Land use and climate change: Anthropogenic effects on arthropod communities and functional traits

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Summary

Today, the world's surface is strongly influenced by human activities and thus the present-day geological era has been termed the Anthropocene. One of the strongest anthropogenic drivers is land use influencing habitats and species worldwide. Additionally, global climate is shaped by human activities, and since climatic conditions have strong effects on the distribution and fitness of organisms, this is the also one of the most important anthropogenic impacts on ecosystems. Hence, both factors affect diversity of species and habitats, but also ecosystem functioning and services.

Analysing species diversity is a well-established method to draw conclusions on ecosystem functioning, because the stability of ecosystems increases with species richness and abundance. It is also possible to measure species' responses in ecosystems, using functional diversity as a predictor. Species traits are features or measurable properties that may be related to the effect or response of a species in an ecosystem (e.g. nutrition specialisation or distribution) and play an important role to determine functional diversity. In this thesis, I analyse and combine the effects of land use and temperature on arthropods in general but also on moths as a case study, which is an unattended but diverse taxonomic group. I consider different levels as (1) Arthropod communities in general, (2) moths as a functional group, (3) morphological variability of single species, and (4) physiological variability of single individuals and show how specialists and generalists differ in their response and effect traits and how these differences have effects on the different levels.

Main parts of this thesis were performed in the Biodiversity-Exploratories, a research platform that focuses on effects of land-use intensity on biodiversity and ecological processes in forests and grasslands in three different regions in Germany

The first study focussed on beech herbivory affected by harvesting intensity and beech dominance. For this purpose, we determined leaf damage and collected Arthropod herbivores in three different regions distributed across Germany. The results suggest a general negative effect of intensive land-use on forest herbivores and the strongest negative effect appeared early in the growing season. For the second and third study, we collected more than 5000 moths from the same three regions, and focussed on grasslands. We determined 461 different species, assigned several interspecific life-history traits (describing specialisation on resources or reproductive strategies), and additionally measured morphological traits (body mass and wing area) of more than 2000 individuals. In the second study, we analysed the effect of land-use intensity (as grazing, mowing and fertilisation) on species diversity and trait composition in moth communities. With increasing land-use intensity, a general decrease of species diversity across all regions was apparent, but also a shift to generalised species, which leads to functional homogenisation in ecosystems. Mowing had the strongest negative effect. The third study focused on intraspecific effects based on morphological changes with increasing land-use intensity. We found several species that benefit from the application of fertilisers due to an increasing body mass, which enhances reproduction success of insects. Such species are mostly generalists, but were still not able to increase their abundance in stronger managed habitats in contrast to other species. In the fourth study, we analysed transpiration and metabolic rate from 557 different arthropod individuals of forest and grassland sites. For this I developed a simple and effective method to measure water loss of several samples within a short period, which we describe in detail in this chapter. Specimen from grassland sites, representing arid habitats in contrast to forests, show generally lower water loss rates. These species developed strategies decreasing cuticular transpiration, resulting in a higher effect of respiratory transpiration on total water loss. In the fifth study, we kept caterpillars of 30 species in different temperature treatments analysing the survival and growth rate in response to the surrounding temperature. Additionally we measured transpiration and metabolic rate. All species showed in general a lower survival rate and increasing growth, transpiration and metabolic rate with higher temperature and especially specialists face a higher risk from increasing temperature.

Hence, this thesis shows similar effects of land use and climate change, as both drivers lead to a general loss of diversity and a shift towards more generalistic communities. Communities of specialists are, however, important to decrease homogenisation and thus receive ecosystem functions. These results provide important information for national and international policies and to support the development of sustainable land-use methods and to reduce climate change.

Zusammenfassung

Unser Planet ist durch menschliche Einflüsse so stark geprägt, dass die aktuelle geologische Ära auch als Anthropozän bezeichnet wird. Durch ihren weltweiten Einfluss auf Lebensräume und Arten, gilt Landnutzung in diesem Zusammenhang als einer der stärksten anthropogenen Faktoren. Auch das Weltklima wird hauptsächlich durch den Menschen geprägt und da klimatische Bedingungen einen starken Einfluss auf die Verbreitung und Fitness von Organismen haben, gilt auch Klimawandel als einer der wichtigsten Faktoren durch den Menschen auf Ökosysteme. Beide Faktoren haben einen starken Einfluss auf die Diversität von Arten und Habitaten, aber auch auf Ökosystemfunktionen und Dienstleistungen.

Die Stabilität eines Ökosystems steigt mit der Anzahl der darin lebenden Arten und Individuen. Die Untersuchung der Diversität von Arten ist eine sehr etablierte Methode, um Rückschlüsse auf Ökosystemfunktionen zu ziehen. Analysen funktioneller Diversität ermöglichen, die Reaktionen und Eigenschaften der Arten im Ökosystem zu messen. Die Eigenschaft einer Art (engl. „species trait“) beschreibt dabei Merkmale, die mit dem Einfluss dieser Art auf das Ökosystem in Verbindung stehen (bspw. Nahrungsspezialisierung oder Verbreitung). Sie spielt eine wichtige Rolle für die Vorhersagbarkeit funktioneller Diversität. In dieser Arbeit analysiere und vergleiche ich die Effekte von Landnutzung und Temperatur auf Arthropoden im Allgemeinen, aber auch auf Nachtfalter als Fallbeispiel, da sie eine oft vernachlässigte und dennoch sehr diverse taxonomische Gruppe darstellen. Ich betrachte verschiedene Ebenen, wie (1) die Gemeinschaft von Arthropoden im Allgemeinen, (2) Nachtfalter als funktionelle Gruppe, (3) morphologische Veränderungen einzelner Nachtfalterarten, und (4) physiologische Veränderungen einzelner Individuen von Nachtfaltern. Außerdem zeige ich, wie sich Spezialisten und Generalisten in ihren Reaktionen und Eigenschaften unterscheiden und welchen Effekt diese Unterschiede auf den verschiedenen Ebenen haben. Wesentliche Abschnitte dieser Arbeit wurden im Rahmen der Biodiversitäts-Exploratorien durchgeführt, ein Projekt in dem Wissenschaftler den Einfluss von Landnutzung auf Diversität und Ökosystemprozesse in Wäldern und im Grünland in drei Regionen innerhalb Deutschlands untersuchen.

Die erste Studie konzentriert sich auf den Effekt von Holzernte und dem relativen Buchenanteil zu anderen Baumarten in Wäldern auf Herbivore (Pflanzenfresser) von

Buchen. Wir haben in drei verschiedenen Regionen in Deutschland den Blattschaden von Buchen bestimmt und pflanzenfressende Arthropoden gesammelt. Die Ergebnisse zeigten einen allgemeinen negativen Effekt intensiver Landnutzung auf waldlebende Herbivore, der zu Beginn der Vegetationsperiode am stärksten war. Für die zweite und dritte Studie haben wir über 5000 Nachtfalter im Grünland der gleichen drei Gebiete gesammelt. Wir haben 461 verschiedene Arten bestimmt und ihnen Eigenschaften zugeordnet, welche die Fitness (bspw. Spezialisierung von Ressourcen oder Strategien der Reproduktion) der Arten beschreiben (engl. „Life-history taits"). Zusätzlich haben wir morphologische Eigenschaften (Körpergewicht und Flügelfläche) von über 2000 Individuen gemessen. In der zweiten Studie haben wir den Effekt von Landnutzung (Beweidung, Mahd und Düngung) auf die Diversität und Eigenschaften der Gemeinschaften untersucht. Mit steigender Landnutzung (besonders durch Zunahme der Mahd) nahm die Diversität der Arten ab. Zusätzlich nahm der relative Anteil von Generalisten zu, was zu funktioneller Homogenisierung in Ökosystem führt. Die dritte Studie hat sich auf intraspezifische morphologische Veränderungen mit steigender Landnutzung konzentriert. Wir haben einige Arten gefunden, die von zunehmender Düngung profitieren. Sie zeigten eine Zunahme ihrer Körpergröße was den Reproduktionserfolg erhöht. Diese Arten waren größtenteils Generalisten und haben sich im Vergleich zu den anderen Arten nicht besser auf stark genutzten Flächen etablieren können. In der vierten Studie untersuchten wir die Transpiration und den Metabolismus von 557 Arthropoden von Wald- und Grünlandflächen. Hierfür habe ich eine einfache und dennoch effektive Methode entwickelt und detailliert beschrieben, welche Wasserverlustraten mehrerer Proben in kurzer Zeit messen kann. Grünland stellt ein vergleichsweises arides Habitat dar und dessen Arthropoden wiesen generell niedrigere Wasserverlustraten auf, als Waldarthropoden. Sie reduzierten ihre kutikuläre Transpiration, wodurch sich der relative Anteil der respiratorischen Transpiration erhöht hat. Für die fünfte Studie haben wir Raupen von 30 verschiedenen Arten bei unterschiedlich temperierten Bedingungen gehalten, ihre Überlebens- und Wachstumsrate in Abhängigkeit zur Temperatur untersucht, sowie deren Transpiration und Metabolismus gemessen. Alle Arten zeigten eine niedrigere Überlebensrate und eine erhöhte Wachstumsrate sowie einen Anstieg von Transpiration und Metabolismus mit steigenden Temperaturen. Vor allem Spezialisten zeigten ein stärkeres Aussterberisiko mit einem Temperaturanstieg.

Meine Studien zeigen ähnliche Effekte von Landnutzung und Klimawandel auf Ökosysteme. Beide Faktoren führen zu einem generellen Diversitätsverlust und einer

Verschiebung zu generalistischen Gemeinschaften. Allerdings sind spezialisierte Gemeinschaften wichtig, um Homogenisierung zu reduzieren und Ökosystemfunktion stabil zu halten. Die Ergebnisse liefern somit wichtige Informationen für nationale und internationale Strategien um die Entwicklung nachhaltiger Landnutzung zu unterstützen und den Klimahandel zu reduzieren.

Glossary of important terms

Community: An assemblage of species interacting in the same area and in a particular time.

Homogenisation: A process by which species immigration and extinction increase the taxonomic or functional similarity between habitats.

Ecosystem functioning: Multiple biological, geochemical or physical ecosystem processes (e.g. soil retention, pollination, resource consumption) that reflect the performance of an ecosystem.

Ecosystem services: Anthropogenic benefits of ecosystems (e.g. food production).

Functional performance: The rate of an ecological process.

Functional traits: Features or measurable properties of an organism, and are usually described by physiological processes (e.g. photosynthesis), life-history processes (e.g. reproduction), morphology (e.g. body size), individual fitness or performance measures (Violle *et al.* 2007).

Generalists: Species, which are able to use a variety of resources or to develop on different environmental conditions.

Specialists: Species, which persist only in a narrow range of environmental conditions.

CHAPTER 1

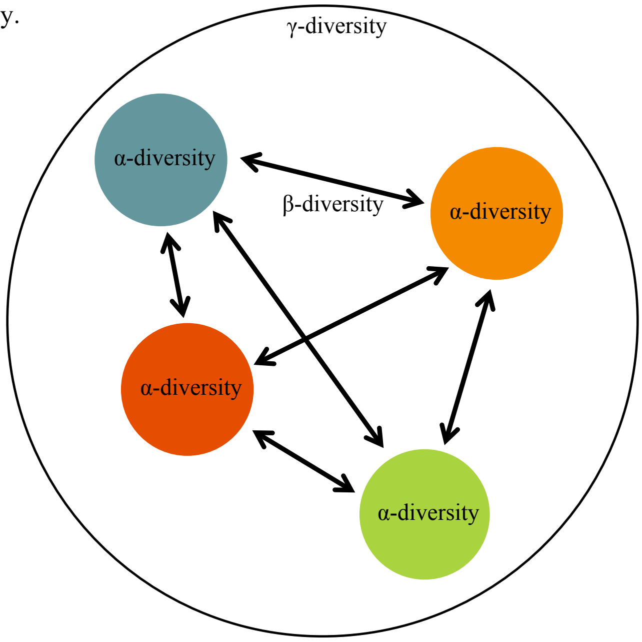
General Introduction

What is biodiversity?

Biodiversity is often described as the number of species and their proportionate abundance in a defined geographic area (species diversity), also called α-diversity. Genetic biodiversity describes the genetic variance within a species. On a broader scale, β-diversity describes the diversity between ecosystems and γ-diversity the diversity of habitats and populations across a landscape (Whittaker 1972; Fig. 1.1). Species diversity is threatened by several factors that also lead to a loss of ecological functions and services (Sala *et al.* 2000). In contrast to the diversity of species, functional diversity measures the complementarity and redundancy of species based on their traits, e.g. nutrition specialisation or distribution (Diaz and Cabido 2001; Petchey and Gaston 2006). Functional diversity is tightly related to species diversity, even if the slope of this relationship depends on the degree of disturbance. Moderately disturbed communities contain most functional groups and species, and thus show the weakest relation, which leads to a heterogeneous species diversity within different functional groups (Biswas and Mallik 2011).

Functional traits have strong effects on ecosystem functioning and thus measuring functional diversity is an effective method considering the effect of biodiversity on ecosystems (Diaz *et al.* 2006).

Fig. 1.1: Differences of α-, β- and γ-diversity.



Functional traits and environmental filtering

Species traits are features or measurable properties, and are usually described by the morphology, physiology or phenology of an organism (Violle *et al.* 2007), for example body size, growth rate, or the ability to perform an ecological process. Life-history traits describe the fitness of an organism (e.g. feeding-niche breadth, distribution, and voltinism). The approach to classify organisms in functional groups is not new (Weiher *et al.* 1999). But as studies about functional ecology have increasingly emerged in the last two decades (Diaz and Cabido 2001; Violle *et al.* 2007), the role of functional traits in determining ecosystem processes becomes particularly relevant. Here, two of the main questions of functional diversity studies are (1) how environmental change affects species composition, and (2) how species influence ecosystem functioning (processes that regulate the flux of energy, e.g. nutrient cycling or decomposition) (Hooper *et al.* 2000)? As I mainly consider environmental filtering, this thesis focuses the first question.

As species have different requirements for successful reproduction, environmental conditions can act as a filter on community composition. For example, species without frost tolerance cannot develop in habitats where temperatures might fall below zero degrees Celsius. In grassland Heteroptera, body size decreases and traits associated with dispersal ability increase with increasing land-use intensity (Simons *et al.* 2016). Environmental gradients can additionally filter traits differently between taxa. Birkhofer *et al.* (2017) found out that Araneae and Auchenorrhyncha are more mobile with increasing land-use intensity, while Chilopoda and Heteroptera show converse responses. For this reason, it is important to analyse the effects of environmental filtering in different taxonomic groups.

Thus, we consider anthropogenic activities as environmental filters and analyse the effect on trait composition in moth communities with a focus on traits associated with the degree of specialisation. We want to identify processes selecting for specialist or generalists and how these selections play a role on community and physiologic levels.

Differences between specialists and generalists

Amongst other properties, functional traits characterise the degree of specialisation of a species, described by its niche breath. For example, some herbivore species feed only on plant species within one genus, whereas others can feed on a variety of different plant taxa.

Multivoltine species (with more than one generation per year) are more generalistic than univoltine (one generation per year) or semivoltine species (one generation in at least two years), because they often have a broader phenological niche. The global distribution can also describe the degree of specialisation as well as the climatic niche, at which a species occurs.

In general, specialists face a higher risk of extinction due to environmental change. On the one hand, generalists are more tolerant and can adapt better to different environmental conditions (Gaston *et al.* 1997). On the other hand, specialists perform better under their optimal conditions than generalists (the 'jack-of-all-trades is master of none' hypothesis; Levins 1968). This means that generalists occur comparatively more often in changing and disturbed environments, whereas rare specialists prefer stable environments (Devictor *et al.* 2008; Rainio and Niemela 2003; Rossetti *et al.* 2017). Thus, the degree of disturbance has a strong effect on species composition in regard to the degree of specialisation. This effect leads to biotic homogenisation, a process that reduces the compositional variation among communities (a decreasing β-diversity) and leads to taxonomic and functional depletion (Mouillot *et al.* 2013; Olden *et al.* 2004), which has been observed for a majority of taxonomic groups (Baiser *et al.* 2012).

Diversity increases the performance and stability of ecosystems, and provides ecosystem functioning and services

Ecosystem services are benefits that ecosystems provide for humanity. They are directly linked to biodiversity (Cardinale *et al.* 2012) and can be classified into four categories (Wallace 2007): provisioning (food and wood production), regulating (pollination, erosion, flood regulation), cultural (spiritual, educational, recreational), and supporting services (nutrient cycling, photosynthesis).

It is important for human wellbeing to protect ecosystems and to understand the mechanism of biodiversity, functional performance, stability and environmental filtering. Functional performance can be described as the rate of an ecological process, e.g. resource consumption and depends on biodiversity (Naeem *et al.* 1994). However, high functional performance can either be achieved by several equally productive species, but also by a single dominant species (Grime 1998). The stability of ecosystems is driven by its diversity, but also by higher abundance and asynchrony across species (Blüthgen *et al.* 2016; Figge

2004; Kühsel and Blüthgen 2015; Schindler *et al.* 2010; Tilman *et al.* 1998; Yachi and Loreau 1999). For example, the portfolio effect implies that the dynamic of an ecosystem is often less variable and thus more stable than the dynamic of each single species occurring in this ecosystem (Yachi and Loreau 1999). Cardinale *et al.* (2012) reviewed the impact of biodiversity on ecosystem functioning and services, and summarised six consensus statements: (1) biodiversity increases the efficiency of communities to convert resources into biomass. (2) Biodiversity leads to stability of ecosystem functioning over a long term. (3) The responses of different ecosystem processes on biodiversity are nonlinear and as biodiversity decreases the change of ecosystem processes increases. (4) Key species in species rich communities lead to higher productivity. (5) Diversity loss across trophic levels has larger effects than diversity loss in one level. (6) Functional traits have strong effects on the productivity of ecosystem functioning.

