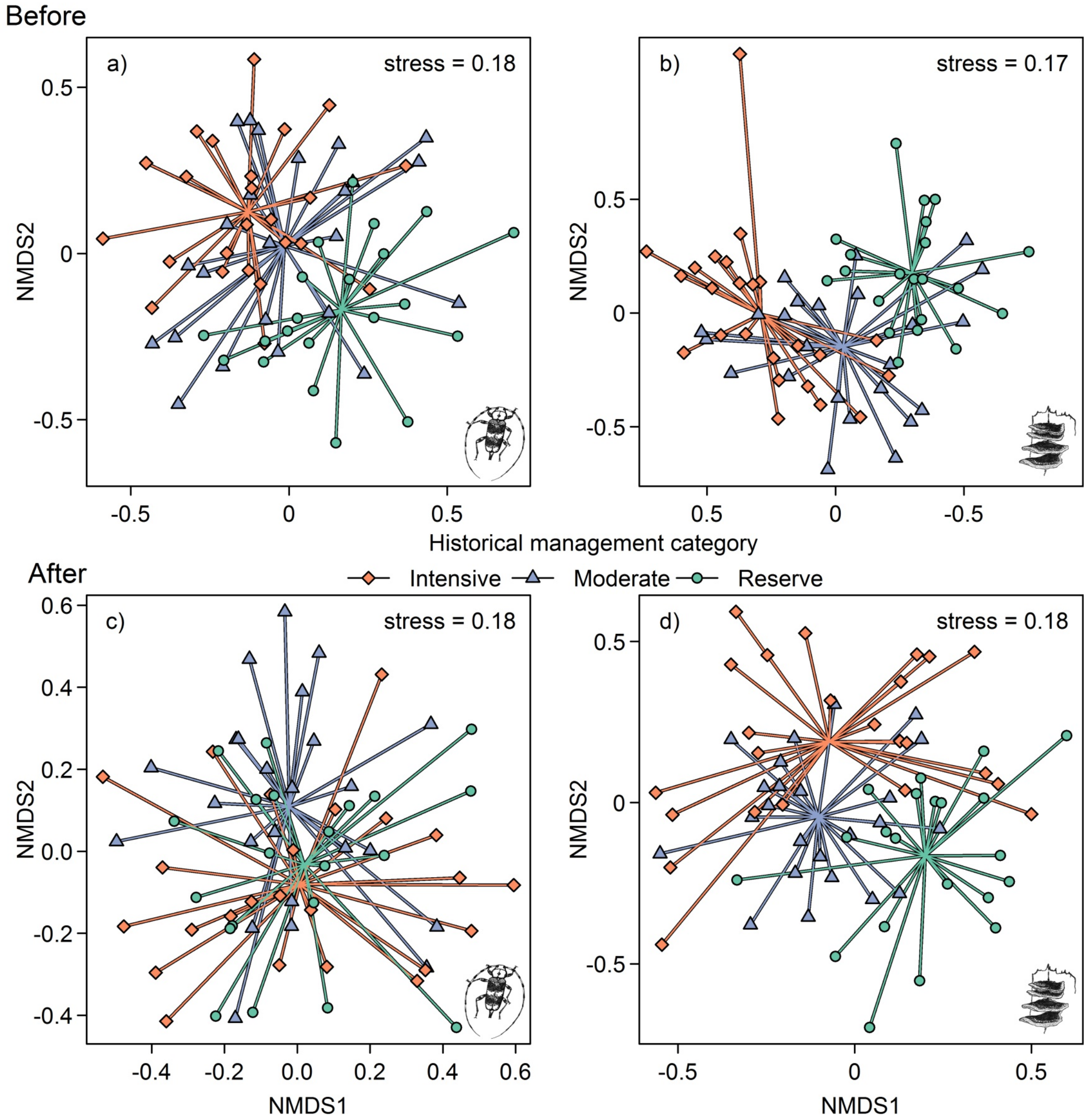


Fig. S4.8.9: NMDS ordinations of (a, c) saproxylic beetle and (b, d) fungal communities (a, b) before and (c, d) after 10 years of dead-wood enrichment. All NMDSs were calculated with 4 dimensions. Note that each spiderplot shows the centroid of the respective management category (intensive, intensively managed; moderate, moderately managed; reserve, strictly protected).

Chapter 5: General Discussion

In the previous chapters 2 and 3 I found declines in lentic water beetle and macro-moth communities. Water beetles living in small to middle-sized water bodies in southern Germany decreased in diversity and abundance with shifts in community compositions. In forest-dwelling moths, I found clearly declining species numbers, abundance and biomass. Dietary specialists and dark coloured species declined more severely than dietary generalists and light-coloured species. However, species numbers increased at one location with a management strategy (coppice with standards) which has become rare in Europe. This indicates that certain management strategies could mitigate insect decline. This is in line with the results in Chapter 3, where I showed that an integrative nature conservation strategy can change diversity and community patterns of saproxylic organisms so that they resemble protected areas.

5.1 Results in the context of the current research

The results of Chapter 2 and 3 corroborate that the observed insect communities decline at a rate of 1-2 % per year and that specialists are especially affected by these declines. However, these trends are also visible in habitats which were considered to be more resilient until now. For example, recent studies found positive trends for forest insect communities (Juslén et al., 2016b; Potocký et al., 2018) and freshwater insect communities (Pilotto et al., 2020; Van Klink et al., 2020). Insect communities are as diverse as the taxon in itself. This means that one should be extremely careful not to over-interpret large-scale meta-analyses, and to consider if the datasets which are included in the analyses comprise also all scope relevant taxa and habitats. Furthermore it is important to account for possible, complex sampling histories in order to draw robust conclusions (Welti et al., 2020). Especially regarding conservation and possible conservation strategies it is important to have knowledge about the development of the communities at the local and regional scale (Primack et al., 2018). However, this information is often missing or too limited in time or space. With Chapter 2 and 3, I try to bridge this gap in missing diversity development data at local and regional scales. It is postulated that at local scale biodiversity remains stable because of the arrival of non-native species (Vellend et al., 2017b). However, I could not detect the arrival of non-native species on my study sites. Although new, warm-adapted species appeared over time (e.g. Hydrovatus cuspidatus, which is a warm-adapted species known to increase in central/northern Europe (Scheers, 2014)), they could not compensate for the general loss of species. As this principle was developed for plants and vertebrates (Vellend et al., 2017a; Primack et al., 2018) it might not be easily applicable to insects. Furthermore, the generality of this principle has also already been questioned (Cardinale et al., 2018). Results in Chapter 3 show that local moth diversity increased significantly in a coppice with standards forest between the late 1970s and today.

However, this is probably not due to an increase of non-native species but merely reflects the ecological value of coppice with standards management. Coppice-with-standards forests feature regular dynamics of changing light and thus temperature regimes (Baeten et al., 2009). Consequently, the coppicing in that area can be regarded as a conservation strategy. However, it is important to create mosaics of different coppicing stages in order to support high diversity of different taxa (Weiss et al., 2020). In addition to the positive effects on moth communities coppicing can also promote unique assemblages of saproxylic beetles (Vandekerkhove & Thomaes, 2015). However, for saproxylic species diversity, not only the micro-climate (e.g. light availability) but especially the habitat amount (e.g. dead-wood volume) is often the limiting factor in managed forests in Central Europe, were human activities reduced the availability of dead wood remarkably (Lassauce et al., 2011). The results in Chapter 5 showed that constant addition of dead wood in managed forests can help to align the patterns of managed forests with patterns of forest reserves. Thus, dead-wood enrichment might help to mitigate declines of saproxylic organisms in forests.

5.2 Trends in insect communities – possible causes

Although during the last decades an increasing number of studies showed mostly negative trends in insect communities (Wagner, 2020 and references therein), the causality for these trends is still unclear. However, most scientist agree at least on one aspect, that these declines have anthropogenic causes (Ripple et al., 2017). These causes can be grouped into climate change related factors like temperature and atmospheric carbon dioxide levels, and into management related factors like nitrogen input, pesticides and land use change in general (Chapter 1). As insect decline already started in the second half of the twentieth century (Asher et al., 2001; Conrad et al., 2004, 2006; Thomas et al., 2004b), it is probable that factors like agricultural intensification and habitat deterioration and destruction were initially responsible for declines (Hallmann et al., 2019). Furthermore, in many cases there was no acceleration or quick increase of insect decline over the past five decades (Conrad et al., 2004; Dirzo et al., 2014; Fox et al., 2015). This indicates that recent environmental stressors like neonicotinoids, increased CO2-levels and temperature are not per se responsible for the decline, at least in Europe (but see Frampton & Dorne, 2007). The results of Chapter 2 suggest that a combination of decreasing habitat availability and increasing nitrogen input drives water beetle declines. More precisely, moor-species are threatened by desiccation of the moor-habitats. In addition, increasing nitrogen input leads to a deterioration of the habitat quality. On the other hand, raw-soil specialists are dependent on a constant creation/ appearance of suitable habitat. This should be considered in conservation planning (see below). It is less intuitive to interpret the results of Chapter 3 regarding the causes of declines in moth species richness, due to a lack of environmental variables available for this data set. However, the stronger decline of dark species and of habitat specialists suggests that there might be multiple causes for the decline. Light colour is known to be positively selected with global warming (Zeuss et al., 2014). Even though it is unclear, how this phenomenon should affect nocturnal ectotherms like moths, it has recently been shown that moth coloration varies with elevation and thus with temperature (Heidrich et al., 2018; Wu et al., 2019). Hence, the stronger decline of dark moths in Chapter 3 might be caused by a temperature increase, which would be a direct cause of climate change. Note that this suggestion is rather hypothetical due the lack of information on changes in temperature on the observed study sites. A decrease of dietary specialists and partly even an increase of generalists suggests changes in the plant communities in forests. These trends are probably driven by homogenization of management practices (e.g. even-aged high forest management) and increasing nitrogen inputs, which in turn leads to a homogenization of plant communities (Keith et al., 2009; De Schrijver et al., 2011; Dirnböck et al., 2014; Reinecke et al., 2014). On the other hand, there are also indications for increasing air quality. For example, species richness of Erebidae increased over time. This family contains a multitude of species feeding on lichens, which react negatively to air pollution (Pescott et al., 2015). The fact that lichen feeding species increase is therefore an indication for an increase in lichens and thus increasing air quality. This pattern was also observed in the Netherlands and the UK (Conrad et al., 2004; Groenendijk & Ellis, 2011; Fox, 2013). Thus, most probably, declines (and rarely increases) are driven by complex interactions between climate change related and management related factors. Equally complex experimental approaches would be required in order to disentangle these effects reliably.

5.3 Current development and conservation

There is more and more evidence that insect communities are declining (Montgomery et al., 2020; Wagner, 2020), and I showed (chapters 2 & 3) that they even do so in habitats, where indications were positive so far. Nevertheless, scientists are still calling for more data in order to further increase our knowledge and to validate the currently observed trends (Habel et al., 2019a; Kunin, 2019; Thomas et al., 2019). This call is completely legitimate, and it is indeed important to continue to collect data in a standardized way in order to continue or set up good time-series data. However, scientists as well as politicians should not forget to investigate practical and appropriate conservation strategies before there is nothing left to preserve (Lindenmayer et al., 2013; Forister et al., 2019). Protection of at least small patches of habitats is often not effective enough in order to protect insect communities as e.g. negative spill over effects from adjacent land can happen (Hallmann et al., 2017; Rada et al., 2019). Thus, studies as described in Chapter 4 are important in order to prove the efficiency of conservation measures. This is especially true for certain habitats like forests, where only few such studies have been done so far (but see Merckx et al., 2012; Heikkala et al., 2016). However, also the increasing number of natural disturbance events in forests (Senf & Seidl, 2020) can be a chance for more dynamic and habitat amount (e.g. dead wood) in European forests, which to some extent could be seen as a natural conservation measure. In open habitats, there is research on effects of conservation efforts on insect biodiversity e.g. in agro-environmental schemes (Thiere et al., 2009; Boetzl et al., 2019; Krimmer et al., 2019) in lentic water bodies (Marchetti et al., 2010) or in urban habitats where potentials of roadsides are being investigated (Mody et al., 2020). For all these management approaches it would be advisable to schedule long-term monitoring schemes in order to study how long the respective measures show positive effects and if, or at which time another intervention would be needed. Studying insect communities is indispensable in order to develop evidence-based management strategies. However, there is also the problem how to interpret and communicate the findings. The narrative of scientific studies has increasingly become alarmistic based on misinterpretation of the data or without sufficient proof of the fact that the observed trends are indeed as startling as interpreted (Lister & Garcia, 2018; Leather, 2019; Sánchez-Bayo & Wyckhuys, 2019). This trend to over-emphasize insect decline has already been pointed out (Cardoso & Leather, 2019; Cardoso et al., 2019; Komonen et al., 2019; Simmons et al., 2019; Montgomery et al., 2020), and recently a publication by Saunders et al. (2019), urged scientists to come back to a more scientific, evidence-based narrative. Thus, it should be also best practice to report, that there are taxa or species which are not declining (see Brooks et al., 2012; Hunter et al., 2014; Wagner, 2020). Such balanced narratives are important in order to assure science driven conclusions and consequently evidence-based management decisions with broad support from the general population.