Consequently, a high spatio-temporal variety and diversity of species and ecological functions (e.g. pollination) stabilise the performance of ecosystems. However, several reviews reported a global decline of biodiversity in terrestrial and aquatic ecosystems for centuries (Butchart *et al.* 2010; De'ath *et al.* 2012; Dirzo and Raven 2003; Dudgeon *et al.* 2006), known as the sixth wave of extinction (Barnosky *et al.* 2011). Here, human activities prevail as one of the main drivers of this loss due to direct and indirect effects (Gren *et al.* 2016; Sala and Knowlton 2006). According to a ranking of the importance of drivers changing biodiversity until 2100 developed by Sala *et al.* (2000), land use and climate change will have the largest effect on terrestrial ecosystems, followed by nitrogen decomposition, biotic exchange and elevated carbon dioxide concentration We thus analyse the consequences of land-use intensity and climate change to see and possible correlations of these effects on ecosystems.

Land use as an environmental filter

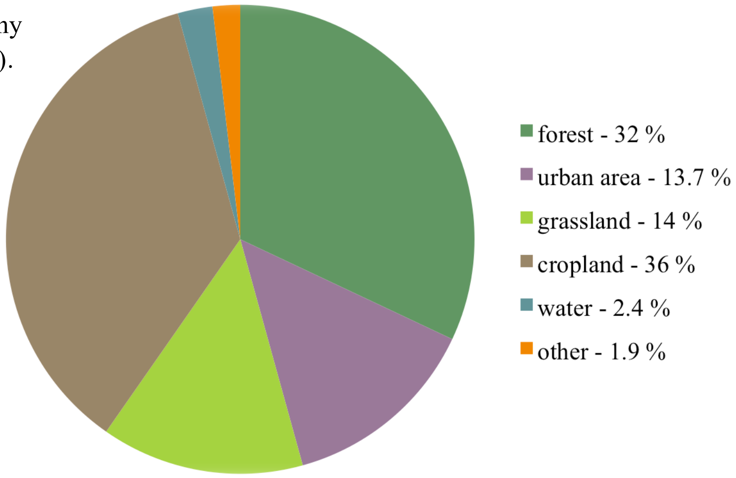
During the last centuries, anthropogenic processes have changed the global land cover massively (Ramankutty and Foley 1999). One method to measure the human impact in ecosystem processes is the ‘human appropriation of net primary production’ (HANPP). It describes the difference between the total net primary production and the net primary production remaining after removal via human activities (Haberl *et al.* 2001). Human activities remove up to 25 % of the global net primary production, mostly through harvesting (Haberl *et al.* 2007).

Forests cover approximately 30 % of the global land cover, and more than half of this area belongs to only five countries (the Russian Federation, Brazil, Canada, the United States of America and China; FAO 2010). The conservation of forests is of great importance due to their ability to conserve water and soil, control desertification and flood risk, and protect coast strips (Bradshaw *et al.* 2007; Bruijnzeel 2004; Graham 2004; Oyama and Nobre 2003). In 2010, almost 50 % of the total carbon stock is stored in world's forests, which is about 289 gigatonnes (FAO 2010; Malhi and Grace 2000). The forest area, which is annually transformed to agricultural land decreased in the last centuries, but still amounts to about 13 million ha per year (FAO 2010). In contrast, grassland areas expanded from 500 million ha to 3.3 billion ha in the last 300 years (Klein Goldewijk and Ramankutty 2004).

The strongest anthropogenic land-cover change is still located in tropical areas. The patterns of land-cover change, however, are similar in Europe. Nevertheless, this trend changed during recent years as well; cropland declined between 1990 and 2006 whereas grasslands, forests and urban areas are increasing (Kuemmerle *et al.* 2016). In Germany, 13 % of the total grassland area was converted between 1991 and 2013 (Umweltbundesamt 2015). Mean land allocation of the European Union suggests similar distributions on a larger scale, as in Germany and forest cover constitutes 38 % and grassland cover 16 % (Statistisches-Bundesamt 2016).

Especially, harvesting intensity in forests and mowing events in grasslands go along with a high degree of disturbance and they mostly decrease the occurrence and diversity of arthropods (Gossner *et al.* 2014b; Humbert *et al.* 2010; Savilaakso *et al.* 2009; Schowalter

Fig. 1.2: Land allocation in Germany (Source: Statistisches-Bundesamt 2016).



1995). Nevertheless, management strategies in forests and grasslands differ massively in their degree of disturbance. Today, only 32 % of Germany is covered with forests (Statistisches-Bundesamt 2016), even if they are considered to be the most natural habitats (Fig. 1.2). Thus, before silviculture started in the Middle Ages, 100 % of Germany was covered with forests (Küster 2001; Wulf *et al.* 2010). Nevertheless, total forest cover increased again during the last decades and the amount of matured forests became more dominant since the new millennium started (BMEL 2016). Since the late seventies, multifunctional strategies enforced to enhance sustainable silviculture and today forests are mainly extensively managed (Höltermann and Oesten 2001). Large-area clear-cuttings do not occur, timber harvesting removes nutrients only partly, and forest are usually not fertilised (BMEL 2016). Hence, between 2000 and 2014 the amount of PEFC (Programme for the Endorsement of Forest Certification) certified forests increased from 27.3 % to 66.4 % (Umweltbundesamt 2015). In contrast, grasslands constitute no permanent existing natural landscapes in Germany, as they should be managed much more radically to avoid succession (Gaisler *et al.* 2004; Moog *et al.* 2002). Mowing events remove almost 100 % of the above ground plant biomass and thus rapidly change the whole landscape. Mowing is often coupled with fertilisation (Blüthgen *et al.* 2016), which enables a faster plant-biomass production and thus facilitates several mowing events per year (Rose *et al.* 2012), but a surplus can also lead to eutrophication (Hautier *et al.* 2014). In contrast, grazing represents an extensive component of land use, but pastures also produce less plant biomass than fertilized hay meadows (Zhou *et al.* 2006). Nevertheless, the amount of intensively used hay meadows is still increased in Germany to enhance crop output and quality, and the total amount of grassland cover decreases (BfN 2014; Umweltbundesamt 2015).

A general negative effect of land-use intensity in grassland and forest sites has been reported for several taxa of plants and animals (Chaudhary *et al.* 2016; Kay *et al.* 2017; Martinez-Jauregui *et al.* 2016; Paillet *et al.* 2010; Socher *et al.* 2012; Weiner *et al.* 2014). Grazing and mowing in grassland and harvesting in forests leads to disturbance events in ecosystems. As already mentioned, the degree of disturbance plays an important role on the effect on biodiversity. The *intermediate disturbance hypothesis* is the most widespread hypothesis, explaining the effect of disturbance: undisturbed habitats usually lead to a disequilibrium of species, because a few species benefit more of the environmental conditions compared to the majority. Soon after a disturbance event, new species have the opportunity to colonize open niches. As long as disturbance events are still infrequent, the time of colonization is, however, short and only those species that can quickly develop, will colonize the habitat. Increasing number of disturbance events facilitates the time of colonization and competition, which leads to an equilibrium of species and an increase of biodiversity. If the frequency of disturbance events is too high, biodiversity will decrease, because only the most resistant species can survive and will eliminate the rest (Connell 1978). This means that extensive management strategies in grassland and forest sites could actually favour biodiversity. Studies confirming this effect on animals, however, are rare (but see Uchida and Ushimaru 2014). This suggests that most land-use management exceeds the amount that is beneficial for biodiversity. In this thesis, I investigate this assumption.

Biodiversity research in the Biodiversity-Exploratories

Main parts of this thesis were performed in the framework of the Biodiversity-Exploratories (hereafter: BE). This interdisciplinary research consortium was founded in 2006 to investigate changes of biodiversity and their impact on ecological processes. The main questions of the BE are: How does the biodiversity of different taxa or levels relate to each other (e.g. plant diversity on herbivore diversity)? What is the role of biodiversity in ecosystem processes? And how does land-use intensification influence biodiversity and ecosystem processes?

The BE are three long term and large-scale areas across Germany (Fig. 1.3). 'Schorfheide-Chorin' is dominated by glacially formed lowland in the northern part of Germany. The altitude is between 2 and 139 m a.s.l. and the annual precipitation is about 520-580 mm. Almost half of the area in this lake district is dominated by forest sites (mainly dry bilberry-pine-forest). The 'Hainich-Dün' region with its national park is in central Germany between 285-550 m a.s.l. and has an annual precipitation of 630 to 800 mm. The national park was founded in 1997 and is characterized by an unmanaged mixed beech forest, whereas the surrounding landscape is dominated by agricultural land. The 'Schwäbische Alb' is in the centre of a calcareous mountain range in south Germany. The region is dominated by a patchwork of grassland and forest sites. The altitude is between 460-860 m a.s.l. and the annual precipitation is 800-930 mm.

The three BE can also be considered as a gradient across Germany, with increasing altitude and precipitation from north to south. Along this gradient it is possible to analyse patterns on a large scale. In each exploratory, study sites were chosen in the forest and in the grassland (50 sites each) that represent the complete land-use gradient within the corresponding region. Depending on the extent and main focus of fieldwork activities, it is possible to use a subset of nine sites per region and habitat type (27 grassland and forest sites each) that show the same land-use gradient and are investigated more intensely by the research group. In contrast to several studies about heterogeneous land-use effects, the BE thus provides a representative and replicable land-use gradient.

Climate change and its consequences

In contrast to land use affecting ecosystems directly, anthropogenic activities can additionally have an indirect effect via climate change. The earth's surface temperature increased during the last three decades continuously and was warmer than any decade since 1850. Between 1980 and 2012 the average temperature increased by 0.85 °C and during the last century the global mean sea level rose by 0.19 metres. Since 1750 anthropogenic carbon dioxide emission amounts to 2040 gigatonnes CO_2, of which 40% are atmospheric. The remaining carbon dioxide is accumulated in plants, soil and in the ocean. Furthermore, the number of extreme events (heat waves, heavy precipitation events, droughts, cyclones, wildfires) has increased. It is uncontroversial that human activities are one of the main drivers and it is predicted that this will continue for the next decades. Representative Concentration Pathways (RCP's) are based on different scenarios of future anthropogenic emission, driven by climate policy, population size, and lifestyle. Depending on the RCP scenarios, global surface temperature will on average increase about 2 °C until 2100 (IPCC 2014).

Temperature is the main climatic driver in terrestrial ecosystems and has a strong effect on the occurrence, phenology, and metabolism of organisms (Chown 2002; Forrest 2016; Kühsel and Blüthgen 2015). Global warming act as an environmental filter on communities that change their species composition as species will be able to emigrate poleward or to higher altitudes depending on their dispersal ability

Fig 1.3: Location of the three Exploratories Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb distributed across Germany (source: BEO).

(Hickling *et al.* 2006; Regniere *et al.* 2012), or occur earlier in the season (Fitter and Fitter 2002 for plants; Forister and Shapiro 2003 for butterflies). In general, metabolic processes, such as respiration, increase exponentially with temperature (Brown *et al.* 2004). Temperature has a stronger effect on the growth and development of ectothermic insects than on endothermic mammals (Bale *et al.* 2002), which makes them particularly dependent. We thus investigated water loss and transpiration rate of arthropod communities in response to climatic conditions in their habitat, and analysed development and fitness rate of moth larvae exposed to higher temperatures.

Lepidoptera can be considered as a model group for arthropods

Due to their ecological relevance and variance, moths can be considered as model organisms for studies of conservation, ecology, and evolution (Boggs *et al.* 2003) and main parts of this thesis were performed on moths. Lepidoptera are the second largest animal order, comprising about 160,000 species in 124 families (Coleoptera contain about 400,000 species) (Kristensen *et al.* 2007). They are divided into three not taxonomic groups: Butterflies and skippers are monophyletic groups, whereas moths are paraphyletic. The latter contains about 85 % of all Lepidoptera and is traditionally divided into macromoths and micromoths. In contrast to butterflies and skippers, moths are usually nocturnal and males often have feathery antennas. They are highly variable in size, morphology, phenology, and degree of specialisation. For example, wing length ranges from 2.5 mm (*Stigmella maya*) to 300 mm (*Attacus atlas*). Some species are widely distributed, for example the codling moth (*Cydia pomonella*), that occurs on all continents except Antarctica and Greenland (Kumar *et al.* 2015).

Moths have a substantial impact on other organisms, because of their role as food resource. Imagoes make up a substantial part of the diet of many bat species and for example the blue tit alone eats 150 trillion caterpillars per year in Great Britain (Fox *et al.* 2006). Additionally, caterpillars as the larval stage are usually phytophagous and thus provide ecological important services, like nutrient recycling. Some species like the gypsy moth (*Lymantria dispar*) are well known as pests in agriculture and forest systems. This species can consume nearly 100 % of available host plants during outbreak events (Kosola *et al.* 2001). Moths additionally use a scarcely used niche as nocturnal pollinators, as most pollinators are usually diurnal.

Research objectives

In this thesis I evaluate direct (land use) and indirect (climate change) anthropogenic effects on arthropods and especially moths as a model organism on different levels. Hence, the main aims are:

I. How do Arthropod communities, functional traits and the degree of specialisation respond on land use and climate change?
II. Does intraspecific trait variation differ with increasing land use and climate change?
III. Which physiologic processes can affect these responses to land use and climate change and how do generalists and specialists differ?

Structure of this thesis

Chapter 2: Tree species composition and harvest intensity affect herbivore density and leaf damage on beech, *Fagus sylvatica*, in different landscape contexts

Increasing forest management is characterised by harvesting intensity and the amount of native tree species that decreases relatively due to the plantation of conifers. The effect of these components on herbivores, that provide an important ecosystem process are not completely understood, because studies usually focus either on a single aspect of forest management, or analyse this effect only on a local scale. We focussed on the effect of tree species composition and harvesting intensity on herbivore arthropods in German forests. We mainly analysed herbivore induced leaf damage and the density of leaf related herbivores across different height levels in beech trees.

Chapter 3: Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists

To analyse effects of land-use to herbivores in detail, we started focusing on moths as model organisms. Here, we analysed how the diversity and occurrence of 178 grassland moth species is influenced by land-use intensity in general, and by its components grazing, mowing and fertilisation in detail. We additionally observed possible shifts of life-history traits across a land-use gradient.

Chapter 4: Intraspecific trait variation and responses to land use: body mass and wing loading in grassland moth communities

As chapter 3 focuses on interspecific variability of moths, we investigated their intraspecific plasticity in **chapter 4**. In this study, we measured body weight and wing length of the same individuals from chapter 3 and additionally calculated its wing loading, a proxy for flight ability. We analysed how these intraspecific morphological traits vary across the land-use gradient and whether patterns correlate with the occurrence of species according to land use. We also investigated how morphological changes of species correlated with the degree of specialisation.

Chapter 5: An efficient method to measure water loss in arthropods: desiccation adaptation hypothesis re-examined

Due to increasing global temperatures, insects face a higher risk of desiccation and need to develop strategies to avoid water loss. On a global scale, species from xeric habitats have lower transpiration rates (cuticular and metabolic), than those from mesic habitats. In **chapter 5**, we developed a simple method, to measure water loss of arthropods of different habitats. We thus measured water loss and metabolic rate of 557 individuals of several arthropod orders from a forest site and two different grassland sites.

Chapter 6: Thermal reaction norms of moth species and their host plant specialisation: specialists face a dual risk

Temperature has a strong effect on development and survival of moth’s larvae. In general, physiological rate increases exponentially with temperature, which leads to a faster development. In **chapter 6**, we analysed these effects on 30 moth species to investigate differences relating to their degree of specialisation.

Abstract

Most forests are exposed to anthropogenic management activities that affect tree species composition and natural ecosystem processes. Changes in ecosystem processes such as herbivory depend on management intensity, and on regional environmental conditions and species pools. Whereas influences of specific forest management measures have already been addressed for different herbivore taxa on a local scale, studies considering effects of different aspects of forest management across different regions are rare. We assessed the influence of tree species composition and intensity of harvesting activities on arthropod herbivores and herbivore-related damage to beech trees, *Fagus sylvatica*, in 48 forest plots in three regions of Germany. We found that herbivore abundance and damage to beech trees differed between regions and that – despite the regional differences - density of tree-associated arthropod taxa and herbivore damage were consistently affected by tree species composition and harvest intensity. Specifically, overall herbivore damage to beech trees increased with increasing dominance of beech trees – suggesting the action of associational resistance processes – and decreased with harvest intensity. The density of leaf chewers and mines was positively related to leaf damage, and several arthropod groups responded to beech dominance and harvest intensity. The distribution of damage patterns was consistent with a vertical shift of herbivores to higher crown layers during the season and with higher beech dominance. By linking quantitative data on arthropod herbivore abundance and herbivory with tree species composition and harvesting activity in a wide variety of beech forests, our study helps to better understand the influence of forest management on interactions between a naturally dominant deciduous forest tree and arthropod herbivores.

CHAPTER 2

Tree species composition and harvest intensity affect herbivore density and leaf damage on beech, *Fagus sylvatica*, in different landscape contexts

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Introduction

Most forests have been considerably modified by human activities (FAO 2010; Paquette and Messier 2010; Powers 1999). Anthropogenic influences affect forest ecosystems indirectly via activities including hunting, livestock grazing, environmental pollution, human-assisted biological invasions and climate change, but also directly via forest management activities (Jactel *et al.* 2009; Milad *et al.* 2011; Pautasso *et al.* 2010). Whereas it is evident that forest management such as logging and reforestation with mono- and polycultures of native or non-native tree species can affect forest biodiversity (sensu Fischer *et al.* 2010; Wilson 1992) and related ecosystem processes (Gamfeldt *et al.* 2013; Hunter 1999; Petersen *et al.* 2000), the extent of these effects is more difficult to predict and supposedly contingent on the intensity of forest management and on the processes studied (Levers *et al.* 2014; Paillet *et al.* 2010; Riedel *et al.* 2013; Schall and Ammer 2013).

Herbivory, the consumption of plant material by animals, is a fundamental ecosystem process that affects nutrient cycles and plant abundance, and as a consequence resources and habitats for other organisms (Boyd *et al.* 2013; Metcalfe *et al.* 2014; Schowalter 2006). In forests, arthropod herbivores are abundant and diverse (Coley and Barone 1996; Elderd *et al.* 2013; Lewinsohn *et al.* 2005), and both abundance and diversity of herbivores are assumed to contribute to the extent of herbivory in forests (Salazar and Marquis 2012; Schowalter and Lowman 1999; Vehviläinen *et al.* 2007), although the relationship between herbivore abundance, herbivore diversity and herbivory may also be ambiguous (Hartley *et al.* 2010; Nummelin 1992; Peter *et al.* 2014).

Herbivore diversity and abundance on host plants is modified by an array of different factors such as abiotic conditions (Schowalter 2012; Seidl *et al.* 2011), the quality of host plants (Cornelissen *et al.* 2008; Lavandero *et al.* 2009; Poelman *et al.* 2009), and the exposure to competitors and natural enemies (Kaplan and Denno 2007; Letourneau *et al.* 2009; Schmitz and Barton 2014). In forests, these factors may show strong vertical stratification within individual trees (Ulyshen 2011), and they may also be strongly influenced by tree species composition (Barbosa *et al.* 2009; Jactel and Brockerhoff 2007). Following the vertical stratification of resources and conditions within tree crowns, many arthropod herbivores show a stratified spatial distribution in the canopy (Leksono *et al.* 2005; Su and Woods 2001; Ulyshen 2011). Although a distinct stratification of arthropods has been described for both tropical and temperate forests, stratification seems to be no static characteristic of canopy arthropod assemblages, but it may vary between seasons and with tree species identity, tree age and tree neighbourhood (Didham and Springate 2003; Gossner *et al.* 2014a; Ulyshen 2011).

Tree neighbourhood reflects age structure and species composition of neighbour trees and can thus be viewed as one aspect of the more general influence of forest management and tree species composition (tree association) on the abundance and diversity of herbivores on forest trees. Although plants in pure stands may often suffer from stronger herbivory than those in mixed stands, both positive and negative effects of plant association on herbivore damage have been reported (Agrawal *et al.* 2006; Heiermann and Schütz 2008; Plath *et al.* 2012). Plant associations can increase or decrease herbivore density or herbivore damage and are referred to as "associational susceptibility" (AS) and "associational resistance" (AR) respectively (Barbosa *et al.* 2009). In forest systems, both AS and AR have been documented as a consequence of tree association, which is most commonly measured as tree diversity or dominance of a focal tree species (Jactel and Brockerhoff 2007; Koricheva *et al.* 2006). For example, insect herbivory on oaks and alders was lower in monocultures, whereas herbivory on birch was higher in pure birch stands (Vehviläinen *et al.* 2007). To explain such contrasting effects of plant association on plant damage, different hypotheses have been established. These hypotheses consider both bottom-up and top down processes (see Jactel *et al.* 2005; Poveda *et al.* 2008 for review of associational resistance hypotheses), and the influence of variation in species characteristics (Castagneyrol *et al.* 2014; Plath *et al.* 2012).

Tree association in forests is strongly determined by forest management, which influences tree species composition and quality (Forkner and Marquis 2004; Hermy and Verheyen 2007), and thus directly and indirectly affects the abundance of herbivores (Savilaakso *et al.* 2009; Schowalter *et al.* 1986). Besides determining tree association, forest management involves harvesting practices, which may, for example, change forest microclimate, host plant quality, host plant quantity, and enemy pressure (Forkner *et al.* 2006; Jactel *et al.* 2009). As a consequence of these changes in the abiotic and biotic environment, harvesting can have intensity-dependent effects on herbivores and on related damage to trees (Schowalter 1995; Summerville 2011; Watt 1992). These effects may either decrease or increase herbivore populations and herbivore diversity depending on species characteristics such as dependence on specific hosts and successional stages of forest (Paquette *et al.* 2006; Rosenvald and Lohmus 2008). In addition to the potentially strong influence of forest management on herbivore populations and herbivore diversity, all the effects should be regarded in the context of larger-scale environmental variation (including climate, edaphic conditions, landscape heterogeneity) and regional species pools. These factors can have a strong impact on herbivore abundance and damage, and they may dilute, overlay or interact with the effects of forest management (Franklin *et al.* 2003; Schowalter 1995; Summerville and Crist 2008).

Considering the varying and interacting effects of tree association, harvest intensity and regional environmental conditions on herbivores and their damaging activity, a simultaneous assessment of these factors appears necessary to achieve generalizable information on the major determinants of herbivory in forest ecosystems. In our study, we investigated herbivore density and damage to European beech trees (*Fagus sylvatica* L.) growing in forests with different management histories in three regions of Germany, to clarify the role of forest management on herbivore abundance and on related damage to trees across a variety of silvicultural and abiotic conditions. We focused on beech forests since European beech is the dominating tree species of the potential natural vegetation in Central Europe (Ellenberg and Leuschner 2010; Packham *et al.* 2012). Despite their dominant role in European forests, beech trees appear to suffer relatively low damage and to host a less speciose and abundant arthropod assemblage than other common deciduous trees such as oak and maple (Brändle and Brandl 2001; Sobek *et al.* 2009; Yela and Lawton 1997). As increasing abundance and species-area relationships are generally related to increasing species richness (Brändle and Brandl 2001; Kennedy and Southwood 1984), the relatively low infestation and species richness of arthropod herbivores on beech emphasizes the need for investigations on determinants of herbivore-beech interactions.

Specifically, we investigated whether (1) herbivore abundance and damage vary between regions differing in various environmental conditions for the same forest type (beech forest) and whether (2) forest management, estimated by beech dominance and harvest intensity, affects herbivore abundance and damage under consideration of expected regional effects. In addition to regional patterns, we (3) also considered herbivore distribution and damage by specific arthropod taxa within tree crowns (Paillet *et al.* 2010).

Material and Methods

Ethics statements

Permits for field work were issued by the responsible state environmental offices of Brandenburg, Thüringen and Baden-Württemberg (according to § 72 BbgNatSchG). The study sites comprise state forests and protected areas such as the National Park Hainich and some nature reserves within the biosphere reserves Schwäbische Alb and Schorfheide-Chorin, as well as in the forest of Keula, Hainich-Dün. No species that are protected by European or national laws were sampled during this study.

Study area

The study was conducted in the framework of the German Biodiversity Exploratories Project (http://www.biodiversity-exploratories.de). The Biodiversity Exploratories Project addresses effects of land use on biodiversity and biodiversity-related ecosystem processes (Fischer *et al.* 2010).

Leaf damage by herbivores was assessed in November 2012 (year 1) from fallen leaves and in May and July 2013 (year 2) from live leaves. The assessments in year 2 were also used to quantify herbivore load on study trees. Assessments were carried out in forest plots in the three Biodiversity Exploratories (from north to south) “Schorfheide-Chorin” (Schorfheide; a glacial formed landscape in North-East Germany, 3 - 140 m a.s.l., 13°23’27” - 14°08’53” E / 52°47’25” - 53°13’26” N), “Hainich-Dün” (Hainich; a hilly region in Central Germany, 285 - 550 m a.s.l., 10°10’24” - 10°46’45” E / 50°56’14” - 51°22’43” N), and “Schwäbische Alb” (Alb; a low-mountain range in South-West Germany, 460 - 860 m a.s.l., 09°10’49” - 09°35’54” E / 48°20’28” - 48°32’02” N). Schorfheide is characterized by the lowest annual precipitation (520 - 580 mm), with a mean annual temperature of 6 - 7°C. It is followed by Hainich (630 - 800 mm, 6.5 - 8°C) and Alb (800 - 930 mm, 8 - 8.5°C). More details on the Biodiversity Exploratories can be found in Fischer *et al.* 2010.

Sample processing

In year 1, fallen leaves were collected on each corner of 15 plots in Hainich and in Alb Exploratories. These plots included three different forest types (n = 5 plots per type and region): uncultivated, young and old beech forest. Leaf damage was then calculated as the percentage of leaf damage for 50 leaves randomly chosen per corner that were scanned and afterwards subjected to a pixel analysis using the software Image J (Rasband 1997). Per cent leaf damage was calculated by estimating the number of pixels of the leaf area missing due to herbivory (attributable to chewing herbivores, not mines and galls) and by relating this number to the number of pixels of the whole leaf including intact and damaged leaf parts (Mody and Linsenmair 2004). In year 2, we collected live leaves of five beech trees randomly chosen in 16 plots per region. Additionally to beech forest, conifer forest (pines at Schorfheide and spruces at Hainich and Alb) was added in year 2 (n = 4 plots per Exploratory). For each selected beech tree, leaves of a lower and an upper position within the tree crown were considered, henceforth termed "crown position". The leaves from heights below 2 meters were sampled with secateurs, whereas leaves from higher crown positions were sampled with a telescopic stick with a clipper at the end controlled by dint of a rope. To ensure that no arthropods escaped due to dropping during branch cutting, we collected those arthropods in a textile funnel positioned underneath the cut branch. The height of the sampled crown positions ranged between 10 cm and 10 m, and depended on the height of the sampled trees and on the accessibility of leaves by the 'telescopic stick technique' described above. The size of the sampled trees ranged from less than 1 meter high to fully-grown mature beeches. We estimated the height of the sampled tree (between 20 cm and 30 m) and counted the leaves of one branch per crown position (between 8 and 132 leaves, mean 36), estimated the percentage leaf damage attributable to chewing herbivores of each counted leaf with the aid of sample 'leaf area loss' cards (sensu Adams *et al.* 2009, see Supplementary Material S2.1: Fig. S2.1.1) and collected or registered all herbivores, galls and mines on the branch as a measure of herbivore load. In case that we encountered oaks (*Quercus petraea* Liebl. and *Q. robur* L.) or sycamore maples (*Acer pseudoplatanus* L.) in the plot, we analysed herbivory and herbivores of three individuals of these tree species as well (and sampled only three beeches). We conducted the surveys in May when leaf-flushing in *F. sylvatica* starts, and during the midseason in July. We started each survey at Schorfheide followed by Hainich and Alb, an order that represented expression of tree phenology in the field (J. Mangels personal observation).

Mean values of leaf damage were calculated for each sampled tree per plot and per survey. Mean values were calculated in a similar way of the total number of herbivores, galls and mines per leaf for the surveys in year 2, as an estimator of herbivore density. We additionally calculated the coefficient of variation (CV) of herbivore damage across different trees within a plot, and compared damage patterns in different tree heights (two crown positions differing in height within a tree) based on a vertical stratification index $VS = LD_U/(LD_U+LD_L)$, where LD_U is the leaf damage assessed at the upper crown position and LD_L the damage at the lower position. For VS between 0 and 0.5, herbivore damage is higher in lower parts; values exceeding 0.5 indicate higher damage in the upper crown position. To compare leaf damage experienced by *F. sylvatica* with damage of other tree species, we conducted the same assessments of herbivore damage for individuals of *Q. robur/petraea* (n = 26) and *A. pseudoplatanus* (n = 70).

Forest management intensity

Defining forest management is a complex issue. The intensity usually varies gradually, which is not well mirrored in simple categorical classifications. To consider different aspects of forest management intensity, we used a combination of two predictor variables: (1) 'beech dominance' in the study plots, and (2) 'harvest intensity', measured as the proportion of harvested tree volume in the study plots ('Iharv': Kahl and Bauhus 2014). Beech dominance was assessed as the percentage of beech trees (in the shrub and the tree layer) among all tree individuals in the plot area (Boch *et al.* 2013 and Fabrice Grassein, unpublished). The original forests in our study are dominated by beech - a higher proportion of beech trees thus assumedly reflects a lower management intensity. Beech dominance was also negatively related to tree diversity in the studied forest plots (beech dominance vs. Shannon diversity index: $r = -0.416$, $p < 0.0001$). Harvested tree volume in the study plots was quantified by Kahl and Bauhus as the ratio of harvested volume to the sum of standing, harvested and dead wood volume (Kahl and Bauhus 2014). In accordance with Kahl and Bauhus, we use the same term *Iharv* for harvested tree volume to address harvest intensity in our analyses.

Data analysis

Data were analysed in generalized linear models (commands 'glm' for the model) using the statistical software package R 2.15.1 (R Core Team 2012) with the package 'nlme' (Pinheiro *et al.* 2014). Leaf damage or herbivore densities were the response variables used in the model, with region (Schorfheide, Hainich and Alb), beech dominance and harvest intensity as the three fixed effect terms in a hierarchical order. The significance of the effect terms was tested using Chi^2-tests (command “anova” based on sequential models of "type I"), and the differences between regions were assessed by Tukey post hoc tests following ANOVA. The data were transformed when necessary (see Tab. 2.1) to comply with the assumptions of variance homogeneity (Bartlett test) and normal distribution (Shapiro-Wilk test) of the residuals, and quasi-Poisson distribution was assumed when transformation was unsuccessful. In addition to the deviance and significance level of the GLM factors, we also show the linear regression coefficient for beech dominance and harvest intensity on response variables for a simple interpretation of response directions. To summarize impacts of forest management that may also appear via changes in beech dominance, an additional model for leaf damage was used where beech dominance was removed from the model. To elucidate the interaction effects between region and the continuous predictor variables beech dominance and harvest intensity, we additionally analysed their effects on the response variables separately per region within the same generalized linear model. Finally, to compare leaf damage across different tree species, we used ANOVA (command ‘aov’) followed by Tukey post hoc tests.

Tab. 2.1: Relationship between average leaf damage and the total density of herbivore groups. Generalized mixed model; for the direction of the effects, the linear regression coefficient (r) between the residuals of the previous predictors and the respective response variable are shown. VS = vertical stratification index, CV = coefficient of variation of leaf damage, R. fagi = Rhynchaenus fagi. Distribution: n (normal) and qp (quasi-Poisson); data transformation for n given in parentheses. Significance levels: . ($p < 0.1$), * ($p < 0.5$), ** ($p < 0.01$) and *** ($p < 0.001$). Degrees of freedom are 1 for beech dominance, 1 for harvest intensity, and 2 for region in May and July (but 1 in November). Effect of harvest intensity in reduced model without beech dominance.
a) *r* = -0.35**, b) *r* = -0.07; c) *r* = -0.22. See Supplementary Material S2.1: Tab. S2.1.1 for complementary analysis of significant interaction effects.

		Distribution		Region (R)		Beech dominance (B)			Harvest intensity (M)			Interactions
Response			Null-Deviance	Deviance		Deviance	*r*		Deviance	*r*		
Leaf damage	May	n (log+1)	17.50	11.76	***	1.07	0.43	***	0.52	-0.26	**a)	RxB*, BxM***
	July	n (^1/3)	74.87	47.55	***	1.35	0.22	ns	0.05	-0.04	ns b)	
	Nov	n	37	27.34	***	0.1	0.1	ns	0.44	-0.20	ns c)	RxM*
VS	May	n	0.87	0.32	***	0.08	0.37	*	0	-0.1	ns	
	July	n	0.74	0.08	*	0.18	0.53	***	0.02	0.2	ns	
CV	May	n (log+1)	1.74	0.09	ns	0.09	-0.23	ns	0.02	-0.08	ns	
	July	n	3.77	0.22	ns	0.04	0.12	ns	0.30	-0.31	*	
	Nov	n (^1/3)	0.08	0.01	*	0	0.26	ns	0	-0.01	ns	
Chewers	May	qp	1.46	0.88	***	0	0.02	ns	0	-0.14	ns	
	July	n (^1/4)	0.01	0.01	***	0	-0.16	ns	0	0.29	*	BxM**
Weevils excl.	May	n (^1/6)	$6.51e^{-5}$	$7.08e^{-6}$	ns	$9.27e^{-7}$	-0.07	ns	$1.19e^{-6}$	-0.13	ns	
R. fagi	July	qp	0.15	0.02	**	0	0.07	ns	0.06	0.37	***	RxM*
R. fagi	May	qp	0.62	-		0	0.08	ns	0.01	-0.13	ns	
	July	qp	0.63	-		0	0.34	ns	0.01	-0.14	ns	
Caterpillars	May	n	0.001	$8.77e^{-5}$	*	$6.79e^{-6}$	0.12	ns	$6.41e^{-6}$	-0.05	ns	
	July	n (sqrt)	0.04	0		0	0.11	ns	0	0.23	*	RxM***
Aphids	May	qp	2.75	0.1	***	0.77	-0.3	***	0	-0.1	ns	
	July	qp	14.13	4.64	***	0.62	-0.22	*	0.23	-0.19	ns	RxB***, BxM*
Mines	May	qp	10.77	9.33	***	0.11	0.2	*	0.04	0.13	ns	BxM***
	July	n (^1/3)	0.17	0.06	***	0	-0.14	ns	0	0.12	ns	RxBxM*
Galls	May	n (^1/4)	2.64	0.8	***	0.28	0.09	**	0.10	0.14	.	
	July	n (^1/3)	3.51	1.81	***	0.01	0.15	ns	0.01	-0.13	ns	RxB***

Results

Leaf damage by chewing herbivores differed considerably between regions (Fig. 2.1, Tab. 2.1), and both the proportion of *F. sylvatica* (beech dominance) and harvest intensity affected the amount of leaf damage and the density of different taxonomic groups of herbivores when the regional differences were accounted for (Fig. 2.2, Tab. 2.1). Damage of live leaves was highest in Alb (mean ± *SD*: 5.3 ± 2.9% in May and 8.1 ± 3.5% in July) and significantly lower in the two other regions (1.0–1.8 ± 0.4–1.9 %) (Fig. 2.1, Tab. 2.1). Similar results were observed for herbivore damage estimated on fallen leaves, with higher damage in Alb (3.2 ± 0.7%) than in Hainich (1.3 ± 0.5%) (Fig. 2.1c, Tab. 2.1).