5.4 Analyses of temporal insect communitiy data

When authors criticize the discourse and lack of data, another major point of criticism is data analyses and the possible interpretations of certain analyses (Didham et al., 2020 and references therein). The study design is one important criterion when it comes to possible analyses and possible interpretations of those. In Chapter 4 I analysed a data set which features 2 points in time. This makes direct assessment of development of insect communities over time virtually impossible, because of the yearly fluctuations, that can occur by one or two orders of magnitude from generation to generation (r-selected), in nearly all insect populations (Scott & Anderson, 2003; Martikainen & Kaila, 2004; Wagner, 2020). In order to get reliable results from such a sampling scheme, the plot number would have to be higher than 200, which was shown for pollinators (Lebuhn et al., 2013). Therefore, I opted for a comparison of within sampling year structures, rather than a direct comparison. However, the sampling design featuring plots in three different historical management categories might be adequate for a real-time series in the future in order to study the development of the communities in a forest where an integrative conservation strategy is applied (see Doerfler et al., 2017). The temporal extend of the data in Chapter 2 is more appropriate because it extends over 2-3 years of water body samplings in each of the three sampled decades (1990s, 2000s, 2010s), thus making the detection of trends more likely and reducing the odds of false trend detection. However, the number of sampled years (7 years) is still too low in order to perform proper cross validation (Arlot & Celisse, 2010) or left and right censoring analyses (Fournier et al., 2019; Didham et al., 2020). Recent analyses show that 10 to 15 single sampling years are required in order to detect non-random trends in abundance through time (White, 2019; Didham et al., 2020). Furthermore, it would be advisable to include new water bodies which match the characteristic of raw-soil water bodies along the time series in order to study if those specialist species are still present at the landscape scale. If this is not done, the loss of species can only refer to the studied habitat patches and remains unclear at the landscape scale. Including new sampling units to such studies should be a viable approach for most ephemeral habitats or habitats which undergo succession faster than the actual time-series. The dataset used in Chapter 3 fitted the requirements of a minimum of 10 individual sampling years (White, 2019) as it spanned over 41 years with 20 or more sample years (depending on the subset). Additionally, cross-validation as well as right censoring was applied and showed the consistency of the results. One downside of this data set is that over whole Bavaria the study plots are neither temporally nor spatially equally sampled. In fact, the data set is merely an accumulation of plots sampled over time with nearly 100 plots sampled only once and 50 plots sampled only twice during the whole study period. This shows how difficult it is to gather data with optimal spatio-temporal cover. However, the strategy of analysing a few constantly sampled plots and complement these analyses by less frequently sampled but spatially more extensive plots (as applied in Chapter 3) is not far away from what Didham et al. (2020) recommend in order to get reliable results.

5.5 Future directions

Studying and verifying insect decline is a difficult problem (Wagner et al 2020) and will most likely also be difficult in the future. It is not possible to observe every aspect of insect community development with climate change under laboratory conditions. The huge variety of landscape factors, which influence communities, and the sheer size of ecosystems make an entire reconstruction in laboratories more or less impossible. Furthermore, the annual decline rates in species richness and abundance seem to be quite subtle (1-2 %) at the moment (Conrad et al., 2006; Hallmann et al., 2017; Rada et al., 2019; Wepprich et al., 2019). This means that it takes a few decades until the losses become apparent. Nevertheless, they can still be calamitous before becoming apparent (Wagner, 2020). This is why it needs immediate, monitored actions in order to buffer the loss of insects as good as possible (Forister et al., 2019). At this point it is important to mention that even if conservation efforts need to be harmonized at larger scale, they have to be adapted to the local conditions (Primack et al., 2018; Pilotto et al., 2020). It is important to acknowledge that there are differences between biota, and to try to understand possible reasons for these differences. Thus, conservation efforts should be wisely chosen in order to take account of different biota and to avoid negative effects of the applied measures on target or non-target taxa (Habel et al., 2016a). Furthermore, conservation at the local scale is not only important in order to preserve species richness but also for preserving ecological processes, functional and phylogenetic diversities

(Pearson, 2016). Thus, even if one might find stable or increasing trends in insect richness it does not mean that conservation efforts should be stopped, as there may be other aspects of the ecosystem which are still impaired. Consequently, in the future not only species richness but also other aspects like species turnover indices should be analysed in time-series data (Hillebrand et al., 2018). Case studies remain the backbone of biodiversity projections in the future (Sala et al., 2000; Warren et al., 2018), thus the maximum of habitats and taxa should be sampled and analysed at every possible scale in order to be able to get reliable forecasts for biodiversity developments. With a multitude of scientific baselines for conservation of insects one should not forget that it is only one of several shortfalls which conservationists have to overcome. Public awareness about the importance of insects in ecosystems and political will for their protection will be crucial for effective insect conservation today and in future (Cardoso et al., 2011).

5.6 Conclusions

This work might give the reader the impression, that more questions are left open then answered. However, it represents a substantial addition to the knowledge about insect decline, possibilities to counteract it and illustrates which pitfalls should be avoided if possible, in order to produce reliable results. It shows the development of insect communities in habitats and taxonomic groups which were under-sampled in at least the studied habitats and indicates that insect decline is a general pattern even in habitats which have been shown to be more stable in the past. Documenting and studying insect communities in their natural habitat will always be challenging because of their complexity and the multitude of factors affecting the communities and each other. Thus, it will be important to cope with analytical problems in the future and to perform analyses with caution in order to get reliable results. For example, time spans of data sets should be maximized while checking for robustness of the results using left, right-censoring and cross-validation techniques. Nevertheless, the knowledge gaps that are still existing should not be an excuse for a lack of action. Contrary, since we are not able to assess the magnitude of species loss, conservation efforts should be implemented immediately based on the knowledge we have so far. Conservation efforts paired with a constant monitoring may be the only chance for certain species, communities, or even habitats to cope with the changing world we are living in.

References

Abellán, P., Arribas, P., & Svenning, J.C. (2012) Geological habitat template overrides late Quaternary climate change as a determinant of range dynamics and phylogeography in some habitat-specialist water beetles. Journal of Biogeography, 39, 970–983.

Allan, E., Bossdorf, O., Dormann, C.F., ... , Fischer, M. (2014) Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences of the United States of America, 111, 308–313.

Altermatt, F. (2010) Tell me what you eat and I'll tell you when you fly: Diet can predict phenological changes in response to climate change. Ecology Letters, 13, 1475–1484.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26, 32–46.

Arlot, S. & Celisse, A. (2010) A survey of cross-validation procedures for model selection. Statistics Surveys, 4, 40–79.

Arnott, A.S.E., Jackson, A.B., & Alarie, Y. (2006) Distribution and potential effects of water beetles in lakes recovering from acidification. The North American Benthological Society Distribution, 25, 811–824.

Asch, M. Van & Visser, M.E. (2007) Phenology of Forest Caterpillars and Their Host Trees: The Importance of Synchrony. Annual Review of Entomology, 52, 37–55.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G., & Jeffcoate, S. (2001) The millennium atlas of butterflies in Britain and Ireland. Oxford University Press, Oxford.

Augenstein, B., Ulrich, W., & Habel, J.C. (2012) Directional temporal shifts in community structure of butterflies and ground beetles in fragmented oligotrophic grasslands of Central Europe. Basic and Applied Ecology, 13, 715–724.

Austin, M.P., Scientific, T.C., & Smith, T.M. (1989) A new model for the continuum concept. Vegetatio, 83, 35–47.

Ayres, M.P. & Lombardero, M.J. (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment, 262, 263–286.

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerkhove, K., Roelandt, B., Beeckman, H., & Verheyen, K. (2009) Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. Applied Vegetation Science, 12, 187–197.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., & Press, M.C. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology, 8, 1–16.

Baranov, V., Jourdan, J., Pilotto, F., Wagner, R., & Haase, P. (2020) Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years. Conservation Biology, 34, 1241-1251.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Tiago, B., Marshall, C., Mcguire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., & Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? Nature, 471, 51–57.

Bässler, C., Ernst, R., Cadotte, M., Heibl, C., & Müller, J. (2014) Near-to-nature logging influences fungal community assembly processes in a temperate forest. Journal of Applied Ecology, 51, 939–948.

Bässler, C., Hothorn, T., Brandl, R., & Müller, J. (2013) Insects Overshoot the Expected Upslope Shift Caused by Climate Warming. PLoS ONE, 8, e65842.

Batzer, D.P., Palik, B.J., & Buech, R. (2004) Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota. Journal of the North American Benthological Society, 23, 50–68.

Begon, M.E., Townsend, C.R., & Harper, J.L. (2005) Ecology: From Individuals to Ecosystems. Blackwell Publishing, Oxford.

Bell, J.R. & Shortall, C.R. (2020) Are insects declining and at what rate? An analysis of standardised , systematic catches of aphid and moth abundances across Great Britain. Insect Conservation and Diversity, .

Belyea, L.R. & Lancaster, J. (1999) Assembly Rules within a Contingent Ecology. Oikos, 86, 402–416.

Benton, T.G., Bryant, D.M., Cole, L., & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: A historical study over three decades. Journal of Applied Ecology, 39, 673–687.

Beudert, B., Bässler, C., Thorn, S., Noss, R., Schröder, B., Dieffenbach-fries, H., Foullois, N., & Müller, J. (2015) Bark Beetles Increase Biodiversity While Maintaining Drinking. Conservation letters, 8, 272–281.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., & Kunin, W.E. (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. Science, 313, 351–355.

Biggs, J., Fumetti, S. von, & Kelly-Quinn, M. (2017) The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. Hydrobiologia, 793, 3–39.

Bilton, D.T., Mcabendroth, L., Bedford, A., & Ramsay, P.M. (2006) How wide to cast the net? Cross-taxon congruence of species richness , community similarity and indicator taxa in ponds. Freshwater Biology, 51, 578–590.

Blaschke, M., Helfer, W., Ostrow, H., Hahn, C., Loy, H., Bußler, H., & Krieglsteiner, L. (2009) Naturnähezeiger – Holz bewohnende Pilze als Indikatoren für Strukturqualität im Wald. Natur und Landschaft, 84, 560–566.

Blasius, B.J. & Merritt, R.W. (2002) Field and laboratory investigations on the effects of road salt (NaCl) on stream macroinvertebrate communities. Environmental Pollution, 120, 219–231.

Boddy, L. (2001) Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins, 49, 43–56.

Boetzl, F.A., Krimmer, E., Krauss, J., & Steffan-Dewenter, I. (2019) Agri-environmental schemes promote ground-dwelling predators in adjacent oilseed rape fields: Diversity, species traits and distance-decay functions. Journal of Applied Ecology, 56, 10–20.

Bouget, C. & Duelli, P. (2004) The effects of windthrow on forest insect communities: A literature review. Biological Conservation, 118, 281–299.

Bouget, C., Larrieu, L., Nusillard, B., & Parmain, G. (2013) In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodiversity and Conservation, 22, 2111–2130.

Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S., & Pocock, M.J.O. (2020) Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. Insect Conservation and Diversity.

Boyes, D.H., Fox, R., Shortall, C.R., & Whittaker, R.J. (2019) Bucking the trend: The diversity of Anthropocene “winners” among British moths. Frontiers of Biogeography, 11, 1–15.

Brito, M.M., Ribeiro, D.B., Raniero, M., Hasui, É., Ramos, F.N., & Arab, A. (2014) Functional composition and phenology of fruit-feeding butterflies in a fragmented landscape: Variation of seasonality between habitat specialists. Journal of Insect Conservation, 18, 547–560.

Brooks, D.R., Bater, J.E., Clark, S.J., Monteith, D.T., Andrews, C., Corbett, S.J., Beaumont, D.A., & Chapman, J.W. (2012) Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. Journal of Applied Ecology, 49, 1009–1019.

Brunet, J. & Isacsson, G. (2009) Restoration of beech forest for saproxylic beetles — effects diversity and distribution. Biodiversity and Conservation, 18, 2387–2404.

Bußler, H. & Müller, J. (2006) Wir brauchen differenzierte Konzepte im Waldnaturschutz. AFZ-DerWald, 4, 174–175.

Cáceres, M. De & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. Ecology, 90, 3566–3574.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., & Purvis, A. (2005) Multiple Causes of High Extinction Risk in Large Mammal Species Multiple Causes of High Extinction Risk in Large Mammal Species. Science, 309, 1239–1241.

Cardinale, B.J., Gonzalez, A., Allington, G.R.H., & Loreau, M. (2018) Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. Biological Conservation, 219, 175–183.

Cardoso, P., Barton, P.S., Birkhofer, K., et al. (2020) Scientists' warning to humanity on insect extinctions. Biological Conservation, 242, 108426.

Cardoso, P., Branco, V.V., Chichorro, F., Fukushima, C.S., & Macías-Hernández, N. (2019) Can we really predict a catastrophic worldwide decline of entomofauna and its drivers? Global Ecology and Conservation, 20, e00621.

Cardoso, P., Erwin, T.L., Borges, P.A.V., & New, T.R. (2011) The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation, 144, 2647-2655.

Cardoso, P. & Leather, S.R. (2019) Predicting a global insect apocalypse. Insect Conservation and Diversity, 12, 263–267.

Carvalho, P.D., Thomaz, S.M., & Bini, L.M. (2005) Effects of temperature on decomposition of a potential nuisance species: the submerged aquatic macrophyte Egeria najas planchom (Hydrocharitaceae). Brazilian Journal of Biology, 65, 51–60.

Cayrou, J. & Céréghino, R. (2005) Life-cycle phenology of some aquatic insects : implications for pond conservation. Aquatic Conservation: Marine and freshwater ecosystems, 15, 559–571.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., & Palmer, T.M. (2015) Accelerated modern human – induced species losses : Entering the sixth mass extinction. Advancement of Science, 1, 9–13.

Chao, A., Chiu, C.-H., & Jost, L. (2014a) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill Numbers. Annual Review of Ecology, Evolution, and Systematics, 45, 297–324.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., & Ellison, A.M. (2014b) Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecological Monographs, 84, 45–67.

Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation : standardizing samples by completeness rather than size. Ecology, 93, 2533–2547.

Chapman, A.D. (2009) Numbers of Living Species in Australia and the World. Australian Biological Resources Study, Canberra.

Chase, J.M. (2007) Drought mediates the importance of stochastic community assembly. PNAS, 104, 17430–17434.

Chase, J.M., McGill, B.J., Thompson, P.L., et al. (2019) Species richness change across spatial scales. Oikos, 128, 1079–1091.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., & Vrska, T. (2005) Dead wood in European beech (*Fagus sylvatica*) forest reserves. Forest Ecology and Management, 210, 267–282.

Clarke, A. & Fraser, K.P.P. (2004) Why does metabolism scale with temperature? Functional Ecology, 18, 243–251.

Clarke, K.R. & Warwick, R.M. (2001) Change in marine communities: An approach to statistical analysis and interpretation. PRIMER-E Ltd, Plymouth.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., & Longino, J.T. (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology, 5, 3–21.

Connell, J.H. (1978) Diversity in Tropical Rain Forests and Coral Reefs Joseph. Science, 199, 1302–1310.

Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., & Woiwod, I.P. (2006) Rapid declines of common , widespread British moths provide evidence of an insect biodiversity crisis. Biological

Conservation, 132, 279–291.

Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R., & Warren, M.S. (2004) Long-term population trends in widespread British moths. Journal of Insect Conservation, 8, 119–136.

Cornelissen, T. (2011) Climate Change and Its Effects on Terrestrial Insects and Herbivory Patterns. Neotropical Entomology, 40, 155–163.

Coulthard, E., Norrey, J., Shortall, C., & Harris, W.E. (2019) Ecological traits predict population changes in moths. Biological Conservation, 233, 213–219.

Coviella, C.E. & Trumble, J.T. (1999) Effects of elevated atmospheric carbon dioxide on insect-plant interactions. Agricultural and Forest Entomology, 13, 700–712.

Crossley, M.S., Meier, A.R., Baldwin, E.M., Berry, L.L., Crenshaw, L.C., Hartman, G.L., Lagos-Kutz, D., Nichols, D.H., Patel, K., Varriano, S., Snyder, W.E., & Moran, M.D. (2020) No net insect abundance and diversity declines across US Long Term Ecological Research sites. Nature Ecology and Evolution, 4, 1368–1376.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., & Wotton, B.M. (2001) Climate change and forest disturbances. BioScience, 51, 723–734.

Dantas de Miranda, M., Pereira, H.M., Corley, M.F.V., & Merckx, T. (2019) Beta diversity patterns reveal positive effects of farmland abandonment on moth communities. Scientific Reports, 9, 1–9.

Davies, B., Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Sear, D., Bray, S., & Maund, S. (2008) Comparative biodiversity of aquatic habitats in the European agricultural landscape. Agriculture, Ecosystems and Environment, 125, 1–8.

Death, R.G. & Zimmermann, E.M. (2005) Interaction between disturbance and primary productivity in determining stream invertebrate diversity. Oikos, 111, 392–402.

Dehling, D.M., Hof, C., Brändle, M., & Brandl, R. (2010) Habitat availability does not explain the species richness patterns of European lentic and lotic freshwater animals. Journal of Biogeography, 37, 1919–1926.

Desender, K., Dekoninck, W., Dufrêne, M., & Maes, D. (2010) Changes in the distribution of carabid beetles in Belgium revisited: Have we halted the diversity loss? Biological Conservation, 143, 1549–1557.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude Thermal Safety margin. PNAS, 105, 6668–6672.

Deutscher Holzwirtschaftsrat (2017) Der Wald in Deutschland – eine Erfolgsgeschichte. DHWR, Berlin.

Devictor, V., van Swaay, C., Brereton, T., et al. (2012) Differences in the climate debts of birds and butterflies at a continental scale. Nature Climate Change, 2, 121–124.

Didham, R.K., Basset, Y., Collins, C.M., Leather, S.R., Littlewood, N.A., Menz, M.H.M., Müller, J., Packer, L., Saunders, M.E., Schönrogge, K., Stewart, A.J.A., Yanoviak, S.P., & Hassall, C. (2020) Interpreting insect declines: seven challenges and a way forward. Insect Conservation and Diversity, 13, 103–114.

Dietmar, R., Michel, V., Graf, R., & Ralf, N. (2007) Definition von Boden-Klima-Räumen für die Bundesrepublik. Nachrichtenblatt Deutscher Pflanzenschutzdienst, 59, 155–161.

Dirnböck, T., Grandin, U., Bernhardt-Römermann, M., Beudert, B., Canullo, R., Forsius, M., Grabner, M.-T., Holmberg, M., Kleemola, S., Lundin, L., Mirtl, M., Neumann, M., Pompei, E., Salemaa, M., Starlinger, F., Staszewski, T., & Uzieblo, A.K. (2014) Forest floor vegetation response to nitrogen deposition in Europe. Global Change Biology, 20, 429–440.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., & Collen, B. (2014) Defaunation in the Anthropocene. Science, 345, 401–406.

Dixon, A.F.G. (2003) Climate change and phenological asynchrony. Ecological Entomology, 28, 380–381.

Doerfler, I., Müller, J., Gossner, M.M., Hofner, B., & Weisser, W.W. (2017) Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity.

Forest Ecology and Management, 400, 607–620.

Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M., & Woodward, G. (2012) Warming alters community size structure and ecosystem functioning. Proceedings of the Royal Society B: Biological Sciences, 279, 3011–3019.

Dubovskiy, I.M., Whitten, M.M.A., Kryukov, V.Y., Yaroslavtseva, O.N., Grizanova, E. V., Greig, C., Mukherjee, K., Vilcinskas, A., Mitkovets, P. V., Glupov, V. V., & Butt, T.M. (2013) More than a colour change: Insect melanism, disease resistance and fecundity. Proceedings of the Royal Society B: Biological Sciences, 280, 1–10.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., & Sullivan, C.A. (2006) Freshwater biodiversity: Importance, threats, status and conservation challenges. Biological Reviews of the Cambridge Philosophical Society, 81, 163–182.

Van Duinen, G.J.A., Brock, A.M.T., Kuper, J.T., Leuven, R.S.E.W., Peeters, T.M.J., Roelofs, J.G.M., Van Der Velde, G., Verberk, W.C.E.P., & Esselink, H. (2003) Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. Wetlands Ecology and Management, 11, 447–459.

Dukes, J. S., Pontius, J., Orwig, D., Garnas, J. R., Rodgers, V. L., Brazee, N., ... & Ehrenfeld, J. (2009) Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Canadian Journal of Forest Research, 39, 231–248.

Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., & Cizek, L. (2018) “ Primeval forest relict beetles ” of Central Europe : a set of 168 umbrella species for the protection of primeval forest remnants. Journal of Insect Conservation, 22, 15–28.

Ellenberg, H. (1988) Vegetation ecology of central Europe. Cambridge University Press, Cambridge.

Ellwood, E.R. & Diez, J.M. (2012) Disentangling the paradox of insect phenology : are temporal trends reflecting the response to warming ? Oecologia, 168, 1161–1171.

Ettema, C.H. & Wardle, D.A. (2002) Spatial soil ecology. Trends in Ecology and Evolution, 17, 177–183.

Ewald, J.A., Wheatley, C.J., Aebischer, N.J., Moreby, S.J., Duffield, S.J., Crick, H.Q.P., & Morecroft, M.B. (2015) Influences of extreme weather, climate and pesticide use on invertebrates in cereal fields over 42 years. Global Change Biology, 21, 3931–3950.

Eyre, M.D., Foster, G.N., & Foster, A.P. (1990) Factors affecting the distribution of water beetle species assemblages in drains of eastern England. Journal of Applied Entomology, 109, 217–225.

Faccoli, M. (2009) Effect of Weather on *Ips typographus* (Coleoptera Curculionidae) Phenology , Voltinism , and Associated Spruce Mortality in the Southeastern Alps. Environmental Entomology, 38, 307–316.

Fairchild, G.W., Cruz, J., Faulds, A.M., Short, A.E.Z., & Matta, J.F. (2003) Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. Journal of the North American Benthological Society, 22, 224–240.

Fairchild, G.W., Faulds, A.M., & Matta, J.F. (2000) Beetle assemblages in ponds:effects of habitat and site age. Freshwater Biology, 44, 523–534.

Fairchild, W.L. & Eidt, D.C. (1993) Perturbation of the aquatic invertebrate community of acidic bog ponds by the insecticide fenitrothion. Archives of Environmental Contamination and Toxicology, 25, 170–183.

Fajer, E.D. (1989) The effects of enriched CO2 atmospheres on plant-insect herbivore interactions : growth responses of larvae of the specialist butterfly , Junonia coenia (Lepidoptera : Nymphalidae). Oecologia, 81, 514–520.

Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R., & Wilson, J.D. (2000) Analysis of population trends for farmland birds using generalized additive models. Ecology, 81, 1970–1984.

Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L., Ranganathan, J., & Tallis, H. (2008) Should agricultural policies encourage land sparing or wildlife-friendly farming? Frontiers in Ecology and the Environment, 6, 380–385.

Flechtner, G. (1983) Höhenzonierung von Vorkommen und Struktur von Lebensgemeinschafen mitteleuropäischer Swimmkäfer. Verh. SIEEC X. Budapest, 1–18.

Florencio, M., Serrano, L., Gómez-Rodríguez, C., Millán, A., & Díaz-Paniagua, C. (2009) Inter- and intra-annual variations of macroinvertebrate assemblages are related to the hydroperiod in Mediterranean temporary ponds. Hydrobiologia, 634, 167–183.

Forister, M.L., Fordyce, J.A., Nice, C.C., Thorne, J.H., Waetjen, D.P., & Shapiro, A.M. (2018) Impacts of a millennium drought on butterfly faunal dynamics. Climate Change Responses, 5, 1–9.

Forister, M.L., Pelton, E.M., & Black, S.H. (2019) Declines in insect abundance and diversity: We know enough to act now. Conservation Science and Practice, 1, 1–8.

Forkner, R.E., Marquis, R.J., Lill, J.T., & Corff, J. Le (2008) Timing is everything? Phenological synchrony and population variability in leaf-chewing herbivores of Quercus. Ecological Entomology, 33, 276–285.

Forsman, A., Polic, D., Sunde, J., Betzholtz, P.E., & Franzén, M. (2020) Variable colour patterns indicate multidimensional, intraspecific trait variation and ecological generalization in moths. Ecography, 43, 823–833.

Fournier, A.M.V., White, E.R., & Heard, S.B. (2019) Site-selection bias and apparent population declines in long-term studies. Conservation Biology, 33, 1370–1379.

Fox, R. (2013) The decline of moths in Great Britain: A review of possible causes. Insect Conservation and Diversity, 6, 5–19.

Fox, R., Brereton, T.M., Asher, J., August, T.A., Botham, M.S., Bourn, N.A.D., Cruickshanks, K.L., Bulman, C.R., Ellis, S., Harrower, C.A., Middlebrook, I., Noble, D.G., Powney, G.D., Randle, Z., Warren, M.S., & Roy, D.B. (2015) The State of the Uk's Butterflies 2015. Butterfly Conservation, Wareham.

Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D., & Roy, D.B. (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. Journal of Applied Ecology, 51, 949–957.

Frampton, G.K. & Dorne, J.L.C.M. (2007) The effects on terrestrial invertebrates of reducing pesticide inputs in arable crop edges: A meta-analysis. Journal of Applied Ecology, 44, 362–373.

Franzén, I., Vasaitis, R., Penttilä, R., & Stenlid, J. (2007) Population genetics of the wood-decay fungus Phlebia centrifuga P. Karst. in fragmented and continuous habitats. Molecular Ecology, 16, 3326–3333.

Frazer, B.D. & Gilbert, N. (1976) Coccinellids and aphids: A quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). Journal of the Entomological Society of British Columbia, 73, 33–56.

Frenne, P. De, Rodríguez-Sánchez, F., Anthony, D., Baeten, L., Verstraeten, G., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., & Pet, P. (2013) Microclimate moderates plant responses to macroclimate warming. PNAS, 110, 18561–18565.

Fritz, S.C., Engstrom, D.R., & Juggins, S. (2004) Patterns of early lake evolution in boreal landscapes: A comparison of stratigraphic inferences with a modern chronosequence in Glacier Bay, Alaska. Holocene, 14, 828–840.

Fukami, T., Dickie, I.A., Paula Wilkie, J., Paulus, B.C., Park, D., Roberts, A., Buchanan, P.K., & Allen, R.B. (2010) Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecology Letters, 13, 675–684.

Galewski, K. (1971) A study on morphobiotic adaptions of European species of the Dytiscidae (Coleoptera). Polskie Pismo Entomologiczne, 44, 486–702.

Galloway, J.N., Dentener, F., Capone, D.G., Boyer, E., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Michaels, A.F., Porter, J.H., Townsend, A.R., & Vörösmarty, C.J. (2004) Nitrogen cycles: past, present, and future. Biogeochemistry, 70, 153–226.

García-Barros, E. (2015) Multivariate indices as estimates of dry body weight for comparative study of body size in Lepidoptera. Nota Lepidopterologica, 38, 59–74.

Gatter, W., Ebenhöh, H., Gatter, W., & Scherer, F. (2020) 50-jährige Untersuchungen an migrierenden Schwebfliegen , Waffenfliegen und Schlupfwespen belegen extreme Rückgänge (Diptera:

Syrphidae , Stratiomyidae ; Hymenoptera : Ichneumonidae). Entomologische Zeitschrift, 130, 131–142.

Gibbs, J.P. & Stanton, E.J. (2001) Habitat fragmentation and arthropod community change: Carrion beetles, phoretic mites, and flies. Ecological Applications, 11, 79–85.

Gilchrist, R. & Drinkwater, D. (2000) The use of the Tweedie distribution in statistical modelling. COMPSTAT (ed. by J.G. Bethlehem and P.G.M. Van der Heijden), pp. 313–318. Utrecht.

Gilliam, F.S. (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. Journal of Ecology, 94, 1176–1191.

Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M., & Brown, J.H. (2002) Effects of size and temperature on developmental time. Nature, 417, 70–73.

Gioria, M., Schaffers, A., Bacaro, G., & Feehan, J. (2010) The conservation value of farmland ponds: Predicting water beetle assemblages using vascular plants as a surrogate group. Biological Conservation, 143, 1125–1133.

Gordo, O. & Sanz, J.J. (2005) Phenology and climate change: A long-term study in a Mediterranean locality. Oecologia, 146, 484–495.

Gossner, M.M., Floren, A., Weisser, W.W., & Linsenmair, K.E. (2013a) Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. Forest Ecology and Management, 302, 404–413.

Gossner, M.M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W., & Müller, J. (2013b) Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology, 27, 605–614.

Gossner, M.M., Lewinsohn, T.M., Kahl, T., et al. (2016) Land-use intensification causes multitrophic homogenization of grassland communities. Nature, 540, 266–269.

Gossner, M.M., Schall, P., Ammer, C., Ammer, U., Engel, K., Schubert, H., Simon, U., Utschick, H., & Weisser, W.W. (2014) Forest management intensity measures as alternative to stand properties for quantifying effects on biodiversity. Ecosphere, 5, 1–111.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E.L. (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science, 2010, 1–16.

Grau, R., Kuemmerle, T., & Macchi, L. (2013) Beyond "land sparing versus land sharing": environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. Current Opinion in Environmental Sustainability, 5, 477–483.

Grime, J.P. (1973) Competitive Exclusion in Herbaceous Vegetation. Nature, 242, 344–347.

Groenendijk, D. & Ellis, W.N. (2011) The state of the Dutch larger moth fauna. Journal of Insect Conservation, 15, 95–101.

Grove, S.J. (2002) Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics, 33, 1–23.

Grunditz, C. & Dalhammar, G. (2001) Development of nitrification inhibition assays using pure cultures of Nitrosomonas and Nitrobacter. Water research, 35, 433–440.

Gutiérrez-Estrada, J.C. & Bilton, D.T. (2010) A heuristic approach to predicting water beetle diversity in temporary and fluctuating waters. Ecological Modelling, 221, 1451–1462.

Haase, P., Pilotto, F., Li, F., Sundermann, A., Lorenz, A.W., Tonkin, J.D., & Stoll, S. (2019) Moderate warming over the past 25 years has already reorganized stream invertebrate communities. Science of the Total Environment, 658, 1531–1538.

Habel, J.C., Augenstein, B., Schmitt, T., & Ulrich, W. (2016a) Managing towards extinction: Diverging developments of plant and ground beetle assemblages following restoration of calcareous grasslands. Basic and Applied Ecology, 17, 668–677.

Habel, J.C., Samways, M.J., & Schmitt, T. (2019a) Mitigating the precipitous decline of terrestrial European insects : Requirements for a new strategy. Biodiversity and Conservation, 28, 1343–1360.

Habel, J.C., Segerer, A., Ulrich, W., Torchyk, O., Weisser, W.W., & Schmitt, T. (2016b) Butterfly community shifts over two centuries. Conservation Biology, 30, 754–762.

Habel, J.C., Segerer, A.H., Ulrich, W., & Schmitt, T. (2019b) Succession matters: Community shifts in moths over three decades increases multifunctionality in intermediate successional stages. Scientific Reports, 9, 1–8.

Habel, J.C., Trusch, R., Schmitt, T., Ochse, M., & Ulrich, W. (2019c) Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. Scientific Reports 9, 1–9.

Hacker, H. & Müller, J. (2009) Die Nachtschmetterlingszönosen von Fichten- und Douglasien-Forsten im Bereich temperater Laubwälder Oberfrankens. Beiträge zur bayerischen Entomofaunistik, 9, 65–70.

Hacker, H.H. & Müller, J. (2006) Die Schmetterlinge der bayerischen Naturwaldreservate: eine Charakterisierung der süddeutschen Waldlebensraumtypen anhand der Lepidoptera (Insecta). Arbeitsgemeinschaft Bayerischer Entomologen e.V., Bamberg.

Hallmann, C., Zeegers, T., Klink, R. Van, & Jongejans, E. (2018) Analysis of insect monitoring data from De Kaaistoep and Drenthe. Radboud University, Nijmegen.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & De Kroon, H. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE, 12, 1–21.

Hallmann, C.A., Zeegers, T., Klink, R. Van, Vermeulen, R., Wielink, P. Van, Spijkers, H., Deijk, J. Van, & Teenis, W. Van (2019) Declining abundance of beetles , moths and caddisflies in the Netherlands. Insect Conservation and Diversity, 13, 127–139.

Halme, P. & Kotiaho, J.S. (2012) The importance of timing and number of surveys in fungal biodiversity research. Biodiversity and Conservation, 21, 205–219.

Hannah, L., Carr, J.L., & Lankerani, A. (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation, 4, 128–155.

Hansch, C. & Fujita, T. (1963) p-σ-π Analysis. A Method for the Correlation of Biological Activity and Chemical Structure. Journal of the American Chemical Society, 178, 1616–1626.

Hanski, I. (1998) Metapopulation dynamics. Nature, 396, 41–49.

Harris, J.E., Rodenhouse, N.L., & Holmes, R.T. (2019) Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. Biological Conservation, 240, 108219.

Harvey, J.A., Heinen, R., Armbrecht, I., et al. (2020) International scientists formulate a roadmap for insect conservation and recovery. Nature Ecology and Evolution, 30–32.

Hastie, T.J. & Tibshirani, R.J. (1990) Generalized additive models. Monographs on Statistics and Applied Probability, 43, 205–208.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., & Totland, Ø. (2009) How does climate warming affect plant-pollinator interactions? Ecology Letters, 12, 184–195.

Heidrich, L., Friess, N., Fiedler, K., Brändle, M., Hausmann, A., Brandl, R., & Zeuss, D. (2018) The dark side of Lepidoptera: Colour lightness of geometrid moths decreases with increasing latitude. Global Ecology and Biogeography, 27, 407–416.

Heikkala, O., Martikainen, P., & Kouki, J. (2016a) Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. Biological Conservation, 194, 39–47.

Heikkala, O., Seibold, S., Koivula, M., Martikainen, P., Müller, J., Thorn, S., & Kouki, J. (2016b) Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. Forest Ecology and Management, 359, 51–58.

Heilmann-Clausen, J. & Christensen, M. (2003) Fungal diversity on decaying beech logs - implications for sustainable forestry. Biodiversity and Conservation, 12, 953–973.

Heilmann-Clausen, J. & Christensen, M. (2004) Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management, 201, 105–117.

Heilmann-Clausen, J. & Christensen, M. (2005) Wood-inhabiting macrofungi in Danish beech-forests - conflicting diversity patterns and their implications in a conservation perspective. Biological Conservation, 122, 633–642.

Heino, J. (2000) Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity , habitat size and water chemistry. Hydrobiologia, 418, 229–242.

Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J., & Huntley, B. (2002) Responses of butterflies to twentieth century climate warming: Implications for future ranges. Proceedings of the Royal Society B: Biological Sciences, 269, 2163–2171.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. Ecology, 54, 427–432.

Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., Filstrup, C.T., Harpole, W.S., Hodapp, D., Larsen, S., Lewandowska, A.M., Seabloom, E.W., Van de Waal, D.B., & Ryabov, A.B. (2018) Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. Journal of Applied Ecology, 55, 169–184.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018) Biodiversity along temperate forest succession. Journal of Applied Ecology, 55, 2756–2766.

Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M., & Crone, E.E. (2011) Predicting insect phenology across space and time. Global Change Biology, 17, 1289–1300.

Hof, C., Brändle, M., & Brandl, R. (2008) Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. Global Ecology and Biogeography, 17, 539–546.

Holden, J., Shotbolt, L., Bonn, A., Burt, T.P., Chapman, P.J., Dougill, A.J., Fraser, E.D.G., Hubacek, K., Irvine, B., Kirkby, M.J., Reed, M.S., Prell, C., Stagl, S., Stringer, L.C., Turner, A., & Worrall, F. (2007) Environmental change in moorland landscapes. Earth-Science Reviews, 82, 75–100.

Horn, H.S. (1975) Markovian properties of forest succession. Ecology and evolution of communities (ed. by M.L. Cody and J.M. Diamond), pp. 196–211. Belknap Press, Cambridge.

Horn, H.S. (1981) Some Causes of Variety in Patterns of Secondary Succession. Forest Succession (ed. by D.C. West, H.H. Shugart, and D.B. Botkin), pp. 24–35. Springer, New York.

Hsieh, T.C., Ma, K.H., & Chao, A. (2016) iNEXT: R, iNterpolation and EXTrapolation for species diversity.

Hunter, M.D. (2001) Effects of elevated atmospheric carbon dioxide on insect-plant interactions. Agricultural and Forest Entomology, 3, 153–159.

Hunter, M.D., Kozlov, M. V., Itämies, J., Pulliainen, E., Bäck, J., Kyrö, E.-M., & Nimelä, P. (2014) Current temporal trends in moth abundance are counter to predicted effects of climate change in an assemblage of subarctic forest moths. Global Change Biology, 20, 1723–1737.

Hyvärinen, E., Kouki, J., & Martikainen, P. (2006) Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in finnish boreal forests. Conservation Biology, 20, 1711–1719.

Jäch, M.A. & Balke, M. (2008) Global diversity of water beetles (Coleoptera) in freshwater. Hydrobiologia, 595, 419–442.

Jeffries, J.M., Marquis, R.J., Forkner, R.E., & Jeffries, J.M. (2006) Forest Age Influences Oak Insect Herbivore Community Structure , Richness , and Density. 16, 901–912.

Jeffries, M.J. (1994) Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology, 32, 603–612.

Jeffries, M.J. (2011) The temporal dynamics of temporary pond macroinvertebrate communities over a 10-year period. Hydrobiologia, 661, 391–405.

Jiménez, E., Giménez, J.B., Ruano, M. V, Ferrer, J., & Serralta, J. (2011) Effect of pH and nitrite concentration on nitrite oxidation rate. Bioresource Technology, 102, 8741–8747.

Juslén, A., Cardoso, P., Kullberg, J., Saari, S., & Kaila, L. (2016a) Trends of extinction risk for Lepidoptera in Finland: The first national Red List Index of butterflies and moths. Insect Conservation and Diversity, 9, 118–123.

Juslén, A., Pykälä, J., Kuusela, S., Kaila, L., Kullberg, J., Mattila, J., Muona, J., Saari, S., & Cardoso, P. (2016b) Application of the Red List Index as an indicator of habitat change. Biodiversity and Conservation, 25, 569–585.

Karl, T.R. & Trenberth, K.E. (2003) Modern Global Climate Change. Science, 302, 1719–1723.

Kehl, S. & Dettner, K. (2007) Flugfähigkeit der in Deutschland vorkommenden adephagen Wasserkäfer

(Coleoptera , Hydradephaga). Entomologie heute, 19, 141–161.

Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E., & Bullock, J.M. (2009) Taxonomic homogenization of woodland plant communities over 70 years. Proceedings of the Royal Society B, 276, 3539–3544.

Kettlewell, H.B.D. (1959) Darwin ' s Missing Evidence. Scientific American, 200, 48–53.

Kholin, S.K. & Nilsson, A.N. (1998) Regional enrichment of predacious water beetles in temporary ponds at opposite east-west ends of the Palearctic. Journal of Biogeography, 25, 47–55.

Klapwijk, M.J., Csóka, G., Hirka, A., & Björkman, C. (2013) Forest insects and climate change : long-term trends in herbivore damage. Ecology and Evolution, 3, 4183–4196.

Klepzig, K.D., Ferro, M.L., Ulyshen, M.D., Gimmel, M.L., Mahfouz, J.B., Tiarks, A.E., & Carlton, C.E. (2012) Effects of small-scale dead wood additions on beetles in southeastern U.S. pine forests. Forests, 3, 632–652.

Klink, R. Van, Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., & Chase, J.M. (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science, 368, 417–420.

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., & Fontaine, C. (2017) Artificial light at night as a new threat to pollination. Nature, 548, 206–209.

Komonen, A., Halme, P., & Kotiaho, J.S. (2019) Alarmist by bad design : Strongly popularized unsubstantiated claims undermine credibility of conservation science. Rethinking Ecology, 4, 17–19.

Komonen, A., Kuntsi, S., Toivanen, T., & Kotiaho, J.S. (2014) Fast but ephemeral effects of ecological restoration on forest beetle community. Biodiversity and Conservation, 23, 1485–1507.

Komonen, A. & Müller, J. (2018) Dispersal ecology of dead wood organisms: implications for connectivity conservation. Conservation Biology, 32, 535-545.

Koptur, S., Rodriguez, M.C., Oberbauer, S.F., Weekley, C., & Herndon, A. (2002) Herbivore-free time? Damage to new leaves of woody plants after Hurricane Andrew. Biotropica, 34, 547–554.

Kraut, A., Liira, J., & Lõhmus, A. (2016) Beyond a minimum substrate supply: Sustaining saproxylic beetles in semi-natural forest management. Forest Ecology and Management, 360, 9–19.

Kremen, C. & Merenlender, A.M. (2018) Landscapes that work for biodiversity and people. Science, 362, 1–9.

Krimmer, E., Martin, E.A., Krauss, J., Holzschuh, A., & Steffan-Dewenter, I. (2019) Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. Agriculture, Ecosystems and Environment, 284, 106590.

Kunin, W.E. (2019) Robust evidence of declines in insect abundance and biodiversity. Nature, 574, 641–642.

Kurze, S., Heinken, T., & Fartmann, T. (2018) Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species. Oecologia, 188, 1227–1237.

Langevelde, F. Van, Braamburg-Annegarn, M., Huigens, M.E., Groendijk, R., Poitevin, O., Van Deijk, J.R., Ellis, W.N., Van Grunsven, R.H.A., De Vos, R., Franzén, M., & WallisDeVries, M.F. (2018) Declines in moth populations stress the need for conserving dark nights. Global Change Biology, 24, 925–932.

Larson, D.J. (1985) Structure in Temperate Predaceous Diving Beetle Communities (Coleoptera : Dytiscidae). Holarctic Ecology, 8, 18–32.

Lassauce, A., Paillet, Y., Jactel, H., & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators, 11, 1027–1039.

Leather, S.R. (2019) "Insectageddon" - bigger headlines, more hype, but where's the funding? https://simonleather.wordpress.com/2019/02/15/insectageddon-bigger-headlines-more-hype-but-wheres-the-funding/, February 15, 2019

Lebuhn, G., Droege, S., Connor, E.F., Gemmill-Herren, B., Potts, S.G., Minckley, R.L., Griswold, T., Jean, R., Kula, E., Roubik, D.W., Cane, J., Wright, K.W., Frankie, G., & Parker, F. (2013) Detecting

Insect Pollinator Declines on Regional and Global Scales. Conservation Biology, 27, 113–120.

Limpens, J., Granath, G., Gunnarsson, U., et al. (2011) Climatic modifiers of the response to nitrogen deposition in peat-forming sphagnum mosses: A meta-analysis. New Phytologist, 191, 496–507.

Lincoln, D.E., Couvet, D., & Sionit, N. (1986) Response of an insect herbivore to host plants grown in carbon dioxide enrichted atmospheres. Oecologia, 69, 556–560.

Lindenmayer, D.B., Piggott, M.P., & Wintle, B.A. (2013) Counting the books while the library burns: Why conservation monitoring programs need a plan for action. Frontiers in Ecology and the Environment, 11, 549–555.

Lischeid, G. (2001) Das Klima am Westrand des Steigerwaldes. Bayrisches Forum Ökologie, 90, 169–174.

Lister, B.C. & Garcia, A. (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. PNAS, 115, 1–10.

Lønsmann Iversen, L., Rannap, R., Thomsen, P.F., Kielgast, J., & Sand-jensen, K. (2013) How do low dispersal species establish large range sizes? The case of the water beetle Graphoderus bilineatus. Ecography, 36, 770–777.

Macgregor, C.J., Williams, J.H., Bell, J.R., & Thomas, C.D. (2019) Moth biomass increases and decreases over 50 years in Britain. Nature Ecology & Evolution, 3, 1645–1649.

Mangels, J., Fiedler, K., Schneider, F.D., & Blu, N. (2017) Diversity and trait composition of moths respond to land- use intensification in grasslands: generalists replace specialists. Biodiversity and Conservation, 26, 3385–3405.

Marchetti, M.P., Garr, M., & Smith, A.N.H. (2010) Evaluating wetland restoration success using aquatic macroinvertebrate assemblages in the sacramento valley, California. Restoration Ecology, 18, 457–466.

Martikainen, P. & Kaila, L. (2004) Sampling saproxylic beetles: lessons from a 10-year monitoring study. Biological Conservation, 120, 175–185.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., & Rauh, J. (2000) Species richness of Coleoptera in mature and old-growth boreal forests in southern Finland. Biological Conservation, 94, 199–209.

Martín-Vertedor, D., Ferrero-García, J.J., & Torres-Vila, L.M. (2010) Global warming affects phenology and voltinism of *Lobesia botrana* in Spain. Agricultural and Forest Entomology, 12, 169–176.

Mcmahon, T.A., Halstead, N.T., Johnson, S., Raffel, T.R., Romansic, J.M., Crumrine, P.W., & Rohr, J.R. (2012) Fungicide-induced declines of freshwater biodiversity modify ecosystem functions and services. Ecology Letters, 15, 714–722.

Memmott, J., Craze, P.G., Waser, N.M., & Price, M. V. (2007) Global warming and the disruption of plant-pollinator interactions. Ecology Letters, 10, 710–717.

Menzel, A., Sparks, T.H., Estrella, N., et al. (2006) European phenological response to climate change matches the warming pattern. Global Change Biology, 12, 1969–1976.

Merckx, T., Feber, R.E., Hoare, D.J., Parsons, M.S., Kelly, C.J., Bourn, N.A.D., & Macdonald, D.W. (2012a) Conserving threatened Lepidoptera: Towards an effective woodland management policy in landscapes under intense human land-use. Biological Conservation, 149, 32–39.

Merckx, T., Marini, L., Feber, R.E., & MacDonald, D.W. (2012b) Hedgerow trees and extended-width field margins enhance macro-moth diversity: Implications for management. Journal of Applied Ecology, 49, 1396–1404.

Merckx, T. & Pereira, H.M. (2015) Reshaping agri-environmental subsidies: From marginal farming to large-scale rewilding. Basic and Applied Ecology, 16, 95–103.

Miguel-Chinchilla, L., Boix, D., Gascón, S., & Comín, F.A. (2014) Macroinvertebrate biodiversity patterns during primary succession in manmade ponds in North-Eastern Spain. Journal of Limnology, 73, 428–440.

Mikkola, K. (1997) Population trends of Finnish Lepidoptera during 1961-1996. Entomologica Fennica, 8, 121–143.