Beech dominance showed a significant positive effect on leaf damage in May, with a significant effect in Hainich, a marginally significant trend in Alb and a weak trend in Schorfheide (Fig. 2.2, Tab. 2.1, see Supplementary Material S2.1: Tab. S2.1.1). Even after accounting for region and beech dominance, harvest intensity had an additional effect on leaf damage in May, where leaf damage decreased significantly with increasing harvest intensity. The effect of harvesting in May remained significant when beech dominance was not considered as a predictor prior to harvesting in a sequential model (Tab. 2.1). The trends for leaf damage in July and for fallen leaves in November were similar, but not significant. Beech dominance and harvesting were not correlated (Pearson *r* = -0.19, *p* = 0.205)

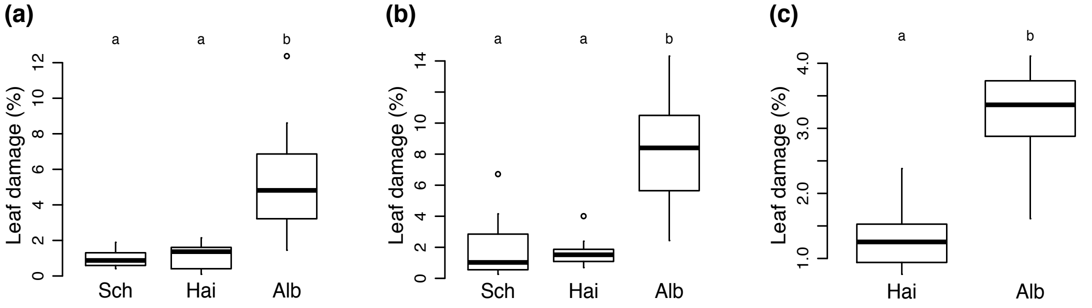

Fig. 2.1: Leaf damage (%) of beech trees in the three study regions – Schorfheide (Sch), Hainich (Hai) and Alb (Alb) – in the surveys in May (a) and July 2013 (b) and November 2012 (c). The letters indicate significant differences between regions (ANOVA, Tukey's post hoc $p < 0.05$).

Region and beech dominance significantly affected the vertical distribution of leaf damage (*VS* index) in May and July (Tab. 2.1). Herbivory was most pronounced in upper crown positions in May in Alb (mean *VS* ± *SD*: 0.61 ± 0.09), but in lower positions in Hainich and Schorfheide (0.44 ± 0.14 and 0.42 ± 0.12, respectively). *VS* values were significantly different from 0.5 (which would indicate a similar herbivory in lower and upper crown positions) in Alb (p = 0.04) and Schorfheide (p = 0.006), but not in Hainich (p > 0.05). Overall-*VS* values in May were not significantly different from 0.5. In July, the majority of herbivory was found in the upper crown positions (Alb: 0.56 ± 0.14, Hainich: 0.57 ± 0.09, Schorfheide: 0.48 ± 0.14), with overall-*VS* values and values from Hainich being significantly higher than 0.5 (p = 0.04 and 0.003 for overall values and Hainich, respectively). These results thus suggest an upward-shift of herbivore feeding in tree crowns during the season at least in Hainich and Schorfheide. In forests with high proportions of beech, herbivory was also more pronounced in higher crown positions (Tab. 2.1).

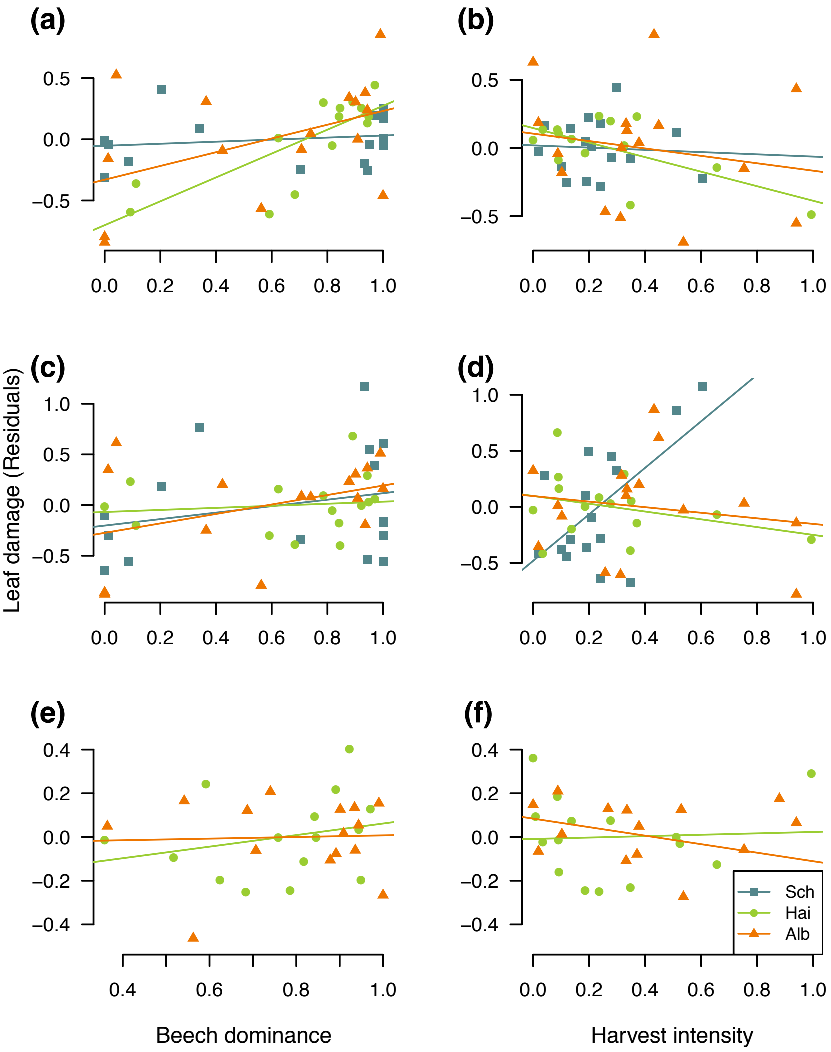

Fig. 2.2: Influence of beech dominance and harvest intensity on leaf damage (residuals) of beech trees. Data were collected in May (a,b), July (c,d) and November (e,f) in the three regions Schorfheide (Sch), Hainich (Hai) and Alb (Alb).

The variation of severity of herbivory across trees, expressed by the coefficient of variation (*CV*) of leaf damage, was not strongly differing between regions (Tab. 2.1). The only difference in *CV* was found between Alb and Hainich for data on fallen leaves, where the *CV* of damage of fallen leaves was significantly lower in Alb (0.25 ± 0.09) than in Hainich (0.38 ± 0.20). Beech dominance showed no effect on *CV* of leaf damage, whereas a weak negative effect (significant only in July) was detected for harvest intensity (Tab. 2.1).

Consistent with leaf damage, the abundance of all herbivore guilds - namely chewers, miners, aphids and galls - and of selected taxa, including weevils and lepidopteran caterpillars, significantly differed between regions (Tab. 2.1). *Rhynchaenus (Orchestes) fagi* L. was the most abundant weevil and represented 95% of all collected weevil individuals. As this species was detected exclusively in Alb, it was treated separately from the remaining weevils; region was removed as factor in the model. The results suggest that beech dominance and harvest intensity have no significant effect on *R. fagi* density. In contrast, beech dominance did have a significant negative effect on the density of aphids (represented by the woolly beech aphid *Phyllaphis fagi L.*) in both surveys, and a significant positive effect on mines and galls in May (Tab. 2.1). Harvest intensity had a positive effect on the density of weevils (excluding *R. fagi*) and on chewers in July (Tab. 2.1). Hence, contrasting responses to harvest intensity were found for leaf damage by chewing herbivores (negative in May) and these herbivore groups (positive) in different months.

A more detailed analysis on the family level of galling arthropods showed a positive effect of beech dominance on gall midges in May ($r = 0.22$; $p = 0.005$) and July ($r = 0.32$; $p < 0.001$) but no effect on gall mites. Analyses on the species level revealed that gall density of the gall mite *Aceria nervisequa* Cane. was positively related to beech dominance in May ($r = 0.11$, $p = 0.027$). Furthermore, beech dominance was positively related to gall density of the gall midges *Mikiola fagi* Hart. (May: $r = 0.26$, $p = 0.016$, July: $r = 0.42$, $p < 0.001$) and *Phegomyia fagicola* Kief. (July: $r = 0.15$, $p < 0.001$). Harvest intensity was positively related to gall density of the gall mite *A. nervisequa* in May ($r = 0.28$, $p = 0.015$) and to the gall midge *P. fagicola* in May ($r = 0.25$, $p = 0.028$).

Across all sites, average leaf damage and the total density of all leaf-chewing herbivores together were significantly positively correlated in May, but not July (Tab. 2.2). This was also confirmed for the caterpillars and for *R. fagi* alone, as well as for leaf mines that were not part of the damage assessment (Tab. 2.2).

Fagus sylvatica showed the lowest level of leaf damage compared to the other two studied tree species in July. Highest damage was found for *Acer pseudoplatanus* (mean ± *SD*: 8.7 ± 11.0 %), followed by *Quercus spp.* (4.2 ± 4.6 %) and *F. sylvatica* (3.8 ± 5.2 %). The factor tree species influenced leaf damage significantly (F = 14.27, $p < 0.0001$). The difference between damage of *F. sylvatica* and *A. pseudoplatanus* was highly significant ($p < 0.0001$). In May, where *Quercus* had not yet flushed leaves, *A. pseudoplatanus* (3.4 ± 6.4%) did not differ significantly from *F. sylvatica* (2.5 ± 3.8%).

Tab. 2.2: Relationship between average leaf damage and the total density of herbivore groups. Spearman rank correlation; data were obtained in May and July and across all sites (n = 48). The correlation between *Rhynchaenus fagi* (R. Fagi) and leaf damage was restricted to the study region ALB (n = 16). Significance levels: *ns* (not significant), * ($p < 0.05$), and *** ($p < 0.001$).

	May		July	
Predictor	*rs*	*p*	*rs*	*p*
Chewers	0.47	***	0.04	ns
Weevils excl.	-0.22	ns	0	ns
R. fagi	0.55	*	0.04	ns
Caterpillars	0.13	ns	-0.03	ns
Aphids	0.14	ns	0.18	ns
Mines	0.59	***	0.13	ns
Galls	-0.05	ns	-0.04	ns

Discussion

In our study we investigated the effects of different aspects of forest management on the abundance of arthropod herbivores and on herbivore-related damage to beech trees, the prevailing tree species in natural Central European forests. Forest management was characterized by (1) changes in beech dominance, assuming that a low proportion of beech trees often represents targeted establishment of other timber species, and (2) by harvest intensity. Our results demonstrated that herbivore damage on beech trees may decline (depending on season) with decreasing beech dominance (i.e. a lower herbivory with increasing management intensity) and that it additionally may decline with increasing harvest intensity. The density of leaf chewers and mines was positively related to leaf damage, and several of the studied arthropod groups were found to respond to beech dominance and harvest intensity, albeit in different ways. An analysis of damage patterns in different tree heights indicated a vertical shift of herbivores to higher crown layers during the season and with higher beech dominance.

Regional differences in herbivore density and leaf damage

The regional differences found for herbivore density and leaf damage are in accordance with other studies showing strong differences in herbivore abundance and impact between study sites differing in climate and other environmental variables (Adams *et al.* 2009; Gossner *et al.* 2014a; Stoeckli *et al.* 2008; Truxa and Fiedler 2012a). Regional differences in abundance of insect species may be related to abiotic but also biotic environmental parameters, and they may occur for widespread as well as for site-restricted species (for a detailed discussion for German beech forests see Andersen 1997; Connor *et al.* 2000; Gering *et al.* 2003; Gossner *et al.* 2014a). Whereas all groups of herbivores varied in abundance across regions in our study, this pattern was particularly obvious for abundance of the beech leaf-miner weevil *R. fagi*. This species can be considered as a key herbivore of beech (Nielsen 1978; Phillipson and Thompson 1983; Rheinheimer and Hassler 2010), and it was the most numerous beetle species in our samples, but was only detected in one of the three regions (Alb). As *R. fagi* is known to occur throughout Germany (Rheinheimer and Hassler 2010), these marked differences in abundance are best explained by fluctuations in population density that are reportedly highly pronounced in this species (Péré *et al.* 2011, and references therein). The importance of this species for herbivore damage in our study was supported by the high correlation of *R. fagi* density and overall leaf damage found in May, and the lower herbivore damage in Hainich and Schorfheide might be partially explained by the absence of this species.

Influence of forest management on leaf damage and herbivore density

Despite the strong regional differences in herbivore communities, consistent effects of tree species composition (beech dominance) and harvest intensity on herbivore density and damage were found. This finding emphasizes the potential importance of forest management for interactions between beech trees and their arthropod herbivores in different environmental contexts and it augments information obtained from qualitative herbivory assessments (Gossner *et al.* 2014a). The increase of damage to beech trees with beech dominance also suggests that some processes described by "*associational resistance hypotheses*" may hold for native Central European beech forests and are not restricted to agricultural (Andow 1991; Letourneau *et al.* 2011) or plantation (Jactel and Brockerhoff 2007; Plath *et al.* 2012; Vehviläinen *et al.* 2006) systems that are strongly influenced by land management. Associational resistance can be based on different processes, which may affect herbivores directly via plant traits such as suitability or appearance of focal plants (bottom-up processes), or via indirect effects on the herbivores' enemies (top-down processes). Different bottom-up processes contribute to associational resistance (see Jactel *et al.* 2005; Poveda *et al.* 2008 for review of associational resistance hypotheses). As most of these hypotheses have been developed in short-lived agricultural systems - where initial host plant colonization is assumedly more important than in long-lived, perennial systems such as forests - or in young experimental forests, it is still a matter of on-going investigations how they apply to mature or near-natural forest systems.

An increase of herbivory in pure stands is often explained by the *resource concentration hypothesis* (Root 1973; Vandermeer 1989). This hypothesis assumes that herbivores maintain higher densities and success in monospecific stands of their host plants, where presence of many conspecific plants enhances accessibility of host plants for specialist herbivores. In mixed stands, plant diversity may protect host plants by physically (Perrin and Phillips 1978), visually (Castagneyrol *et al.* 2013; Finch and Collier 2000) or chemically (Castagneyrol *et al.* 2013; Finch and Collier 2000; Tahvanainen and Root 1972) impeding herbivore access to the host plant. As herbivore species or even stages of the same herbivore species are strongly differing in their foraging behaviour and responses to environmental parameters (Hochuli 2001; Moreau *et al.* 2006), the specific mechanisms underlying an observed damage pattern can only be completely understood when the damaging species have been identified. In our study, this specific identification was obtained for a few species, namely the beech leaf-miner weevil *R. fagi*, the woolly beech aphid *P. fagi* and a few gall makers. The community of chewing herbivores as a whole responded in a positive way to beech dominance. However, the abundance of the only common chewing herbivore species that can be related to the quantified herbivore damage - the weevil *R. fagi* - did not respond to beech dominance in our analysis. The roles of other species need to be elucidated in more detailed studies in beech forests. Nevertheless, possible mechanisms can be deduced from other studies and systems. For example, positive relationships between herbivore damage and host plant dominance may occur in passively dispersing herbivores including early-instar moth larvae, where higher host density increases the probability to land on a suitable host, or for bark beetles, where higher host plant densities allow for build-up of critical population densities (Hochuli 2001; Kemp and Simmons 1979; Speight and Wainhouse 1989).

Increasing tree diversity (decreasing host dominance) may also increase herbivore damage, translating to associational susceptibility (Barbosa *et al.* 2009). This is particularly described for generalist herbivores profiting from mixing different host species, or spilling-over from preferred hosts to less palatable focal plants following exhaustion of the preferred host species (Brown and Ewel 1987; White and Whitham 2000). However, associational susceptibility due to increasing tree diversity is not restricted to generalist herbivores, but it can also occur for specialist herbivores avoiding enemies or competitors (Plath *et al.* 2012), or those that profit from mixing heterogeneous conspecific plants (Castagneyrol *et al.* 2012; Mody *et al.* 2007). In our study, an indication for associational susceptibility was found for infestation of beech by *P. fagi*, which was negatively related to beech dominance in spring and summer. In this case, a higher dominance of host trees may dilute the density of early-season fundatrices (Kareiva 1983), or it may affect the quality of beech trees as a host. Host quality of trees may depend on tree association, for example as a consequence of facilitation and reduced stress in mixed stands during periods of abiotic stress such as drought (Pretzsch *et al.* 2013), which is known to affect the suitability of trees for insect herbivores (Gaylord *et al.* 2013; Gutbrodt *et al.* 2012; Jactel *et al.* 2012), depending on drought intensity (Banfield-Zanin and Leather 2015; Mody *et al.* 2009).

The change in associational effects - from support to suppression of herbivores - by increasing tree diversity (decreasing beech dominance) may also be related to indirect effects of enemies as stated by the *enemies hypothesis* (Riihimaki *et al.* 2005; Root 1973). It is generally assumed that natural enemies of herbivores may profit from increasing plant diversity due to an increasing availability of resource and habitat conditions (Letourneau *et al.* 2011). In forests, these positive effects of increasing tree diversity have been shown for some predator or parasitoid groups but not for others (Jactel and Brockerhoff 2007; Lange *et al.* 2014; Nixon and Roland 2012; Sobek *et al.* 2009). To assess whether top-down processes have contributed to effects of beech dominance on herbivores in our study, further investigations on enemy assemblages and on specific herbivores are required.

Besides effects of beech dominance, we also detected an influence of harvest intensity - defined as the proportion of harvested tree volume - on leaf damage and on abundance of some chewing herbivores. Harvesting activities may lead to a simplification of forest structure, which may provoke a reduction of herbivore abundance or species richness (Ayres and Lombardero 2000; Bouget *et al.* 2012; Grove 2002) in different taxonomic groups (Dodd *et al.* 2012; Paillet *et al.* 2010). These reductions in herbivore occurrence (including both abundance and diversity) may lead to a decrease in leaf consumption, which might explain the observed negative relationship between harvest intensity and herbivore damage in spring and also autumn (see also Gossner *et al.* 2014b, who found a negative relationship between land use intensity and herbivory in grasslands). The decrease in herbivory might also come along with increased enemy pressure in more strongly disturbed forests, which might be possible for some key enemies (Gandhi *et al.* 2008; Sheehan 1986; Way 1977), but is not generally to be expected (Schowalter 2012 and references therein).

Relationship between herbivore density and damage

We found a generally positive relationship between herbivore density and damage although such a pattern may not always be apparent given the conceptual differences between the two parameters: whereas the assessment of damage integrates over a period of time, the activities of specific herbivores are usually fluctuating over the season and with changes in environmental conditions or resource availability (Gaston and McArdle 1994). In our study this shift became apparent by the observed switch of herbivory from lower to higher canopy layers. These shifts may directly track resource availability and quality, but they may also reflect changes in species composition (Ruhnke *et al.* 2009). The shifts in resources and species may also explain why we did not detect effects of beech dominance and harvest intensity on damage later in the season—probably since different effects were masking each other.

Conclusion

Our study showed that the occurrence of arthropod herbivores in forests and resulting damage to forest trees is influenced by host tree dominance and by differences in harvest intensity. Specifically, herbivore damage to beech trees increased with increasing dominance of beech trees and decreased with increasing harvest intensity. These findings appear to be generalizable at least for European beech forests as they were consistent across forests from three regions varying in biotic and abiotic environmental conditions. At the same time, strong temporal and spatial variation in herbivore occurrence and damage to beech, but also to oak and maple trees, point to the highly conditional nature of herbivory as an ecosystem process.

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Abstract

Grasslands belong to the ecologically most relevant habitats in cultural landscapes, but also provide high economic value when used as meadows or pastures. Land-use intensification in grasslands negatively affects plant diversity as well as arthropod communities that depend on plants as food source and habitat, with important consequences for the provision and resilience of ecosystem functioning.

In this study, we analysed 178 moth species to investigate whether species composition, diversity and life-history trait characteristics of moth communities respond to the type and intensity of land use, comparing 26 sites in three different regions of Germany.

Consistent across the three regions, we found that pastures grazed by cattle, horses or sheep harbour fundamentally different moth communities than meadows (mown and fertilized grasslands). Overall land-use intensity (LUI) – i.e. grazing intensity, amount of fertilizer applied and mowing frequency taken together – significantly reduced abundance and species richness as well as diversity. Some 27 % of the species showed significant negative responses to LUI. A shift towards generalist life-history traits was observed: in frequently mown and fertilized meadows, rare specialist species were replaced by ubiquist species, i.e. highly reproductive habitat generalists.

These results show the sensitivity of moths, an important group of arthropod herbivores and pollinators, to land use change in grassland ecosystems. The functional homogenization of life-history traits in plants along land-use gradients is mirrored by their herbivore consumers, leaving high-intensity grasslands less diverse and potentially less resilient to environmental disturbances.

CHAPTER 3

Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists

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Introduction

Grasslands constitute one of the largest biomes covering 26 % of the world land area (FAO 2008). In central Europe, however, grassland ecosystems naturally occur only under particular edaphic or climatic situations (e.g. at high altitudes or in wetlands). Most European grasslands are anthropogenic in origin either as pastures or meadows, with possible conflicting goals in terms of biodiversity conservation, agro-economical and other stakeholder interests.

Therefore, grassland biodiversity is highly contingent on the type (mode of biomass removal through grazing intensity or mowing) and intensity of management (frequency of biomass removal, replenishment of soil nutrients through fertilization). Several studies reported a general loss of grassland biodiversity after intensification of land-use activities by the three most common management interventions, namely grazing, mowing and fertilization (Debinski *et al.* 2011; Johst *et al.* 2006; Krause and Culmsee 2013; Lanta *et al.* 2009; Moranz *et al.* 2012; Öckinger *et al.* 2006a; van den Berg *et al.* 2011). So far, only few studies related community composition and life-history trait variation with the type and intensity of land use (Birkhofer *et al.* 2015a; Bommarco *et al.* 2014; Gossner *et al.* 2014b; Tsiafouli *et al.* 2015).

As grasslands are managed more intensively, land-use practice often moves away from livestock grazing to frequent mowing, accompanied by the application of fertilizer. Extensively used grassland with low disturbance by livestock grazing typically maintains a higher structural diversity and higher plant diversity than more disturbed and intensively managed sites (Boch *et al.* 2013; Socher *et al.* 2012). Grazing by livestock can have direct and indirect effects on the complexity of the grassland vegetation structure by defoliation, treading and manuring (Morris 2000). In contrast, mowing affects all plant and animal populations at once, although interventions last only for very short periods in time. Conceptually, mowing can thus be considered as a pulse disturbance, whereas disturbance via grazing is more persistent and more selective. In the long term, frequently repeated mowing will select for different plant growth forms (e.g. rosettes, Liira *et al.* 2009) than grazing (e.g. plants with physical or chemical defence against grazers, Diaz *et al.* 2007). In common land-use practice, however, mowing is usually combined with the application of fertilizer to grasslands, which increases total biomass production (Simons *et al.* 2014) and favours fast-growing, highly competitive plant species (Liancourt *et al.* 2009), consequently reducing plant diversity (Simons *et al.* 2014; Zechmeister *et al.* 2003).

These changes in the resource composition and plant functional diversity due to land-use intensification are mirrored by the arthropod community. Livestock grazing affects arthropod diversity directly, by unintentional predation and increased disturbance, and indirectly, via selective resource depletion and changes in vegetation structure and abiotic conditions (van Klink *et al.* 2015). Under moderate grazing pressure, high species richness of plants and arthropod herbivores can be maintained or even increased (Kruess and Tscharntke 2002). Mowing, on the other hand, being primarily non-selective for plant taxa or functional groups, also induces high disturbance on the arthropod communities with particularly high fatalities on less mobile larval stages feeding on leaves (Humbert *et al.* 2010). The decline in resource plant species richness and higher plant biomass production due to combined mowing and fertilization (Lee *et al.* 2010; Socher *et al.* 2012) is causing a loss of specialist herbivore species and an increase in generalists (Gámez-Virués *et al.* 2015; Huston and Gilbert 1996; Simons *et al.* 2016). For example, the niche breadth of adult butterflies has been found to increase with the degree of disturbance; mono- and oligophagous specialist species occur more commonly in less disturbed habitats (Börschig *et al.* 2013; Kitahara *et al.* 2000). Many generalist arthropod species also have higher reproductive rates due to a larger number of reproductive cycles per year (i.e. multivoltine species, Börschig *et al.* 2013). Further, species traits such as a wide distribution or high dispersal mobility may improve the likelihood of arthropods to recolonize grassland sites after local extinctions through mowing or grazing (Öckinger *et al.* 2010; Tscharntke *et al.* 2005). Since individual body size is an important constraint on many functional traits, and particularly of mobility and dispersal range (Bartonova *et al.* 2014; Kivelä *et al.* 2013) as well as diet breadth (Kalinkat *et al.* 2013), it will be considered as a major factor of trait variation in this study.

This leads to the following expectations for arthropod communities in the wake of land-use intensification:

(1) Species composition of arthropod communities in grasslands depends on the *type* of land use (mowing and fertilization vs. grazing).

(2) Arthropod abundance and diversity concomitantly decrease in high-intensity grasslands.

(3) At high land-use intensification, generalist life-history traits will prevail over specialist traits.

In this study, we aim to test these predictions by assessing abundance, diversity and trait variation of moth communities from grassland sites distributed over three regions in Central Europe, which comprise meadows managed by mowing as well as pastures grazed by cattle, sheep and horse. The selected grasslands in this large-scale collaborative project (Biodiversity Exploratories) are representative for the three regions and cover a broad range of land-use intensities (Fischer et al. 2010). Land-use intensity (LUI) in these grasslands is quantified by three individual components (fertilization intensity, mowing frequency and grazing intensity) and summarized in a compound index, since the individual components are non-independent (Blüthgen et al. 2012).

Lepidoptera contain more than 160,000 described species and belong to the largest and best-explored arthropod groups (Kristensen *et al.* 2007; New 2004). However, the main focus of studies on land-use intensification has been on diurnal butterflies (Macgregor *et al.* 2015), whereas more than 85 % of Lepidopteran species are moths. Life-history traits and diversity of moths along quantified land-use gradients in grassland have rarely been studied (but see Pavlikova and Konvicka 2012; Rickert *et al.* 2012; Šumpich and Konvička 2012).

Material and Methods

Study area

The study was performed in the framework of the German Biodiversity Exploratory Project (http://www.biodiversity-exploratories.de; Fischer *et al.* 2010). The main objectives of the Biodiversity Exploratory Project are to understand the relationships between biodiversity of different taxa and levels, the role of land use and management for biodiversity, and the role of biodiversity for ecosystem processes. The established experimental plot design is used as a framework for many research projects to enable synthesis across taxa and functional groups.

The Exploratories were established in 2006 in three different regions of Germany: the Biosphere Reserve "Schorfheide-Chorin" (a glacially formed landscape in North-East Germany, 3-140 m a.s.l., 13°23'27''-14°08'53'' E / 52°47'25'' - 53°13'26'' N, mean annual temperature 6 - 7 °C, mean annual precipitation 520 - 580 mm), National Park "Hainich" and its surroundings (a hilly region in Central Germany, 285 - 550 m a.s.l., 10°10'24'' - 10°46'45'' E / 50°56'14'' - 51°22'43'' N, mean annual temperature 6.5 - 8 °C, mean annual precipitation 630 - 800 mm), and the Biosphere Reserve "Schwäbische Alb" (a low-mountain range in South-West Germany, 460 - 860 m a.s.l., 09°10'49''-09°35'54'' E / 48°20'28'' - 48°32'02'' N, mean annual temperature 8 - 8.5 °C, mean annual precipitation 800 - 930 mm).

Sample processing

Micro- and macro-moths were collected once a month between May and August 2014 in Hainich and Alb and in June and July 2014 in Schorfheide, because the highest species richness and abundance is expected during this period (Jonason *et al.* 2014). Nine grassland plots were sampled in both Hainich and Alb and eight in Schorfheide (n = 26), representing different land-use intensities and management methods. Moths represent one of the most diverse groups of arthropods and their abundance varies strongly along the season. To cover the whole variation within the plots, we preferred sampling repeatedly, rather than increasing local sample size. Every night during the sampling periods, three plots (termed A, B and C) were chosen. Moths were attracted using a battery powered (12 V) portable light trap, consisting of a super actinic and a black light tube (230 V, 2 x 20 W, bioform®)

with a twilight sensor, surrounded by a gauze cylinder (height: 180 cm; diameter: 70 cm). Light traps were placed in the centre of a plot to minimize the attraction of moths from adjacent habitats (Merckx *et al.* 2012), because the distance by which moths are attracted to light traps is up to 30 meters (Merckx and Slade 2014; Truxa and Fiedler 2012b). The sensor facilitated a simultaneous onset of the three light-traps after sunset. Every night the observation started with complete darkness (mean = 1.26 h after sunset) and comprised two sampling rounds when moths were manually collected at each trap and its direct surroundings. During the first sampling round, the light traps were visited (in order A, B, C) and directly observed for 20 minutes during which all moths were caught in individual vials. The second observation round reversed the order of plots (C, B, A) and lasted 15 minutes at each site. Thus, for logistic reasons given the travel distance of at least 20 minutes car drive between the three sites, the time between visits and the exposure to light varied between the plots, with longest exposure (sunset to last visit) at plot A and shortest at plot C. In consequence, the traps were illuminated for a total of 138 – 317 minutes (mean = 225.1 minutes) per night. In climate stations permanently installed on the plots, we recorded the mean air temperature two meters above ground per night and plot as a measure of ambient temperature per sampling site and night. All moths were identified to species level using identification guides (Rennwald and Rodeland 2002; Segerer and Hausmann 2011; Steiner *et al.* 2014) and by taxonomic experts (see Acknowledgements).

Land-use intensification

We examined the responses of moth communities to land-use intensity in grasslands using the quantitative index of land-use intensity (LUI) as an explanatory variable. This index combines the intensity of the three main management components applied to anthropogenic grasslands in Central Europe, namely livestock grazing [livestock units • grazing days • ha^{-1} • year^{-1}], mowing [cuts • year^{-1}] and fertilization intensity [kg N • ha^{-1} • year^{-1}] at each site. The index of land-use intensity (LUI_s) for each site *s* combines these three land-use components and is quantified as

$$LUI_s = \sqrt{\frac{F_s}{F_r} + \frac{M_s}{M_r} + \frac{G_s}{G_r}}$$

where intensities of fertilization (F_s), mowing (M_s) and grazing (G_s) on site *s* are standardized by their respective mean intensity across the three regions (F_r, M_r, G_r)

(Blüthgen *et al.* 2012). The land-use information is obtained annually by interviews with the landowners and farmers.

We used the land-use intensity of the year 2013, assuming that the year preceding the survey has the strongest influence on the occurrence of moths. Nevertheless, the LUI is highly correlated between successive years ($r = 0.86$ between 2013 and 2012, $r = 0.84$ between 2013 and 2014; n = 26 sites, for detailed information about the intensity of each plot see Supplementary Material S3.1: Tab. S3.1.1). In addition, the land-use components grazing, mowing and fertilization were evaluated separately as binary explanatory variables (grazed/ungrazed, mown/unmown, fertilized/unfertilized). Note that mowing and fertilization are usually coupled due to prevailing management practices in the study regions (and thus non-independent), whereas grazing trends to be complementary, even if eight plots were managed as mown pastures (see Supplementary Material S3.1: Data S3.1.1, Tab. S3.1.14).

Life-history traits

To analyse how land-use intensification may represent an environmental filter for moth species with particular life-history traits, we categorized the larval feeding niche, wingspan (as a representation of body size), reproductive cycle (expressed through voltinism and hibernation stage), geographic distribution in Europe, and national conservation status of each species based on the literature and supplemented with own data (KF, pers. obs.). The data are provided in Supplementary Material S3.2, the reference list in Supplementary Material S3.1: Literature S3.1.1. Larval feeding niche was classified in four ranks: (1) narrow specialists (host plants within one plant genus), (2) moderate specialists (host plants within one plant family), (3) moderate generalists (host plants recorded from two to four families), and (4) wide generalists (host plants in five or more families). We used the mean wingspan of each species taken from literature records, because it is strongly correlated with body size and is also known to relate to dispersal abilities and reproductive rates (Garcia-Barros 2000), even if such relationships might not be fully consistent across different studies (Betzholtz and Franzen 2011; Sekar 2012; Slade *et al.* 2013). We assume that larger body size supports the recolonization after disturbance events associated with management. As characteristics related to the reproductive cycle, we used two life-history traits. First, we classified voltinism of each species according to the number of generations produced within one year: (1) semivoltine (i.e. all individuals must undergo two periods of hibernation to complete their development), (2) strictly univoltine, and (3) multivoltine (i.e. two or more generations are regularly observed per year). Second, we classified the hibernation stage: (1) egg, (2) larva, (3) pupa, and (4) adult. Species with more advanced hibernation stages appear earlier in spring and have a higher degree of phenological advancement (Diamond *et al.* 2011). Therefore, they have better chances to avoid early-season land-use associated disturbances like mowing. We additionally classified the occurrence of each species across six different biogeographic zones within Europe (subarctic, boreal, continental, Atlantic, alpine and Mediterranean). To quantify the gross distribution we counted the number of zones in which the species occurs. National conservation status of moth species was taken from available red lists and the classification was adapted from the original red list: (1) critically endangered, (2) endangered, (3) vulnerable, (4) near threatened, (5) least concern. Since no nation-wide red list classification is available for micromoths in Germany, we excluded the conservation status for these species (for detailed information on scoring of the traits see Supplementary Material S3.1: Tab. S3.1.2, for life-history traits of each species see Supplementary Material S3.3).

Data selection

For the main analysis, we only included true grassland moth species, i.e. species whose larvae feed on herbs or grasses that regularly occur on meadows and pastures, because only populations of those species are expected to be affected by local land-use activities in the grassland. We thus aimed to exclude moths that were sampled while on dispersal flight or which may have been attracted by the light traps from nearby habitats. In particular, we assigned ‘ecotone species’, whose larvae feed on plants which may occasionally occur on grassland habitats, but mostly towards surrounding forest, hedgerows, neighbouring wetlands, agricultural land, or in stages of vegetation succession after mowing or grazing has been abandoned, and ‘forest species’, whose larvae feed on plants which are never a component of the vegetation community in open grassland. Both ‘ecotone species’ and ‘forest species’ were excluded. For comparison and as an assessment of the robustness of our results, we repeated the complete analysis for the grassland and ecotone species combined, and also for the forest species alone (see Supplementary Material S3.1: Tab. S3.1.8 - S3.1.13, Fig. S3.1.3 - S3.1.8).

Analysing community composition

To see how combined land-use intensification and particular land-use factors affected species composition, we analysed the species abundances per plot by means of a constrained ordination method (dbRDA / CAP). We z-transformed the predictors, square-root-transformed the moth counts and then calculated the Bray-Curtis distance of faunal composition across sites, based on proportional abundances of each species. With this method we converted all predictors to the same scale and minimized the effect of a few highly abundant species. We then tested the influence of land-use factors on moth species composition by running univariate tests (number of permutations = 999). As environmental factors, LUI and its individual components were used.

Analysing diversity trends and trait filtering

We further studied a variety of community-level metrics in response to land-use intensification, namely Shannon species diversity (H), total abundance (A) and observed species richness (S) of moths for each site during each survey. To quantify the average score of the moth assemblage for each life-history trait per site and survey, we calculated community-weighted means (CWM).

The statistical analysis of responses of moth communities (H, A, S, and CWM) to land use was performed in two steps. First, to account for random factor variation in the abiotic conditions we calculated residuals on a linear model (subsequently termed the co-variate model) that described the response variables as a function of the average temperature (in °C), the month (as factorial variable with levels “May”, “June”, “July”, “August”) and the potential influence of exposure to moonlight (Merckx *et al.* 2009). Moon exposure was quantified as the product of its proportional visibility during the observation period (sunset to end of second sampling; min = 0.07, max = 0.09; using http://www.mooncalc.org by Hoffmann 2015) and the proportion of lunar illumination (calculated using the lunar package in R, Lazaridis 2014; min = 0 at new moon; max = 1 at full moon). Controlling for effects of moonlight is important since this factor is known to substantially influence the effectiveness of light traps (Jonason *et al.* 2014). The duration of the observation period had no significant effect on the response variables and was therefore omitted from the co-variate model. Thus, the residual values extracted from the co-variate model are adjusted for any occurring seasonal or temperature-dependent variation in the response values. In the second step of analysis, the residual values of all temporal replicate samples per site were pooled into a single annual mean value for each plot, which was then used as response value in a series of ANCOVAs. These analyses tested whether land use (LUI, or its components grazing, mowing, or fertilization) had a significant effect on moth community attributes (H, A, S, CWM) and if this effect was concordant across the three regions (Alb, Hainich, Schorfheide). For significant results only, we additionally included the interaction effect between land use and region for significant results.