Miller, K.B. & Bergsten, J. (2016) Diving beetles of the world: Systematics and biology of the Dytiscidae. JHU Press, Baltimore.

Minchin, P.R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. Theory and models in vegetation science (ed. by I.C. Prenctice and E. Maarel), pp. 89–107. DR W. Junk Publishers, Dordrecht.

Mitter, C., Davis, D.R., & Cummings, M.P. (2017) Phylogeny and Evolution of Lepidoptera. Annual Review of Entomology, 62, 265–283.

Mody, K., Lerch, D., Müller, A.K., Simons, N.K., Blüthgen, N., & Harnisch, M. (2020) Flower power in the city: Replacing roadside shrubs by wildflower meadows increases insect numbers and reduces maintenance costs. PLoS ONE, 15, 1–29.

Molinari, A., Guadagnini, L., Marcaccio, M., & Guadagnini, A. (2012) Background levels and threshold values of chemical species in three large-scale groundwater bodies in Northern Italy. Science of the Total Environment, 425, 9–19.

Montgomery, G.A., Dunn, R.R., Fox, R., Jongejans, E., Leather, S.R., Saunders, M.E., Shortall, C.R., Tingley, M.W., & Wagner, D.L. (2020) Is the insect apocalypse upon us? How to find out. Biological Conservation, 241, 108327.

Morales-Hidalgo, D., Oswalt, S.N., & Somanathan, E. (2015) Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. Forest Ecology and Management, 352, 68–77.

Müller-Using, S. & Bartsch, N. (2009) Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in Central Germany. European Journal of Forest Research, 128, 287–296.

Müller, J. (2005) Waldstrukturen als Steuergröße für Artengemeinschaften in kollinen bis submontanen Buchenwäldern Inhaltsverzeichnis. TU München,

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I.M.M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., & Gossner, M.M. (2015) Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography, 38, 499–509.

Müller, J., Bußler, H., & Kneib, T. (2008) Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. Journal of Insect Conservation, 12, 107–124.

Müller, J., Engel, H., & Blaschke, M. (2007a) Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany. European Journal of Forest Research, 126, 513–527.

Müller, J., Hothorn, T., & Pretzsch, H. (2007b) Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica* L. Forest Ecology and Management, 242, 297–305.

Müller, J., Mehr, M., Bässler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., Klemmt, H.J., & Brandl, R. (2012) Aggregative response in bats: Prey abundance versus habitat. Oecologia, 169, 673–684.

Müller, J., Noss, R.F., Bussler, H., & Brandl, R. (2010) Learning from a "benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation, 143, 2559–2569.

Nilsson, A.N. (1984) Species Richness and Succession of Aquatic Beetles in Some Kettle-Hole Ponds in Northern Sweden. Holarctic Ecology, 7, 149–156.

Nilsson, A.N., Elmberg, J., & Sjoberg, K. (1994) Abundance and Species Richness Patterns of Predaceous Diving Beetles (Coleoptera, Dytiscidae) in Swedish Lakes. Journal of Biogeography, 21, 197–206.

Nilsson, A.N. & Hájek, J. (2018) A World Catalogue of the Family Dytiscidae, or the Diving Beetles (Coleoptera, Adephaga). .

Nilsson, A.N. & Soderberg, H. (1996) Abundance and species richness patterns of diving beetles (Coleoptera, Dytiscidae) from exposed and protected sites in 98 northern Swedish lakes. Hydrobiologia, 321, 83–88.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., & Wagner, H. (2018) vegan: Community Ecology Package.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R., Bruyn, L.

De, Fuhr, M., Kanka, R., Lundin, L., Luque, S., Magura, T., & Matesanz, S. (2010) Does biodiversity differ between managed and unmanaged forests? A meta-analysis on species richness in Europe. Conservation Biology, 24, 101–112.

Palik, B., Batzer, D.P., Buech, R., Nichols, D., Cease, K., Egeland, L., & Streblow, D.E. (2001) Seasonal pond characteristics across a chronosequence of adjacent forest ages in northern Minnesota, USA. Wetlands, 21, 532–542.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., & Warren, M. (1999) Polewardshifts in geographical ranges of butterfly species associated with regionalwarming. Nature, 399, 579–583.

Parmesan, C. & Yohe, G. (2003) Parmesan & Yohe 2003 A globally coherent fingerprint of climate change impacts across natural systems. .

Parviainen, J. (2005) Virgin and natural forests in the temperate zone of Europe. Forest Snow and Landscape Research, 79, 9–18.

Pasanen, H., Junninen, K., Boberg, J., Tatsumi, S., Stenlid, J., & Kouki, J. (2018) Life after tree death: does restored dead wood host different fungal communities to natural woody substrates? Forest Ecology and Management, 409, 863–871.

Pasanen, H., Junninen, K., & Kouki, J. (2014) Restoring dead wood in forests diversifies wood-decaying fungal assemblages but does not quickly benefit red-listed species. Forest Ecology and Management, 312, 92–100.

Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R., & Thomas, C.D. (2012) Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. Science, 336, 1028–1031.

Pearson, R.G. (2016) Reasons to Conserve Nature. Trends in Ecology and Evolution, 31, 366–371.

Pedersen, E.J., Miller, D.L., Simpson, G.L., & Ross, N. (2019) Hierarchical generalized additive models in ecology: An introduction with mgcv. PeerJ, 2019, 1–42.

Perdomo, G., Sunnucks, P., & Thompson, R.M. (2012) The role of temperature and dispersal in moss-microarthropod community assembly after a catastrophic event. Philosophical Transactions of the Royal Society B: Biological Sciences, 367, 3042–3049.

Perrett, L.A., Johnston, E.L., & Poore, A.G.B. (2006) Impact by association: Direct and indirect effects of copper exposure on mobile invertebrate fauna. Marine Ecology Progress Series, 326, 195–205.

Pescott, O.L., Simkin, J.M., August, T.A., Randle, Z., Dore, A.J., & Botham, M.S. (2015) Air pollution and its effects on lichens , bryophytes , and lichen-feeding Lepidoptera : review and evidence from. Biological Journal of the Linnean Society, 115, 611–635.

Pilotto, F., Kühn, I., Adrian, R., et al. (2020) Meta-analysis of multidecadal biodiversity trends in Europe. Nature Communications, 11, 1-11.

Pinkert, S., Brandl, R., & Zeuss, D. (2017) Colour lightness of dragonfly assemblages across North America and Europe. Ecography, 40, 1110–1117.

Plant, A.R., Bickel, D.J., Chatelain, P., Hauser, M., Cesne, M. Le, Surin, C., Saokhod, R., Nama, S., Soulier-perkins, A., Daugeron, C., & Srisuka, W. (2018) Spatiotemporal dynamics of insect diversity in tropical seasonal forests is linked to season and elevation, a case from northern Thailand. Raffles Bulletin of Zoology, 66, 382–393.

Pope, S.E., Fahrig, L., & Merriam, H.G. (2000) Landscape complementation and metapopulation effects on Leopard Frog populations. Ecology, 81, 2498–2508.

Potocký, P., Bartoňová, A., Beneš, J., Zapletal, M., & Konvička, M. (2018) Life-history traits of Central European moths: Gradients of variation and their association with rarity and threats. Insect Conservation and Diversity, 11, 493–505.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W.E. (2010) Global pollinator declines : trends , impacts and drivers. Trends in Ecology & Evolution, 25, 345–353.

Primack, R.B., Ibáñez, I., Higuchi, H., Lee, S.D., Miller-Rushing, A.J., Wilson, A.M., & Silander, J.A. (2009) Spatial and interspecific variability in phenological responses to warming temperatures. Biological Conservation, 142, 2569–2577.

Primack, R.B., Miller-Rushing, A.J., Corlett, R.T., Devictor, V., Johns, D.M., Loyola, R., Maas, B., Pakeman, R.J., & Pejchar, L. (2018) Biodiversity gains? The debate on changes in local- vs global-scale species richness. Biological Conservation, 219, A1–A3.

Pureswaran, D.S., Roques, A., & Battisti, A. (2018) Forest Insects and Climate Change. Current Forestry Reports, 4, 35–50.

R Core Team (2018) R: A Language and Environment for Statistical Computing.

Rada, S., Schweiger, O., Harpke, A., Kühn, E., Kuras, T., Settele, J., & Musche, M. (2019) Protected areas do not mitigate biodiversity declines: A case study on butterflies. Diversity and Distributions, 25, 217–224.

Reif, J., Storch, D., Vorisek, P., Stastny, K., & Bejcek, V. (2008) Bird-habitat associations predict population trends in central European forest and farmland birds 1 C. Biodiversity and Conservation, 17, 3307–3319.

Reif, J., Voříšek, P., Šťastný, K., & Bejček, V. (2006) Populační trendy ptáků v České republice v letech 1982–2005 (Population trends of birds in the Czech Republic during 1982–2005). Sylvia, 42, 22–37.

Reinecke, J., Klemm, G., & Heinken, T. (2014) Vegetation change and homogenization of species composition in temperate nutrient deficient Scots pine forests after 45 yr. Journal of Vegetation Science, 25, 113–121.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. Conservation biology: the journal of the Society for Conservation Biology, 13, 1220–1222.

Richman, N.I., Böhm, M., Adams, S.B., Alvarez, F., Bergey, E.A., Bunn, J.J., & Dawkins, K.L. (2015) Multiple drivers of decline in the global status of freshwater crayfish (Decapoda: Astacidea). Philosophical Transactions of the Royal Society B, 370, 1–10.

Ripley, B.J. & Simovich, M.A. (2009) Species richness on islands in time: Variation in ephemeral pond crustacean communities in relation to habitat duration and size. Hydrobiologia, 617, 181–196.

Ripple, W.J., Wolf, C., Newsome, T.M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M.I., & Laurance, W.F. (2017) World scientists' warning to humanity: A second notice. BioScience, 67, 1026–1028.

Robinet, C. & Roques, A. (2010) Direct impacts of recent climate warming on insect populations. Integrative Zoology, 5, 132–142.

Rockström, J., Steffen, W., Noone, K., et al. (2009a) Planetary boundaries: Exploring the safe operating space for humanity. Ecology and Society, 14, 1-33.

Rockström, J., W. Steffen, K. Noone, et al. (2009b) A safe operation space for humanity. Nature, 461, 472–475.

Rohr, J.R. & Crumrine, P.W. (2005) Effects of an herbicide and an incecticide on pond community structure and processes. Ecological Applications, 15, 1135–1147.

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., & Imeson, A. (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature, 453, 353–357.

Rosset, V., Angélibert, S., Arthaud, F., Bornette, G., Robin, J., Wezel, A., Vallod, D., & Oertli, B. (2014) Is eutrophication really a major impairment for small waterbody biodiversity? Journal of Applied Ecology, 51, 415–425.

Rouault, G., Candau, J.N., Lieutier, F., Nageleisen, L.M., Martin, J.C., & Warzée, N. (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Annals of Forest Science, 63, 613–624.

Roulin, A. (2014) Melanin-based colour polymorphism responding to climate change. Global Change Biology, 20, 3344–3350.

Sabrosky, C.W. (1953) How many insects are there? Systematic Zoology, 2, 31–36.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L.R., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. Science, 287, 1770–1774.

Samways, M.J., Barton, P.S., Birkhofer, K., et al. (2020) Solutions for humanity on how to conserve insects. Biological Conservation, 242, 108427.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation journal, 232, 8–27.

Saunders, M.E., Janes, J., & O'Hanlon, J. (2019) Moving on from the insect apocalypse narrative: engaging with evidence-based insect conservation. BioScience, 70, 80–89.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., & Ammer, C. (2017) The impact of even- aged and uneven- aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Animal Ecology, 55, 267–278.

Schauer, B., Steinbauer, M.J., Vailshery, L.S., Müller, J., Feldhaar, H., & Obermaier, E. (2017) Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. Biodiversity and Conservation, 27, 853-869.