Pooling the temporal replicates assumes that the variation of observations on plots is Gaussian and no further correction for plot effects is required. The factor 'plot' was not included in our residual model, because the combination of plot and month, as the temporal replicates of samplings per plot, explains all of the variance. Using a linear mixed-effect model for the last step and adding plot as random effect would cause the same conflict between plot and land-use effect.

Analysing land-use niche of species

To further differentiate the responses of individual species to land-use intensity, we characterized the species by their distribution and abundance across the sites, defining their 'land-use niche' (Chisté *et al.* 2016). In particular, we defined the abundance-weighted means (μ_i) of the land-use gradient values of the sites in which species *i* occurs as a measure of its environmental niche optimum relative to the ecological gradient covered by our sampling (see Chisté *et al.* 2016 for land-use niche; Kühsel and Blüthgen 2015 for thermal niche). The species niches were estimated for the aggregate LUI value as well as for its components grazing, mowing and fertilization intensity. We compared the abundance-weighted means to a null model to test whether the observed μ_i does conform to expectations if the species was randomly distributed across the sites (Chisté *et al.* 2016). Therefore, we used 10,000 permutations of species occurrence while fixing the total number of plots in which the species occurs, to compute a distribution of μ_{null} values. For instance, if a species occurred in a total of three sites with mean land use μ_i, each null model computed the mean μ_{null} of any three sites randomly selected from the entire pool of 26 sites. We then calculated the proportion of the 10,000 μ_{null} values below and above the observed μ_i, p ($\mu_{\text{null}} < \mu_i$) and p ($\mu_{\text{null}} > \mu_i$), respectively. The smaller of both p-values defines the level of one-tailed significance. Species that had significantly lower realized μ_i land-use intensity than expected by chance are termed 'losers', whereas species that had a significantly higher

μ_i are termed 'winners'. While this null model approach has high statistical power even for rare species occurring in few plots, the minimum number of sites in which a species needs to occur to significantly deviate from the null model depends on the total number of sites and the number of sites sharing the lowest or highest land-use intensity, e.g. zero fertilization. To restrict the analyses to those species with sufficient power (i.e. a significant result for a hypothetical extreme response), we only included moth species that occurred on three or more sites for LUI, grazing and mowing; for fertilization we only included species that occurred on five or more sites since 15 plots were unfertilized.

Analysing relationship between land-use niche and species traits

Life-history traits were used to analyse patterns of μ_i associated with each trait level. The differences between the categories were assessed by Tukey's post hoc test following ANOVA or ANCOVA in case of body size. Within each category, a one-sample t-test comparing to the mean LUI was used to find differences within each category according to land-use intensification. To assess how mowing and grazing as contrasting management strategies affect the occurrence across all species, we correlated the μ_i of grazing and the μ_i of mowing.

Variance homogeneity and normal distribution was checked with Bartlett's test and Shapiro-Wilk's test, respectively. All statistical analyses were performed in the R environment (R Core Team 2014, version 3.1.2), using the packages lme4 (Bates *et al.* 2014), MASS (Venables and Ripley 2002) and vegan (Oksanen *et al.* 2015).

Results

Between May and August 2015 we recorded and determined 4,811 moth individuals belonging to 461 species from 26 families. After discounting all species that are atypical for grassland habitats, the sample on which the analyses described below was based, comprised 3,237 individuals (178 species, 14 families).

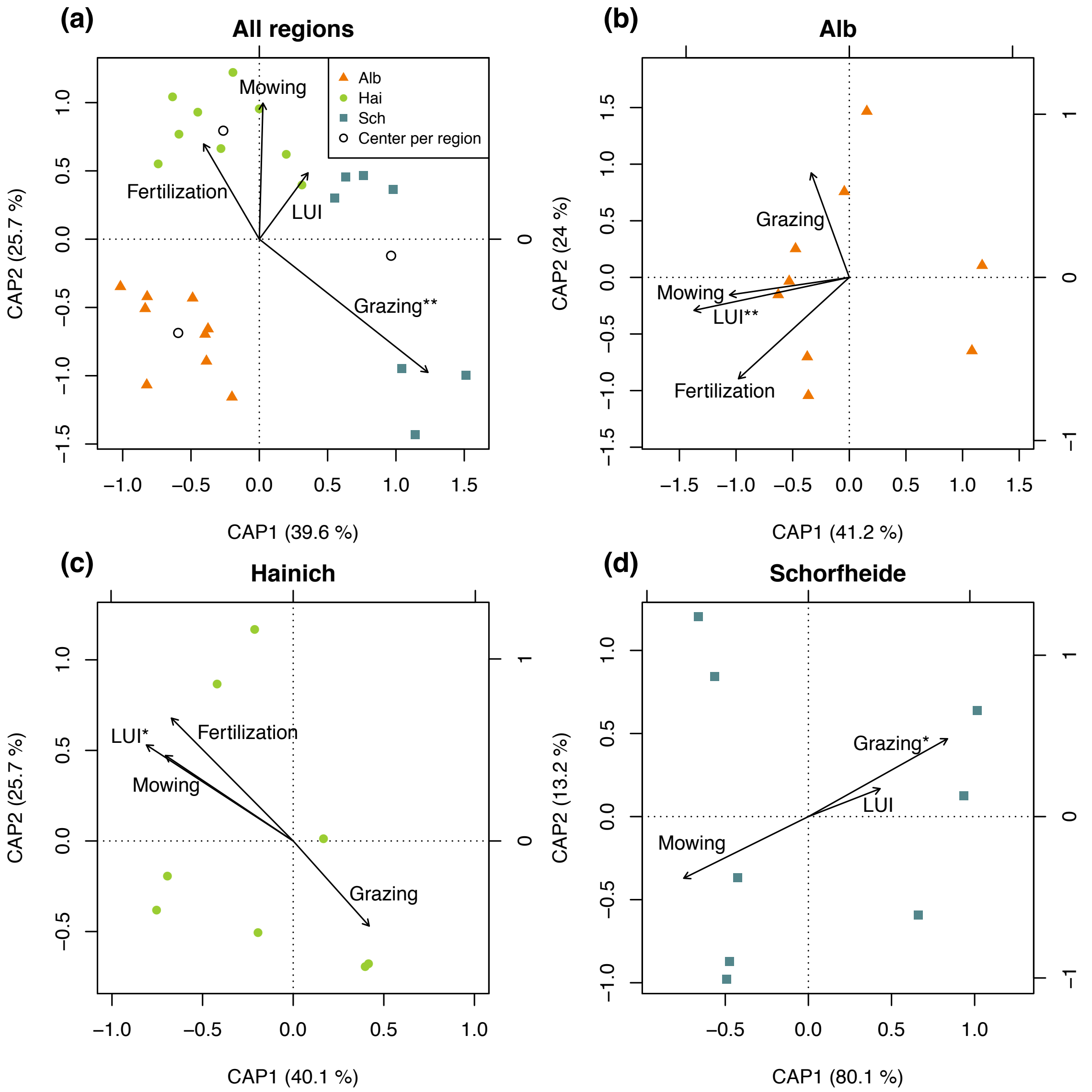

Fig. 3.1: Constrained ordination of moth species composition in all regions (a), and separately for the three regions Schwäbische Alb (Alb) (b), Hainich (Hai) (c) and Schorfheide (Sch) (d). Comparisons of communities were based on quantitative Bray-Curtis distances. Arrows represent the relationships with the respective land-use components. Asterisks indicate a statistically significant effect of the predictor. Detailed information on the statistical results and the residual model are given in the Supplementary Material S3.1.

Community composition

Community composition differed significantly across all three regions (dbRDA: $F = 4.53$, $df = 2$, $p = 0.001$) and was on this large scale significantly affected only by grazing ($F = 2.68$, $df = 1$, $p = 0.004$). The two other factors of land use did not explain significantly the variance in moth species composition. Moth samples from the Alb and the Hainich formed two rather well defined clusters in reduced ordination space, whereas the Schorfheide samples (characterized by the overall lowest sample sizes) appeared more variable with regard to species composition. Within each region, a significant relationship between land-use intensity (i.e. LUI) and moth species composition could be shown in Alb ($F = 2.13$, df = 1, $p = 0.008$) and in Hainich ($F = 1.54$, df = 1, $p = 0.045$), but not in Schorfheide. Of the individual factors describing land use, only grazing had a significant effect in Schorfheide ($F = 3.44$, df = 1, $p = 0.021$; See Fig. 3.1), whereas all other factors did not show any close relationships with moth species composition in any region. In Hainich and Schorfheide, grazing and mowing effects on moth species composition were opposed to each other. In the Alb, in contrast, the effects of mowing and grazing were independent, with mowing largely projected on the first and grazing on the second canonical axis (See Fig. 3.1). For the full list of species in each region and month, see Supplementary Material S3.2.

Diversity trends

After correcting for the variation caused by temperature, moonlight and season by taking the residuals on the covariate-model, we tested the effect of land use on species diversity, abundance and species richness across all survey regions. No response variable was significantly reduced at higher LUI values across all three regions, but an interaction between LUI and region was significant for abundance ($F = 4.46$, $df = 2$, $p = 0.026$). However, among the three land-use dimensions, mowing as a binary explanatory was associated with a decline in diversity ($F = 4.78$, $p = 0.04$), abundance ($F = 10.31$, $p = 0.046$) and richness ($F = 11.43$, $p = 0.047$) (Fig. 3.2c, g & k). No significant effects were observed for grazing and fertilization (ANOVAs testing the effect of grazing, mowing and

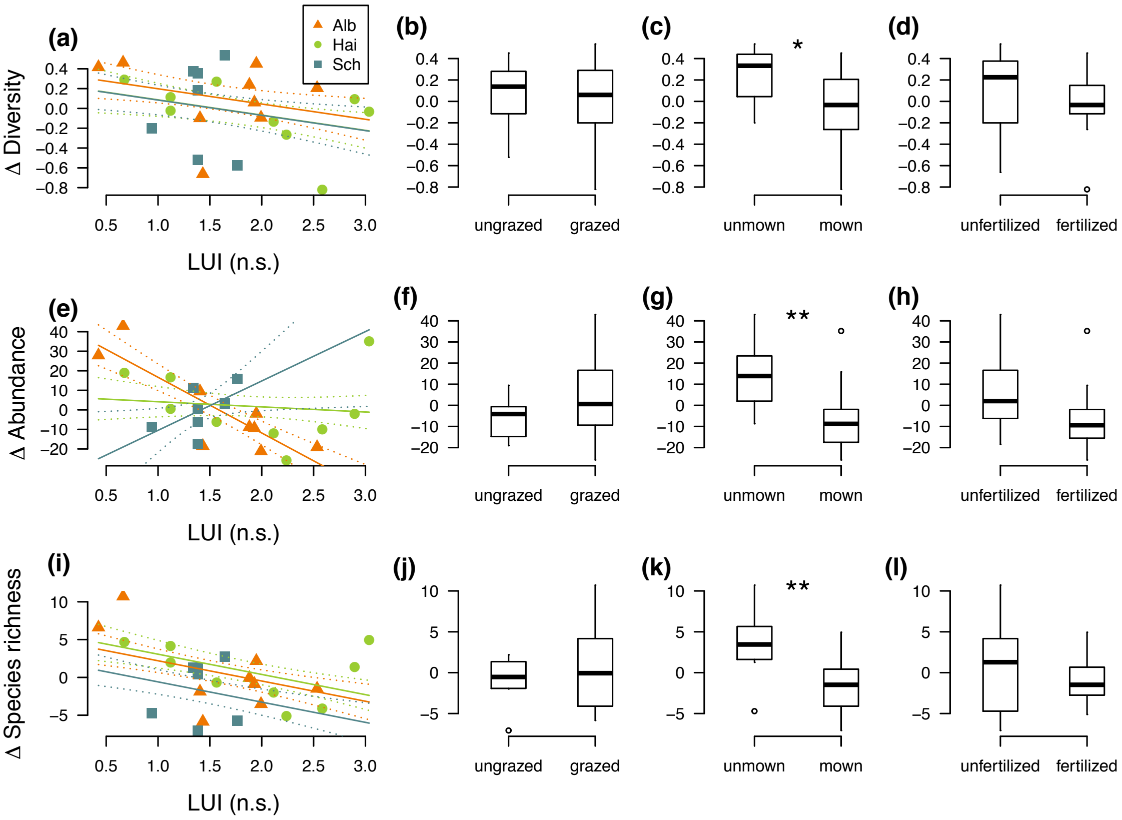

Fig. 3.2: Relationship between residuals of moth diversity [(a) – (d)]; abundance [(e) – (h)] and observed species [(i) – (l)] per site along the standardized integrated land-use intensity index LUI [(a), (e), (i)] for the three regions Schwäbische Alb (Alb), Hainich (Hai) and Schorfheide (Sch). The results are based on a linear model using LUI and region as explanatory variables, after accounting for variation in light-trap samples related to temperature, season and moonlight. The factors grazing mowing and fertilization were examined separately. In contrast to species composition, region had no significant effect in any of the models. Different slopes of the three lines illustrate the interaction between land use and region, if it is significant. Significance levels: n.s. – not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.005$. Please note: We calculated species diversity with mean temperature and moonlight in May (1.13) and in July (2.10), because those months showed the lowest and highest species diversity. Those results are equivalent to 0 on the y-axis. (Observed mean abundance: 18.48 moths per night and site in May, 74.51 in July; observed species richness: 5.68 species per night and site in May, 20.77 in July). Detailed information on the statistical results and the residual model are given in the Supplementary Material S3.1.

fertilization as binary explanatories; Fig. 3.2b - d, 3.2f - h; Supplementary Material S3.1: Tab. S3.1.6).

Trait filtering

Larval feeding niche, voltinism, distribution range and conservation status were all significantly filtered to some extent by land-use intensification. The community-weighted mean (CWM) of the species' larval feeding niche breadth increased significantly with LUI

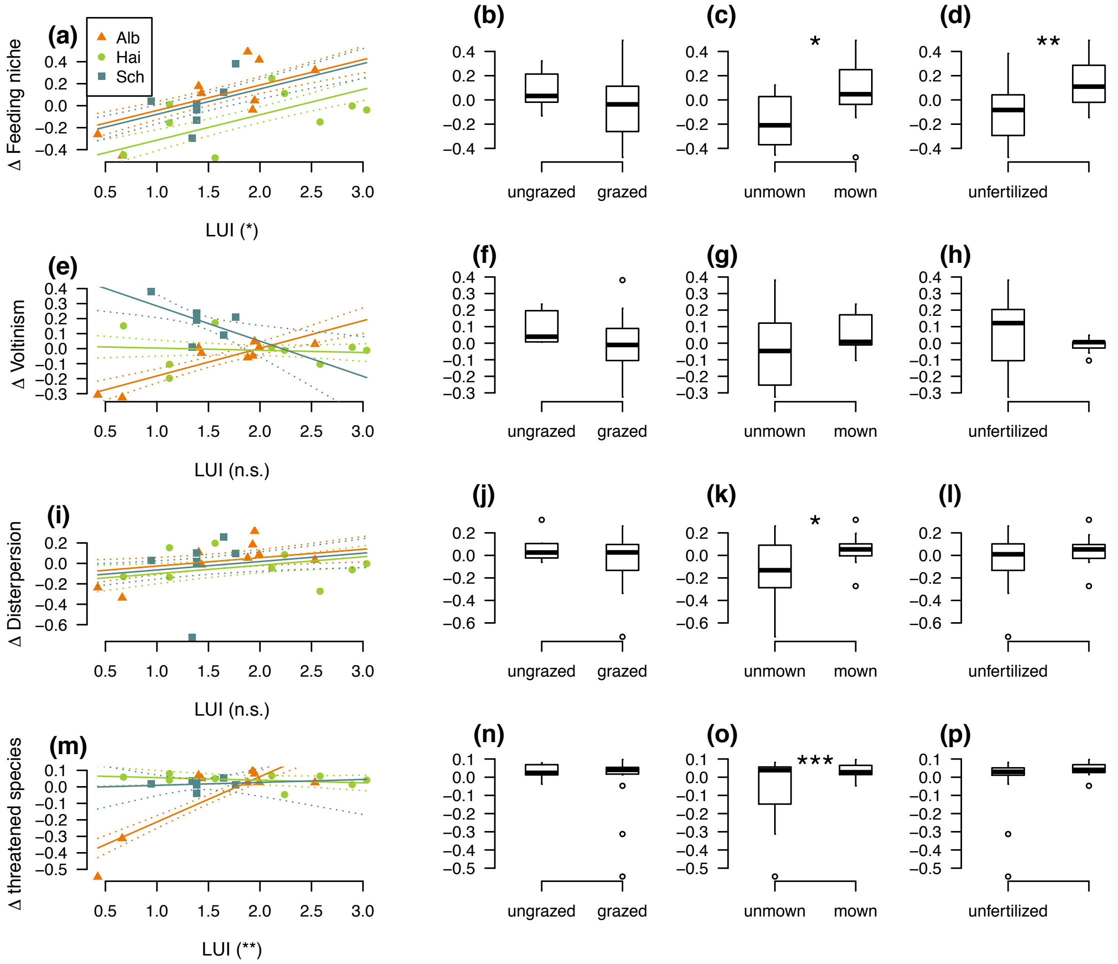

Fig. 3.3: Relationship between residuals of moth traits along the land-use intensity index LUI [(a), (e), (i), (m)] in the three regions Schwäbische Alb (Alb), Hainich (Hai) and Schorfheide (Sch). Shown are those four traits with significant results, namely breadth of larval feeding niche, voltinism, distributional range, and national conservation status. The results are based on a linear model using LUI and region as explanatory variables. Voltinism and vulnerability show a significant interaction effect between LUI and region. The factors Grazing [(b), (f), (j), (n)], Mowing [(c), (g), (k), (o)] and Fertilization [(d), (h), (l), (p)] were additionally examined. Different slopes of the three lines illustrate the interaction between land use and region, if it is significant. Significance levels: n.s. – not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.005$. Please note: We calculated feeding niche with mean temperature and moonlight in May (3.46) and in July (2.6), because those months showed the lowest and highest moth species diversity. Those results are equivalent to 0 on the y-axis. (Observed community-weighted averages: Voltinism: 2.53 in May, 2.28 in July; Distribution: 5.01 in May, 5.47 in July; Red list status: 4.83 in May, 4.99 in July). Detailed information on the statistical results and the residual model are given in the Supplementary Material S3.1.

(*F* = 7.36, *df* = 1, *p* = 0.013), mowing (*F* = 7.97, *df* = 1, *p* = 0.011) and fertilization (*F* = 9.13, *df* = 1, *p* = 0.006), i.e. species in intensively used grasslands were more generalistic in terms of their caterpillar's host ranges. LUI had no consistent effect on the CWM of voltinism (p = 0.649), but an interaction between region and LUI was significant (*F* = 5.59, *df* = 2, p = 0.012), where voltinism decreased with LUI in Alb, increased in Hainich and remained constant in Schorfheide. Grazing caused a weak positive (*p* = 0.071) and mowing a negative (p = 0.056) trend for voltinism (see Fig 3.3, Supplementary Material S3.1: Tab. S3.1.7). The CWM of the species' distribution range increased significantly with mowing (*F* = 4.556, *df* = 1, *p* = 0.045), i.e. species in intensively mown grasslands were on average more geographically widespread within Europe. The CWM of the national conservation status was affected significantly by LUI (*F* = 13.66, *df* = 1, p = 0.002), but this effect varied very substantially across regions (*F* = 13.43, *df* = 2, *p* < 0.0001). The effect of LUI on conservation status was strongly positive in Alb but weakly negative in the other two exploratories. This was due to the fact that the most threatened species were found on xeric grassland, which among our study sites only occur at Alb (see Fig 3.3, Supplementary Material S3.1: Tab. S3.1.7). The analyses of wingspan and hibernation stage did not show any significant filtering effects.

Tab. 3.1: List of species, which were determined as neutral, losers, winners and mid-specialists in relation to the standardized integrated land-use intensity index LUI and its components grazing, mowing and fertilization**.** Results were given by the Null model with its total abundance (A) and number of plots they occurred (n plots). Species are defined as losers, when the *abundance-weighted means* (μ_i) is significantly lower than the expected μ_{Null} giving by the Null model, winners have a significantly higher μ_i, than μ_{Null} and mid-specialists are specialised at medium land-use intensification. For fertilization we only included species that occurred on five or more sites.

Species	Family	A	n plots	LUI	Grazing	Mowing	Fertilisation
Agriphila straminella	Crambidae	322	22	winner	mid spec.	winner	winner
Idaea biselata	Geometridae	5	3	winner	mid spec.	neutral	
Siona lineata	Geometridae	6	4	winner	neutral	neutral	
Autographa gamma	Noctuidae	9	5	winner	mid spec.	neutral	winner
Axylia putris	Noctuidae	8	6	winner	neutral	neutral	winner
Mesoligia furuncula	Noctuidae	9	7	winner	mid spec.	neutral	winner
Mythimna albipuncta	Noctuidae	6	4	winner	neutral	neutral	
Noctua interposita	Noctuidae	8	3	winner	neutral	winner	
Oligia versicolor	Noctuidae	15	6	winner	neutral	winner	winner
Spilosoma lubricipeda	Noctuidae	49	16	winner	loser	winner	neutral
Xestia c-nigrum	Noctuidae	123	24	winner	loser	winner	winner
Celypha rufana	Tortricidae	11	6	winner	neutral	neutral	winner
Pyrausta despicata	Crambidae	80	10	loser	neutral	neutral	loser
Pyrausta purpuralis	Crambidae	13	5	loser	neutral	loser	loser
Acompsia cinerella	Gelechiidae	21	5	loser	neutral	loser	loser

Species	Family	A	n plots	LUI	Grazing	Mowing	Fertilisation
Chiasmia clathrata	Geometridae	104	17	loser	loser	neutral	loser
Epirrhoe alternata	Geometridae	31	13	loser	loser	neutral	neutral
Eupithecia satyrata	Geometridae	6	4	loser	neutral	loser	
Scopula ornata	Geometridae	13	3	loser	mid spec.	loser	
Scotopteryx chenopodiata	Geometridae	53	9	loser	mid spec.	loser	neutral
Xanthorhoe spadicearia	Geometridae	23	6	loser	mid spec.	loser	neutral
Triodia sylvina	Hepialidae	13	5	loser	neutral	loser	loser
Agrotis cinerea	Noctuidae	32	4	loser	mid spec.	loser	
Apamea lithoxylaea	Noctuidae	12	6	loser	mid spec.	neutral	neutral
Apamea monoglypha	Noctuidae	30	16	loser	loser	neutral	neutral
Charanyca trigrammica	Noctuidae	40	7	loser	loser	loser	neutral
Deltote deceptoria	Noctuidae	16	4	loser	neutral	loser	
Hada plebeja	Noctuidae	26	6	loser	mid spec.	loser	neutral
Mythimna conigera	Noctuidae	25	8	loser	neutral	loser	loser
Thalpophila matura	Noctuidae	7	4	loser	neutral	loser	
Xestia xanthographa	Noctuidae	9	3	loser	neutral	neutral	
Oncocera semirubella	Pyralidae	33	7	loser	neutral	loser	loser
Agapeta zoegana	Tortricidae	22	3	loser	neutral	loser	
Agriphila inquinatella	Tortricidae	25	4	loser	neutral	loser	
Crambus pratellus	Tortricidae	23	7	loser	loser	loser	neutral
Eucosma cana	Tortricidae	9	5	loser	neutral	loser	neutral
Ostrinia nubilalis	Crambidae	42	9	neutral	neutral	winner	winner
Arctia caja	Erebidae	12	9	neutral	loser	neutral	neutral
Eupithecia subfuscata	Geometridae	10	9	neutral	loser	neutral	neutral
Eupithecia subumbrata	Geometridae	7	6	neutral	mid spec.	neutral	neutral
Perizoma alchemillata	Geometridae	18	12	neutral	mid spec.	neutral	neutral
Agrotis exclamationis	Noctuidae	109	17	neutral	loser	mid spec.	neutral
Amphipoea fucosa	Noctuidae	39	10	neutral	neutral	neutral	winner
Ceramica pisi	Noctuidae	5	4	neutral	winner	neutral	
Cerapteryx graminis	Noctuidae	3	3	neutral	loser	neutral	
Hoplodrina octogenaria	Noctuidae	25	11	neutral	mid spec.	neutral	neutral
Mythimna ferrago	Noctuidae	12	11	neutral	neutral	mid spec.	winner
Noctua pronuba	Noctuidae	96	18	neutral	loser	neutral	neutral
Ochropleura plecta	Noctuidae	86	19	neutral	mid spec.	mid spec.	neutral
Oligia strigilis	Noctuidae	18	8	neutral	mid spec.	mid spec.	neutral
Phragmatobia fuliginosa	Noctuidae	147	17	neutral	neutral	winner	neutral
Rivula sericealis	Noctuidae	67	9	neutral	loser	neutral	winner
Agapeta hamana	Tortricidae	49	16	neutral	mid spec.	winner	winner
Agriphila tristella	Tortricidae	199	17	neutral	mid spec.	neutral	neutral
Celypha lacunana	Tortricidae	40	16	neutral	loser	neutral	neutral
Chrysoteuchia culmella	Tortricidae	178	19	neutral	loser	winner	neutral
Cnephasia asseclana	Tortricidae	22	11	neutral	loser	neutral	neutral
Cnephasia stephensiana	Tortricidae	15	4	neutral	neutral	loser	
Crambus perlellus	Tortricidae	122	19	neutral	loser	winner	neutral

Land-use niche

Individual species varied massively in their response to land-use. Regarding the aggregate land-use intensity (LUI) index, the observed niche optima (μ_i) significantly differed from expectations under a random distribution (null model, μ_{null}) for 36 of 87 species. In 24 species (27.6 %) a significantly lower μ_i was observed, marking them as losers; whereas 12 species (13.8 %) were winners. For the individual land-use components grazing (losers: 24 species, 27.6 %; winners: 12 species, 13.8 %) and mowing (losers: 19 species, 21.8 %; winners: 10 species, 11.5 %), similar results were found. In addition 17 species (19.5 %) were detected as mid-specialists for grazing and 4 species (4.6 %) for mowing. In contrast, fertilization showed an opposing effect (losers: 7 species, 12 %; winners: 12 species, 20.7 % of the total 58 species for which this analysis was possible) (See Tab. 3.1 for list of species, Supplementary Material S3.1: Tab. S3.1.4 for μ_i, μ_{null} and p-values of all 87 species).

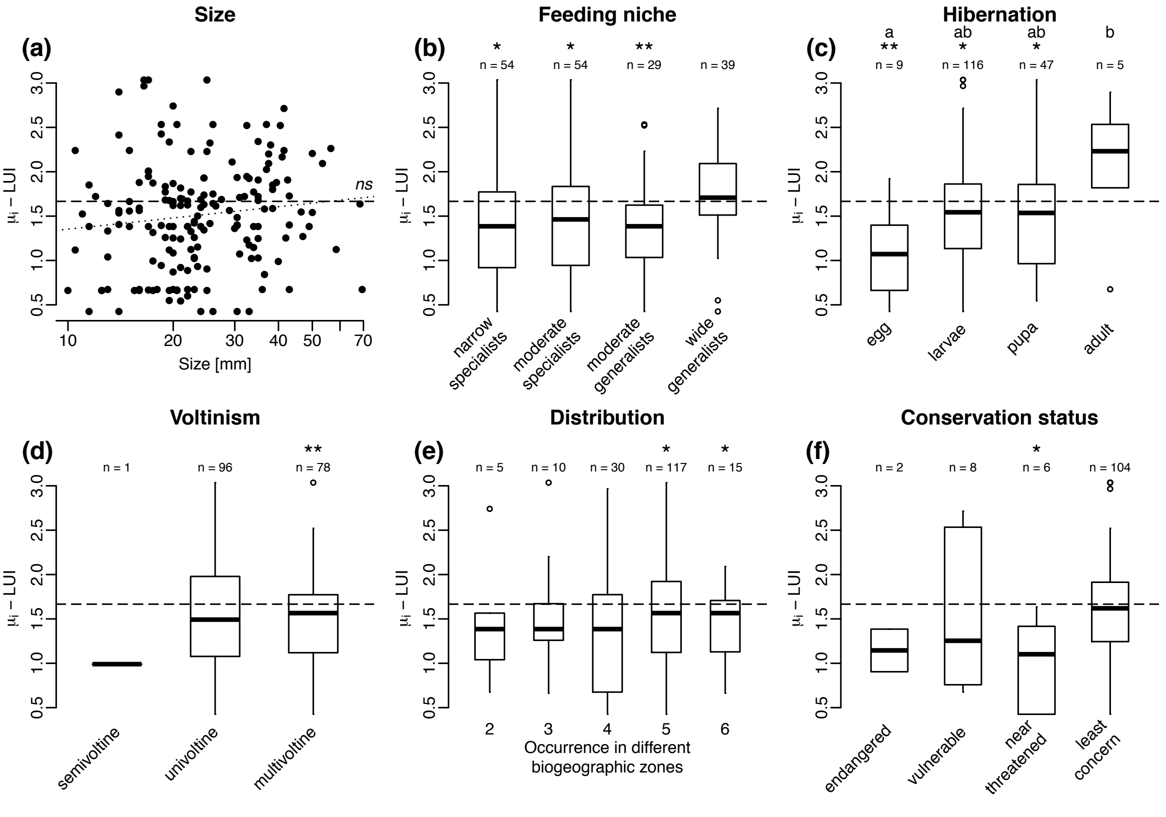

Fig. 3.4: Relationship between the observed niche optima relative to LUI (μ_i) and traits of 178 grassland moth species. The dashed line represents the mean LUI (1.67) observed across all 26 sites. Asterisks represent a significant difference to the mean LUI given by a one-sample t-test. Significant differences between the groups a given by an ANOVA.

Relationship between land-use niches and species traits

The niche optima of species relative to land-use varied with the levels of most life-history traits (see Fig. 3.4). In terms of larval feeding niche, significantly more narrow (p = 0.018) and moderate specialists (p = 0.016) and moderate generalists (p = 0.009) had niche optima at land-use intensities below average (niche optima μ_i significantly < 1.67). Similarly, the analysis of hibernation stage revealed that species that overwinter as eggs (p = 0.006), larvae (p = 0.013) and pupae (p = 0.035), correlate with low LUI values, whereas adult hibernation was unrelated. Multivoltine species, species with broad distribution (5 zones: p = 0.02; 6 zones: p = 0.043) and nearly threatened species (p = 0.027) also were favoured by low LUI. Note that no life-history trait level predicted niche optima above average LUI.

The effects of grazing and mowing intensity on the abundance-weighted means (μ_i) were strongly negatively correlated (rs = -0.302; $p < 0.001$). Grazing had a stronger effect on abundance-weighted means (μ_i) than mowing. Many species preferred sites of below-average grazing intensity (143 species; 35 species above-average grazing). High mowing intensity was avoided by 99 species, versus 79 species that were more abundant on sites with above-average mowing intensity (see Fig. 3.5).

The overall effects of land-use intensity were less pronounced when the analyses were not restricted to genuine grassland moths. Including species that are affiliated with larval host plants that mostly occur in ecotones around the plot area (additional 103 species from

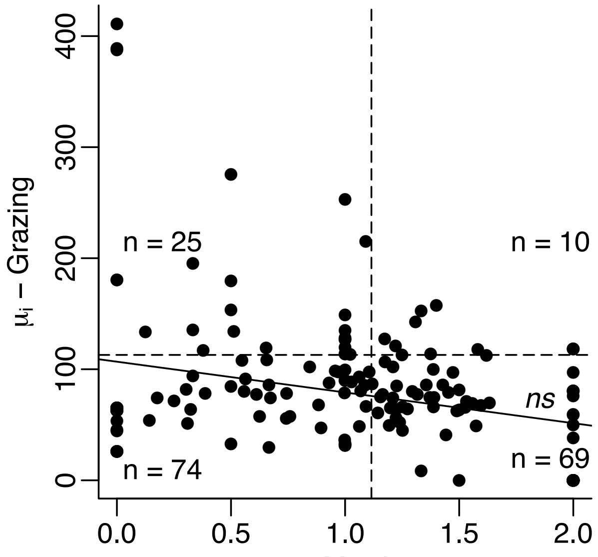

Fig. 3.5: Correlation between the observed niche optima (μ_i) relative to grazing and mowing of 178 grassland moth species. The dotted line represents the correlation between both factors (rs = -0.302; $p <$ 0.0001). The dashed horizontal line represents the mean grazing intensity (112.9 LSU*day/ha) and the dashed vertical line represents the mean mowing intensity (1.12 cuts/year). In each quadrant the total number of species is specified.

14 families, 532 individuals) uncovered overall similar effects as with the true grassland species only. In contrast, considering only those stray species that are not a component of open grassland assemblages as inferred from their larval host plant affiliations (1037 individuals, 179 species, 22 families) did not reveal any statistically significant relationships with land use (see Supplementary Material S3.1: Tab. S3.1.8 – S3.1.13, Fig. S3.1.3-S3.1.8).

Discussion

For the case of nocturnal moths, we found significant effects of land use on the species assemblage, its diversity and composition of life-history traits in grasslands. As expected, species with specialist traits were favoured by low-intensity pasturing while generalists were prevailing in intensely managed meadows.

Differences in community composition matched the differences in land-use intensity consistently across two of the three regions in Germany, regardless of the strong geographic differentiation in species composition. Among the three types of land use considered in this study, grazing had the strongest effect on species composition. We found that grazing and mowing/fertilization had largely opposing effects on the moth assemblages: species characteristic for meadows such as *Agriphila straminella*, *Agriphila tristella* and *Crambus perlellus* declined under more intense livestock grazing and were replaced by other species such as *Anerastia lotella*, *Mythimna pallens* and *Xestia c-nigrum*.

Besides these qualitative effects on species diversity, abundance and richness of moths significantly declined in response to land-use intensification, particularly through mowing. These negative effects were consistent across all three regions.

In correspondence to changes in species composition with land-use intensification, the species traits found in the communities indicate a shift towards more ubiquitous, generalist moth species: with land-use intensification communities were composed of common species which cover a broader geographic distribution range and whose larvae feed on a broader host plant range. Voltinism, i.e. the number of reproductive cycles within one year, showed an inconsistent response, and neither body size nor hibernation stage of grassland moths were detectably filtered by land use.

Similar effects were shown for the land-use niche. Most species had niche optima at low land-use intensity. This pattern was mediated by the components grazing and mowing. In contrast to expectation, species mostly prefer niches associated with a higher application of fertilizers.

Our finding of a reduction in moth diversity, species richness and abundance as well as an increase in generalist prevalence also adds to the evidence of negative effects of land-use intensification on biodiversity that has been demonstrated for moths (Ekroos *et al.* 2010;

Kadlec *et al.* 2009) and a variety of other taxa (Allan *et al.* 2014; Billeter *et al.* 2008). Not all taxa or functional groups are equally affected (Weiner *et al.* 2014; Winfree *et al.* 2008), and our results confirm that land use acts as an environmental filter (Klimek *et al.* 2007; Kühsel and Blüthgen 2015; Loder *et al.* 1998).

Mowing represents a massive pulse disturbance in grassland and has been found to increase the mortality of caterpillars up to forty per cent (Humbert *et al.* 2010). The occurrence of moths, therefore, is likely constrained by the survival rate of their larvae in response to the land-use management regime. In the process of recolonizing the habitat after such a treatment, common ubiquitous moth species are favoured over rare species with narrow larval food niches for stochastic reasons alone. With a plant community being dominated by few fast-growing plant species as a result of fertilizer application, larvae with a broad spectrum of host plants were favoured on such sites. In addition, a trend towards higher reproduction rates of moths (e.g. voltinism) could be found in mown grasslands. Generalists with this set of traits are more likely to colonize new environments and have better abilities to find necessary recourses (Duncan *et al.* 2003). Changes in trait composition towards generalist species in response to land-use intensification have been reported for other traits and arthropod taxa in the same grasslands (e.g. Birkhofer *et al.* 2015b; Börschig *et al.* 2013; Simons *et al.* 2016). This shift to more generalist species may ultimately lead to functional homogenization, defined as the effect of “spatial similarity of a functional variable over time” (Clavel *et al.* 2011). Higher homogenization in intensively managed habitats has been found in several taxa (Finke and Snyder 2008), including butterflies (Börschig *et al.* 2013). In our study, the effect of fertilization, which is expected to affect the development of herbivores due to stoichiometric limitations (Audusseau *et al.* 2015; Fischer and Fiedler 2000; Serruys and Van Dyck 2014), is likely masked by the strong contingency between mowing and fertilization on the study sites of the Biodiversity Exploratories (Blüthgen *et al.* 2016, see Supplementary Material S3.1: Data S3.1.1).