Scheers, K. (2014) On the increase of *Hydrovatus cuspidatus* (Kunze, 1818) and *Graptodytes bilineatus* (Sturm, 1835)(Coleoptera: Dytiscidae) in Belgium. Bulletin SRBE/KBVE, 150, 195–198.

Schelhaas, M.-J., Nabuurs, G.-J., & Schuck, A. (2003) Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology, 9, 1620–1633.

Schenker, N. & Gentleman, J.F. (2001) On judging the significance of differences by examining the overlap between confidence intervals. The American Statistician, 55, 182–186.

Schmidl, J. (2003) Bioindikation stehender Gewässer anhand adephager Wasserkäfer. bioform entomology, Nürnberg.

Schmidl, J. & Bußler, H. (2004) Ökologische Gilden xylobionter Käfer Deutschlands. Naturschutz und Landschaftsplanung, 36, 202–218.

Schrijver De, A., de Frenne, P., Ampoorter, E., van Nevel, L., Demey, A., Wuyts, K., & Verheyen, K. (2011) Cumulative nitrogen input drives species loss in terrestrial ecosystems. Global Ecology and Biogeography, 20, 803–816.

Schuch, S., Bock, J., Krause, B., Wesche, K., & Schaefer, M. (2011) Long-term population trends in three grassland insect groups: a comparative analysis of 1951 and 2009. Journal of Applied Entomology, 136, 321–331.

Schuch, S., Wesche, K., & Schaefer, M. (2012) Long-term decline in the abundance of leafhoppers and planthoppers (Auchenorrhyncha) in Central European protected dry grasslands. Biological Conservation, 149, 75–83.

Scott, J.A. & Epstein, M.E. (1987) Factors Affecting Phenology in a Temperate Insect Community. American Midland Naturalist, 117, 103–118.

Scott, W.A. & Anderson, R. (2003) Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. Biological Conservation, 110, 197–210.

Segerer, A. & Hausmann, A. (2011) Die Großschmetterlinge Deutschlands. The Macrolepidoptera of Germany. Heterocera Press, Budapest.

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S., & Müller, J. (2017) An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology, 98, 1613–1622.

Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., Thorn, S., Ulyshen, M.D., & Müller, J. (2015a) Experimental studies of dead-wood biodiversity - a review identifying global gaps in knowledge. Biological Conservation, 191, 139–149.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., & Müller, J. (2015b) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conservation Biology, 29, 382–390.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarli, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W.W. (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature, 574, 671–674.

Seidl, R. & Rammer, W. (2017) Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. Landscape Ecology, 32, 1485–1498.

Seidl, R., Schelhaas, M., Rammer, W., & Verkerk, P.J. (2014) Increasing forest disturbances in Europe and their impact on carbon storage. Nature Climate Change, 4, 806–810.

Seidl, R., Schelhaas, M.J., & Lexer, M.J. (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology, 17, 2842–2852.

Senf, C. & Seidl, R. (2020) Mapping the forest disturbance regimes of Europe. Nature Sustainability.

Sferra, C.O., Hart, J.L., & Howeth, J.G. (2017) Habitat age influences metacommunity assembly and species richness in successional pond ecosystems. Ecosphere, 8, 1–18.

Sgardeli, V., Zografou, K., & Halley, J.M. (2016) Climate change versus ecological drift: Assessing 13 years of turnover in a butterfly community. Basic and Applied Ecology, 17, 283–290.

Sheppard, L.W., Bell, J.R., Harrington, R., & Reuman, D.C. (2015) Changes in large-scale climate alter spatial synchrony of aphid pests. Nature Climate Change, 6, 610-613.

Shortall, R.C., Moore, A., Smith, E., Hall, J.M., Woiwod, P.I., & Harrington, R. (2009) Long-term changes in the abundance of flying insects. Insect Conservation and Diversity, 2, 251–260.

Simmons, B.I., Balmford, A., Bladon, A.J., Christie, A.P., De Palma, A., Dicks, L. V., Gallego-Zamorano, J., Johnston, A., Martin, P.A., Purvis, A., Rocha, R., Wauchope, H.S., Wordley, C.F.R., Worthington, T.A., & Finch, T. (2019) Worldwide insect declines: An important message, but interpret with caution. Ecology and Evolution, 9, 3678–3680.

Simon-Delso, N., Martin, G.S., Bruneau, E., Delcourt, C., & Hautier, L. (2017) The challenges of predicting pesticide exposure of honey bees at landscape level. Scientific Reports, 7, 1–10.

Sioli, H. (1975) Tropical rivers as expressions of their terrestrial environments. Tropical ecological systems pp. 275–288. Springer, Berlin, Heidelberg.

Skirvin, D.J., Perry, J.N., & Harrington, R. (1997) The effect of climate change on an aphid-coccinellid interaction. Global Change Biology, 3, 1–11.

Slade, E.M., Merckx, T., Riutta, T., Bebber, D.P., Redhead, D., Riordan, P., & Macdonald, D.W. (2013) Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. Ecology, 94, 1519–1530.

Smith, R. V., Doyle, R.M., Burns, L.C., & Stevens, R.J. (1997) A model for nitrite accumulation in soils. Soil Biology and Biochemistry, 29, 1241–1247.

Smith, V.H., Tilman, G.D., & Nekola, J.C. (1999) ScienceDirect - Environmental Pollution: Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution, 100, 179–196.

Speight, M.C.D. (1989) Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg.

Spieles, D.J., Coneybeer, M., & Horn, J. (2006) Community structure and quality after 10 years in two Central Ohio mitigation bank wetlands. Environmental Management, 38, 837–852.

Spitzenberg, D., Sondermann, W., Hendrich, L., & Heckes, U. (2016) Rote Liste und Gesamtartenliste der wasserbewohnenden Käfer (Coleoptera aquatica) Deutschlands. Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 4: Wirbellose Tiere (Teil 2) (ed. by H. Gruttke, M. Binot-Hafke, S. Balzer, H. Haupt, N. Hofbauer, G. Ludwig, G. Matzke-Hajek, and M. Ries), pp. 207–246. Münster.

Stange, E.E. & Ayres, M.P. (2010) Climate Change Impacts: Insects. Encyclopedia of Life Sciences (ELS) pp. 1–7. John Wiley & Sons, Chichester.

Stefanescu, C., Carnicer, J., & Pen, J. (2011a) Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. Ecography, 34, 353–363.

Stefanescu, C., Torre, I., Jubany, J., & Páramo, F. (2011b) Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. Journal of Insect Conservation, 15, 83–93.

Steffen, W., Crutzen, P.J., & McNeill, J.R. (2007) The anthropocene: Are humans now overwhelming the great forces of nature? Ambio, 36, 614–621.

Steiner, A., Ratzel, U., Top-Jensen, M., & Fibiger, M. (2014) Die Nachtfalter Deutschlands - Ein Feldführer. BugBook Publishing, Oestermarie.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., & Drake, B.G. (2003) Elevated CO_2 lowers relative and absolute herbivore density across all species of a scrub-oak forest. Oecologia, 134, 82–87.

Stocker, T.F., Qin, D., & Platner, G.K. (2013) "Climate Change 2013: The Physical Science Basis." 492 Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on 493 Climate Change. Summary for Policymakers (IPCC, 2013).

Stoeckle, B.C., Dworschak, K., Gossner, M.M., & Kuehn, R. (2010) Influence of arthropod sampling solutions on insect genotyping reliability. Entomologia Experimentalis et Applicata, 135, 217–223.

Stokland, J.N., Siitonen, J., & Jonsson, B.G. (2012) Biodiversity in Dead Wood. Cambridge University, Cambridge.

Stork, N.E. (2018) How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? Annual Review of Entomology, 63, 31–45.

Strauss, E.A., Mitchell, N.L., & Lamberti, G.A. (2002) Factors regulating nitrification in aquatic sediments : effects of organic carbon , nitrogen availability , and pH. Canadian Journal of Fisheries and Aquatic Sciences, 56, 554–563.

Suzuki, I., Dular, U., & Kwok, S.C. (1974) Ammonia or Ammonium Ion as Substrate for Oxidation by Nitrosomonas europaea Cells and Extracts. American Society for Microbiology, 120, 556–558.

Sverdrup-Thygeson, A., Gustafsson, L., & Kouki, J. (2014) Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. Biodiversity and Conservation, 23, 513–535.

Thiere, G., Milenkovski, S., Lindgren, P.E., Sahlén, G., Berglund, O., & Weisner, S.E.B. (2009) Wetland creation in agricultural landscapes: Biodiversity benefits on local and regional scales. Biological Conservation, 142, 964–973.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., & Erasmus, B.F.N. (2004a) Article : Extinction risk from climate change. Nature, 427, 145–148.

Thomas, C.D., Jones, T.H., & Hartley, S.E. (2019) " Insectageddon ": A call for more robust data and rigorous analyses. Global Change Biology, 26–27.

Thomas, J.A., Telfer, M.G., Roy, D.B., & Preston, C.D. (2004b) Comparative Losses of British Butterflies , Birds , and Plants and. Science, 303, 1879–1882.

Thompson, L.M., Faske, T.M., Banahene, N., Parry, D., Tobin, P.C., Johnson, D.M., & Grayson, K.L. (2017) Variation in growth and developmental responses to supraoptimal temperatures near latitudinal range limits of gypsy moth *Lymantria dispar* (L .), an expanding invasive species. Physiological Entomology, 42, 181–190.

Thomsen, P.F., Jørgensen, P.S., Bruun, H.H., Pedersen, J., Riis-nielsen, T., Jonko, K., Iwona, S., Rahbek, C., & Karsholt, O. (2015) Resource specialists lead local insect community turnover associated with temperature – analysis of an 18-year full-seasonal record of moths and beetles. Journal of Animal Ecology, 85, 251–261.

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S., & Müller, J. (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters, 19, 163–170.

Thorn, S., Hacker, H.H., Seibold, S., Jehl, H., Bässler, C., & Müller, J. (2015) Guild-specific responses of forest Lepidoptera highlight conservation-oriented forest management - Implications from conifer-dominated forests. Forest Ecology and Management, 337, 41–47.

Thunes, K. (1994) The coleopteran fauna of *Piptoporus betulinus* and *Fomes fomentarius* (Aphyllophorales: Polyporaceae) in Western Norway. Entomologica Fennica, 5, 157–168.

Timmermans, M.J.T.N., Lees, D.C., & Simonsen, T.J. (2014) Molecular Phylogenetics and Evolution Towards a mitogenomic phylogeny of Lepidoptera. Molecular Phylogenetics and Evolution, 79, 169–178.

Townsend, S.A. (2002) Seasonal evaporative concentration of an extremely turbid water-body in the semiarid tropics of Australia. Lakes & Reservoirs: Research and Management, 7, 103–107.

Trenberth, K.E. (2006) The Impact of Climate Change and Variability on Heavy Precipitation, Floods, and Droughts. Encyclopedia of Hydrological Sciences, John Wiley & Sons, Ltd, New-York.

Tudoran, M.M., Marquer, L., & Jönsson, A.M. (2016) Historical experience (1850–1950 and 1961–2014) of insect species responsible for forest damage in Sweden: Influence of climate and land management changes. Forest Ecology and Management, 381, 347–359.

Ubach, A., Páramo, F., Gutiérrez, C., & Stefanescu, C. (2020) Vegetation encroachment drives changes in the composition of butterfly assemblages and species loss in Mediterranean ecosystems. Insect Conservation and Diversity, 13, 151–161.

Urbanek, S. (2013) png: Read and write PNG images.

Vamosi, S.M., Naydani, C.J., & Vamosi, J.C. (2007) Body size and species richness along geographical gradients in Albertan diving beetle (Coleoptera: Dytiscidae) communities. Canadian Journal of Zoology, 85, 443–449.

Vandekerkhove, K. & Thomaes, A. (2015) Saproxylic beetles in non-intervention and coppice-with-standards restoration management in Meerdaal forest (Belgium): an exploratory analysis. iForest, 9, 536–545.

Vellend, M. (2010) Conceptual synthesis in community ecology. Quarterly Review of Biology, 85, 183–206.

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J.L., Messier, J., Myers-Smith, I.H., & Sax, D.F. (2017a) Plant Biodiversity Change Across Scales During the Anthropocene. Annual Review of Plant Biology, 68, 563–586.

Vellend, M., Dornelas, M., Baeten, L., Beauséjour, R., Brown, C.D., De Frenne, P., Elmendorf, S.C., Gotelli, N.J., Moyes, F., Myers-Smith, I.H., Magurran, A.E., McGill, B.J., Shimadzu, H., & Sievers, C. (2017b) Estimates of local biodiversity change over time stand up to scrutiny. Ecology, 98, 583–590.

Vidal, M.C. & Murphy, S.M. (2018) Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. Ecology Letters, 21, 138–150.

Vilén, T., Gunia, K., Verkerk, P.J., Seidl, R., Schelhaas, M., Lindner, M., & Bellassen, V. (2012) Forest Ecology and Management Reconstructed forest age structure in Europe 1950 – 2010. Forest Ecology and Management, 286, 203–218.

Visser, M.E. (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences, 275, 649–659.

Vogel, G. (2017) Where have all the insects gone? Science, 356, 576–579.

Vuorenmaa, J., Forsius, M., & Mannio, J. (2006) Increasing trends of total organic carbon concentrations in small forest lakes in Finland from 1987 to 2003. Science of the Total Environment, 365, 47–65.

Wagner, D.L. (2020) Insect Declines in the Anthropocene. Annual Review of Entomology, 65, 457–480.

Wainwright, C.E., Mitchell, R.M., & Bakker, J.D. (2020) Spatial Sampling Grain Shapes Conclusions about Community Structure and Dynamics. Natural Areas, 40, 51–61.

Warren, R., Price, J., Graham, E., Forstenhaeusler, N., & VanDerWal, J. (2018) The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. Science, 360, 791–795.

Weiser, E.L., Diffendorfer, J.E., Grundel, R., López-Hoffman, L., Pecoraro, S., Semmens, D., & Thogmartin, W.E. (2019) Balancing sampling intensity against spatial coverage for a community science monitoring programme. Journal of Applied Ecology, 56, 2252–2263.

Weiss, M., Kozel, P., Zapletal, M., Hauck, D., Prochazka, J., Benes, J., Cizek, L., & Sebek, P. (2020) Forest Ecology and Management The effect of coppicing on insect biodiversity. Small-scale mosaics of successional stages drive community turnover. Forest Ecology and Management, 118774.

Welti, E.A.R., Joern, A., Ellison, A.M., Lightfoot, D.C., Record, S., Rodenhouse, N., Stanley, E.H., & Kaspari, M. (2020) Meta-analyses of insect temporal trends must account for the complex sampling histories inherent to many long-term monitoring efforts.

Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J., & Haddad, N.M. (2019) Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. PLoS ONE, 14, 1–21.

Wesenberg-Lund, C. (1943) Die Biologie der Süßwasserinsekten. Kopenhagen, Berlin, Wien.

White, E.R. (2019) Minimum Time Required to Detect Population Trends: The Need for Long-Term Monitoring Programs. BioScience, 69, 40–46.

Wiecek, M., Martin, P., & Lipinski, A. (2013) Water mites as potential long-term bioindicators in formerly drained and rewetted raised bogs. Ecological Indicators, 34, 332–335.

Wilson, K., Cotter, S.C., Reeson, A.F., & Pell, J.K. (2001) Melanism and disease resistance in insects. Ecology Letters, 4, 637–649.

Wölfling, M., Uhl, B., & Fiedler, K. (2019) Multi-decadal surveys in a Mediterranean forest reserve – do succession and isolation drive moth species richness? Nature Conservation, 35, 25–40.

Wood, P.J., Greenwood, M.T., & Agnew, M.D. (2003) Pond biodiversity and habitat loss in the UK. Area, 35, 206–216.

Wood, S.N. (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association, 99, 673–686.

Wood, S.N. (2017) Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC, New York.

Wu, S., Chang, C., Mai, G., Rubenstein, D.R., Yang, C., Huang, Y., Lin, H., Shih, L., Chen, S., & Shen, S. (2019) Artificial intelligence reveals environmental constraints on colour diversity in insects. Nature Communications, 10, 1–9.

Xing, S., Bonebrake, T.C., Ashton, L.A., Kitching, R.L., Cao, M., Sun, Z., Chee, J., & Akihiro, H. (2018) Colors of night: climate – morphology relationships of geometrid moths along spatial gradients in southwestern China. Oecologia, 188, 537–546.

Xing, S., Bonebrake, T.C., Tang, C.C., Pickett, E.J., Cheng, W., Greenspan, S.E., Williams, S.E., & Scheffers, B.R. (2016) Cool habitats support darker and bigger butterflies in Australian tropical forests. Ecology and Evolution, 6, 8062–8074.

Yee, D.A. (2014) Ecology , Systematics , and the Natural History of Predaceous Diving Beetles (Coleoptera : Dytiscidae). Springer, Dordrecht.

Yee, D.A. & Juliano, S.A. (2007) Consequences of detritus type in an aquatic microsystem: effects on water quality, micro-organisms and performance of the dominant consumer. Freshwater Biology, 51, 448–459.

Yodzis, P. (1986) Competition, mortality, and community structure. Community ecology pp. 480–491. Harper and Row, New York.

Zahiri, R., Lafontaine, D., Canada, A., Building, K.W.N., Farm, C.E., Schmidt, C., Agency, F.I., Building, K.W.N., Farm, C.E., Holloway, J.D., Kitching, I.J., Museum, N.H., Road, C., Mutanen, M., & Wahlberg, N. (2013) Relationships among the basal lineages of Noctuidae. The Norwegian Academy of Science and Letters, 42, 488–507.

Zeuss, D., Brandl, R., Brändle, M., Rahbek, C., & Brunzel, S. (2014) Global warming favours light-coloured insects in Europe. Nature Communications, 5, 3874.

Zhang, Z., Cazelles, B., Tian, H., Stige, L.C., Bräuning, A., & Stenseth, N.C. (2012) Periodic temperature-associated drought/flood drives locust plagues in China. Proceedings of the Royal Society B: Biological Sciences, 276, 823–831.

Zikeli, S., Jahn, R., & Kastler, M. (2002) Initial soil development in lignite ash landfills and settling ponds in Saxony-Anhalt, Germany. Journal of Plant Nutrition and Soil Science, 165, 530–536.

Ziska, L.H., Pettis, J.S., Edwards, J., Hancock, J.E., Tomecek, M.B., Clark, A., Dukes, J.S., Loladze, I., & Polley, H.W. (2016) Rising atmospheric CO_2 is reducing the protein concentration of a floral pollen source essential for north American bees. Proceedings of the Royal Society B: Biological Sciences, 283, 1–7.

Zytynska, S.E., Doerfler, I., Gossner, M.M., Sturm, S., Weisser, W.W., & Müller, J. (2018) Minimal effects on genetic structuring of a fungus-dwelling saproxylic beetle after recolonisation of a restored forest. Journal of Applied Ecology, 55, 2933-2943.

Author contributions

Statement of individual author contributions

Roth, N., Zoder, S., Zaman, A. A., Thorn, S., & Schmidl, J*. (2020). Long-term monitoring reveals decreasing water beetle diversity, loss of specialists and community shifts over the past 28 years. *Insect Conservation and Diversity*, 13(2), 140-150.				
Participated in	**Author initials, responsibility decreasing from left to right**			
Study design	JS	SZ	NR	
Methods development	JS	SZ		
Data collection	JS	SZ	AAZ	NR
Data analysis & interpretation	NR	JS	ST	
Writing of first draft	NR			
Editing the manuscript	NR	JS	ST	AAZ

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Acknowledgements: The authors thank Jörg Müller for his valuable ideas and suggestions during data analyses and preparation of the manuscript. The authors thank W. Ran for linguistic revision of the manuscript. The authors thank Mareike Kortmann for counterchecking during the revision process.

Roth, N., Hacker, H. H., Heidrich, L., Friess, N., Garcia-Barros, E., Habel, J. C., Thorn, S., Müller, J. (submitted as) Host specificity and species colouration mediate the regional decline of nocturnal moths in central European forests. *Ecography*								
Participated in	**Author initials, responsibility decreasing from left to right**							
Study design	JM	HHH						
Methods development	HHH	JM						
Data collection	HHH	LH	NF	JM				
Data analysis & interpretation	NR	JM	LH	NF				
Writing of first draft	NR							
Editing the manuscript	NR	LH	JM	NF	JH	EGB	ST	HHH

Acknowledgements: We thank the field assistant and students for their help during data acquisition of different subsets in this project. Furthermore, we thank P. Hull for linguistic revision of the manuscript. The research was partly funded by the Hessen State Ministry for Higher Education, Research and the Arts, Germany, as part of the LOEWE priority project Nature 4.0 – Sensing Biodiversity.

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*contributed equally

Acknowledgements: This project was financed by the Bayerisches Staatsministerium für Ernährung, Landwirtschaft und Forsten, grant L55. We thank the Bavarian State Forestry BaySF for cooperation, in particular the forestry department Ebrach with its manager Ulrich Mergner. We thank Karen A. Brune for linguistic revision of the manuscript.

Publication List

Publications as part of the doctoral thesis

Roth, N., Zoder, S., Zaman, A. A., Thorn, S., & Schmidl, J. (2020). Long-term monitoring reveals decreasing water beetle diversity, loss of specialists and community shifts over the past 28 years. Insect Conservation and Diversity, 13(2), 140-150.

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Additional publications

Bae, S., Heidrich, L., Levick, S. R., Gossner, M. M., Seibold, S., Weisser, W. W., ... , Roth, N., ... & Schulze, E. D. (2020). Dispersal ability, trophic position and body size mediate species turnover processes: Insights from a multi-taxa and multi-scale approach. Diversity and Distributions.

Streinzer, M., Roth, N., Paulus, H. F., & Spaethe, J. (2019). Color preference and spatial distribution of glaphyrid beetles suggest a key role in the maintenance of the color polymorphism in the peacock anemone (Anemone pavonina, Ranunculaceae) in Northern Greece. Journal of Comparative Physiology A, 205(5), 735-743.

Müller, J., Varandi, H. B., Babaii, M. R., Farashiani, M. E., Sageb-Talebi, K., Lange, F., Gossner, M. M., Jarzabek-Müller, A., Roth, N., Thorn, S. & Seibold, S. (2018). The diversity of saproxylic insects (Coleoptera, Heteroptera) on four tree species of the Hyrcanian forest in Iran. Journal of Insect Conservation, 22(3-4), 607-625.

Acknowledgements

First, I would like to thank Prof. Dr. Jörg Müller for giving me the opportunity to work on this exciting topic and for funding my position. Thank you for the experiences I could gain during my time as PhD student and for the research experience in your team. Thank you also for motivating me to finish the thesis after I left Fabrikschleichach.

I would like to express my appreciation to Prof.Dr. Jan Habel for being part of my PhD committee, giving useful advices for projects and papers and for being referee of this thesis.

I would like to thank Dr. Simon Thorn for being part of my PhD committee and for his assistance, especially with R.

Furthermore, I am grateful to Dr. Inken Dörfler, Hermann Hacker and Dr. Jürgen Schmidl for sharing their data, which allowed me to conduct the studies, presented in this thesis. Thank you in addition, Jürgen, for your support and for showing me the world of insects and guiding my first steps in insect research.

I wish to acknowledge the support of all my co-authors, which helped me during the writing and revision processes.

Thank you to the FSF-crew for welcoming me as a colleague for 3.5 years. I would like to pay my special regards to my fellow PhD-colleagues with whom I shared the best and the worst moments. Many thanks especially to Mareike for your invaluable support and hints which undoubtedly contributed a lot to the completion of this thesis.

Thank you to the colleagues from the ZooIII and the ZooII in Würzburg, who were welcoming me anytime I came to the Biocenter. I have a special thought for Brigitte, who liked to remind me that there are more important things in life, than work.

Merci à ma famille pour votre soutien illimité.

Thank you to all my friends, and everyone keeping me grounded and connected to the "real world".

Thanks to Jamaican music. Big up and respect to all the creators and artists. "Dancehall a mi everyting".