In contrast to mowing, grazing preserves species that combine life-history traits characteristic for specialists. Livestock grazing, by acting continuously and selectively, maintains a less disturbed habitat structure and more diverse plant resources, particularly with regard to herb species (Socher et al. 2013). Caterpillars of only a small number of moth species in our sample are predominantly or exclusively grass feeding, while the majority of grassland species encountered in our study were herb feeders. The higher diversity of herb species under livestock grazing regimes may explain why moth communities on pastures were more diverse than on meadows. The loss of specialists along with resource homogenization and the subsequent simplification of the functional trait diversity in the arthropod community is an alarming pattern that illustrates how consequences of land-use intensification for the vegetation translate into community shifts at higher trophic levels.

This pattern recurs, considering the land-use niche of moth species. The majority of species preferred low land-use intensity, especially regarding grazing and mowing, i.e. the losers of land-use intensification. Hemerophilous species, i.e. species often associated with anthropogenic land use such as *Oligia versicolor*, *Spilosoma lubricipeda* or *Xestia c-nigrum*, benefit from increasing land-use intensification. Except for the highly polyphagous *S. lubricipeda*, the larvae of all winners live on grasses. In contrast, losers of land-use intensification prefer extensively used habitats. They feed on herbaceous plants that disappear with increasing land use (e.g. *Thymus* and related Lamiaceae for *Pyrausta purpuralis* or *Scopula ornata*, some Fabaceae for *Oncocera semirubella* or *Rhinanthus* for *Perizoma blandiata*). In contrast, more species benefit with increased application of fertilizers. In general, eutrophication decreases the occurrence of diurnal and nocturnal Lepidopteran (Fox *et al.* 2014; Hodgson *et al.* 2014; Öckinger *et al.* 2006b; Van Es *et al.* 1999; Wallisdevries *et al.* 2012). Nevertheless, a few winners do not occur in nutrient-poor grassland (e.g. *Amphipoea fucosa*, *Celypha rufana*, *Mythimna ferrago*), live as ubiquists (e.g. *Autographa gamma*, *Oligia versicolor*) or even prefer nutrient-rich environments (e.g. *Agriphila straminella*, *Axylia putris*, *S. lubricipeda*, *X. c-nigrum). Agapeta hamana* might disappear with even stronger fertilization and the European corn borer (*Ostrinia nubilalis*) is well known as a pest species and benefit from increasing eutrophication. The results suggest that particularly ubiquists or hemerophilous species benefit from land-use intensification, i.e. species that require open grassland vegetation with immature soil disappear.

Finally, smaller species are often more specialized in resources whereas larger species are often more dependent on a particular environment (Loder *et al.* 1998; Summerville *et al.* 2006). This pattern may lead to a contingency between body size and niche breath. We did not find a significant relationship between land-use intensity and average body-size, however.

In this study, we showed that the community composition of moths, a rich and abundant group of arthropods known to maintain important ecosystem processes such as herbivory and pollination, selectively respond to different types of land use. The threats to biodiversity imposed by land-use intensification in the form of mowing and fertilization complement the documented changes in plant communities, as specialised moth species are tied to the fate of their host plants. Such intensive land-use management thus filters for generalist species and nurtures homogeneous communities of plants and consumers that may, in the long run, be less resilient to environmental change (Blüthgen *et al.* 2016; Gámez-Virués *et al.* 2015; Kühsel and Blüthgen 2015). By opting for grazing rather than for mowing and fertilization, land-use managers may contribute to conservation of specialized species and grassland biodiversity.

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Abstract

Intraspecific phenotypic variation in populations promotes a species' persistence in different environments and to tolerate environmental variation, land use and habitat disturbances. Hence, trait composition across species in communities and within populations should be affected by the intensity of land use. Cultural grasslands are regularly disturbed by different kinds of management (mowing, grazing and fertilisation) at varying intensity. For animals, traits associated with mobility and dispersal thus play a key role, and the importance of such traits may increase with land-use intensity. Moreover, resource specialists may be affected more strongly than generalists. Therefore, it is important to understand the relationship between specialisation and dispersal-related traits across species in a community. In this context, land-use intensity affects both, intraspecific variation and community trait composition.

In this study, we analysed the intraspecific variation of morphological traits associated with dispersal ability (body mass, wing area and wing loading) of 67 species of moths (Lepidoptera) across 26 grasslands in three regions. We examined how these selected traits changed with land-use intensity and tested whether phenotypic variability explained the occurrence of moth species along the land-use gradient. Additionally, we analysed how trait variation corresponded to host-plant specialisation of each moth species. Species differed strongly in land-use responses, but a higher number of species significantly increased in body mass and wing loading with increasing land-use intensity, whereas few species decreased in these traits. Increases were most pronounced with increasing fertilization. Especially grass-feeding moths responded positively, corresponding to an increase in grass biomass and quality with fertilizer application. In contrast, species with increasing body mass and wing loading along land-use gradients were not more abundant in intensively managed sites than others. All three morphological traits were correlated interspecific with the species' host plant specialization: the mean trait values were significantly lower for specialised species than for generalists, whereas the intraspecific variance did not change across the range of specialisation. Hence, generalists were larger and additionally profited from fertilization by developing a higher body mass and total wing area. Intraspecific variation together with the specialization of consumers may thus contribute to biodiversity declines and changes in community composition with increasing land-use intensity.

CHAPTER 4

Intraspecific trait variation and responses to land use: body mass and wing loading in grassland moth communities

Jule Mangels, Nico Blüthgen

Introduction

The global decline of biodiversity is mainly caused by land-use intensity (Sala *et al.* 2000), which has also a strong effect of community trait composition (Birkhofer *et al.* 2017; Simons *et al.* 2016). In this context, potential filtering of phenotypic traits become particularly evident and have often been examined in an interspecific context, focusing on the community-weighted means and variance of various traits across species (Gámez-Virués *et al.* 2015; Kühsel and Blüthgen 2015). Such traits include life history, behavioural, physiological or morphological traits. For instance, variation in the shape of wings may be associated with altered flight performance in birds or insects, with consequences for a species' dispersal ability and mobility in different habitats (Chai and Srygley 1990; Claramunt *et al.* 2012; Kennedy *et al.* 2016). To survive in changing environments or in different habitats, organisms can also adjust to altered conditions through phenotypic plasticity, filtering of phenotypes within populations and selection of associated genotypes and thus adaptation over several generations. Ecological consequences of intraspecific trait variation on populations and communities are multifold (reviewed in Bolnick *et al.* 2011). For instance, higher intraspecific variability can buffer populations against temporal fluctuations in environmental conditions, promotes a broader ecological niche and accelerates adaptive eco-evolutionary dynamics (Bolnick et al. 2011).

Land-use interferes with resource allocation and succession in grassland. A certain degree of disturbance is necessary in many semi-natural grasslands to avoid vegetation succession, shrub and tree growth (Huston 1994). The Intermediate Disturbance Hypothesis suggests that maximal diversity can be reached if local disturbances are frequent enough to delay negative effects of asymmetric interspecific competition, as long as the degree of disturbance does not lead to eliminations of the species (Connell 1978). In this context it is necessary to consider the type and intensity of disturbance via land use. In grasslands the three most common components are grazing, mowing and fertilization, and each of these components potentially represents a substantial impact and disturbance on an ecosystem (Debinski *et al.* 2011; Gossner *et al.* 2016; Johst *et al.* 2006; Krause and Culmsee 2013; Lanta *et al.* 2009; Moranz *et al.* 2012; Öckinger *et al.* 2006a; van den Berg *et al.* 2011). In general, the intensity of grazing and mowing are usually opposing managements, and the latter has the strongest effect (Humbert *et al.* 2009). In contrast, grassland fertilization is often coupled with mowing and decreases plant diversity, increases the total plant biomass production and leads to a higher dominance of grass species (Simons *et al.* 2014).

The application of fertilizers may increase food availability – depending on the focal herbivore's diet. Additionally, fertilization improves the nutrient content of plant tissue with variable effects on the individual herbivorous insects' body mass and reproductive strategies such as egg size and quality or number of offspring (Awmack and Leather 2002; Bissoondath and Wiklund 1997; Craig *et al.* 1992; Ebeling *et al.* 2013). Several traits are expected to express an insects' dispersal ability and short-term mobility, e.g. to cope with temporal disturbances. For example, an higher wing area corresponds to a higher acceleration capacity, whereas smaller wings have a positive effect on the intraspecific manoeuvrability in butterflies (Berwaerts *et al.* 2002). Intraspecific phenotypic plasticity can also vary between generations for polyvoltine species. Here, adults of spring generations have a larger abdomen for reproduction and summer generations have larger wings for mobility (Shkurikhin and Oslina 2016). Wing loading combines body mass and wing area: it is defined as body weight divided by the area of the wing (Almbro and Kullberg 2012). The relationship between flight performance and wing loading is controversially debated in the literature (Van Dyck 2012). Nevertheless, decreasing wing loading is associated with long distance-movements, flight speed and manoeuvrability for birds and insects (Betts and Wootton 1988; Stevens *et al.* 2012; Turlure *et al.* 2010; Wickman 1992). Even if low wing loading is associated with lower flight energy (Wickman 1992), dispersal ability should be improved (Turlure *et al.* 2016). In theory, with decreasing disturbance or increasing food supply insects may achieve a higher wing loading – and thus higher investment in body mass relative to lower allocation to wings. Species that show intraspecific trait variation related to mobility should benefit from land-use intensity. As a consequence, they should be more dominant in disturbed areas.

Across a broad taxonomic range, morphological traits are also associated interspecific with host specificity. Two different hypotheses discuss the occurrence of generalists and specialists in disturbed area (Carboni *et al.* 2016): Specialists can perform better in their optimal habitat than generalists (the 'jack-of-all-trades is master of none' hypothesis; Levins 1968). As long as the extent of disturbance does not vary, they could adapt to the local conditions and could also be more abundant in disturbed environments. On the other hand generalists tolerate a broad variety of environmental conditions, whereas specialists exist only in a small range. As a consequence generalists are less vulnerable to disturbance and environmental changes (Clavel *et al.* 2011; Slatyer *et al.* 2013) and should be more common in disturbed habitats (Vazquez and Simberloff 2002).

Large species can be more tolerant against environmental stress and are able to handle a larger environmental variation (Loder *et al.* 1998). While the relationship between body size, distribution and specialisation is discussed by numerous studies (Brändle *et al.* 2000; Davis *et al.* 2013; Komonen *et al.* 2004; Lindstrom *et al.* 1994; Mattila *et al.* 2009), little is known about the effect of host specificity on intraspecific variation. Large species are also more variable in size and this intraspecific variability alters the flexibility to adapt to more variable environmental conditions. A broader variability in host plant identity and thus quality across individuals for generalised species could have caused a higher variability in growth, performance or body mass.

With 160,000 described species, Lepidoptera are the second largest arthropod group (Kristensen *et al.* 2007; New 2004). About 85 % of Lepidopteran are nocturnal moths, but the main focus is still on diurnal butterflies (Macgregor *et al.* 2015). Moths are a very heterogeneous group and play as herbivores (larvae) and pollinators (adults) an important role in ecosystems. Depended by the species, moths can either feed extremely specialistic, but also generalistic on a variety of plant taxa and possess an enormous interspecific variability. For example the atlas moth *Attacus atlas* (Saturniidae) has the largest wing surface area and can reach a wing span of 300 mm, whereas *Stigmella maya* (Nepticulidae) belong with its wing span of 2.5 mm to one of the smallest moths in the world. Due to their ecological importance and variability moths are suitable targets to unravel mechanisms and consequences of trait variation particularly in the context of mobility and dispersal.

In this framework we asked the following questions:

1.) Does the intraspecific variation in morphological traits of moths (body mass, wing area, wing loading) respond to land-use intensity?

2.) Are these possible responses in morphological traits related to the distribution of moths along land-use gradients?

3.) Does the species' degree of dietary specialisation correspond to a smaller mean and reduced intraspecific variation in morphological traits across the moth community?

Material and Methods

Study area

The study was executed in the framework of the German Biodiversity Exploratory Project (www.biodiversity-exploratories.de) funded by the German Research Foundation (DFG). The main objectives of the Biodiversity Exploratory project are to understand the relationship between biodiversity of different taxa and levels, the role of land use and management for biodiversity and the role of biodiversity for ecosystem processes.

The Exploratories are established in three different regions of Germany called the Biosphere Reserve "Schorfheide-Chorin" (a glacial formed landscape in North-East Germany, 3-140 m a.s.l., 13°23'27''-14°08'53'' E / 52°47'25''-53°13'26'' N, mean annual temperature 6-7 °C, mean annual precipitation 520-580 mm), National Park "Hainich" and its surroundings (a hilly region in Central Germany, 285-550 m a.s.l., 10°10'24''-10°46'45'' E / 50°56'14''-51°22'43'' N, mean annual temperature 6.5-8 °C, mean annual precipitation 630-800 mm) and the Biosphere Reserve "Schwäbische Alb" (a low-mountain range in South-West Germany, 460-860 m a.s.l., 09°10'49''-09°35'54'' E / 48°20'28''-48°32'02'' N, mean annual temperature 8-8.5 °C, mean annual precipitation 800-930 mm). (For further information of the Biodiversity Exploratories see Fischer *et al.* 2010).

Sample processing

Nocturnal moths were collected once a month between May and August 2014 in Hainich and Alb and in June and July 2014 in Schorfheide (26 plots), because most species fly during this period (Jonason *et al.* 2014). Every night, moths from three plots were attracted and collected using a battery powered (12 V) portable light trap, consisting of a super actinic and a black light tube (230 V, 2 x 20 W, bioform®) with a twilight sensor, surrounded by a gauze cylinder (height: 180 cm; diameter: 70 cm). The observation started with complete darkness (mean = 1.26 h after sunset) and compiled two sampling rounds. In the first sampling round, traps were visited for 20 minutes. For the second round (15 Minutes) plots were observed in the reversed order than in the first round. The mean illumination for the plots lasts 225.1 minutes (For detailed information about the sampling design and results of diversity and life-history traits see Chapter 3).

Land-use intensity

Land use in grasslands is represented by three main management components, namely grazing (the number of livestock units times the number of days on the pasture per year and hectare), mowing (as number of cuts per year) and fertilization (amount of nitrogen [kg] applied per year per hectare). Moreover, to summarize these components, we used the land-use intensity (LUI) index, for which each component is standardized relative to its mean within each corresponding region and then added (Blüthgen *et al.* 2012). The LUI for each site was sqrt-transformed to improve normality.

Trait measurements

Moths were kept in separated paper bags and dried out for several weeks at 20 °C in airtight boxes including silica gel. For each individual moth, the body mass (dry weight) was determined (Mettler Toledo XS3DU; accuracy ±0.001 mg) and forewing length and width (for one of the forewings) was measured with a sliding calliper. Forewing length (x_i [mm]) was determined as the distance between base and apex, and its width (y_i [mm]) as the distance between tornus and costa. Both measures were then used to estimate forewing area (A_i) for each individual moth of a species i. The true wing area (A_0 [mm^2]) was quantified for a single representative individual for each species, using image analysing software (Image J, freely available at http://imagej.nih.gov/ij/), together with its x_0 and y_0 (Fig. 4.1). We used this method, because we assumed that intraspecific variability of wing shape is negligible compared to body mass and wing area. We then obtained the ratio a_0 between the rectangle area defined by $x_0 \bullet y_0$ versus the measured wing area A_0 as $a_0 = A_0$ [mm^2] / (x_0 [mm] $\bullet$ y_0 [mm]). We assumed a_0 to be constant in each species to calculate the wing area

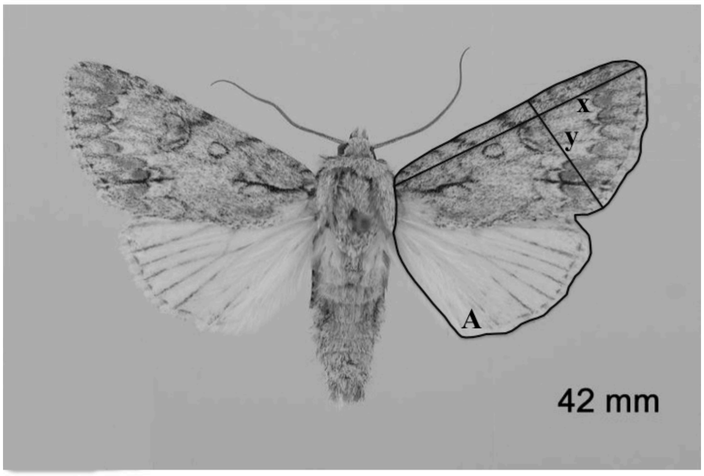


Fig. 4.1: For each moth species, the area (*A*), length (*x*) and width (*y*) of a forewing were measured for a specimen based on digital scanning. The constant *a* represents the ratio between the measured area *A* and the rectangle described by the length and width, i.e. $a = A/(x \bullet y)$. Assuming that the shape of the wing and thus *a* is constant within a species, we then calculated the total wing area of each individual based on individual measurements of forewing length (*x*) and width (*y*) with callipers.

for each individual as A_i [mm^2] = $a_0 \bullet x_i$ [mm] $\bullet$ y_i [mm]. Wing loading was calculated as the ratio of body dry mass/wing area [mg / mm^2] (Almbro and Kullberg 2012). Note that the value of the species-specific constant a_0 allows making realistic comparisons of wing area and wing loading across species with different shapes, but a_0 is irrelevant for describing the relative variability or trends within a species.

Host specificity

To analyse how morphological traits are related to the degree of specialisation, we categorized the larval feeding niche. It was classified in four ranks: (1) narrow specialists (host plants within one plant genus), (2) moderate specialists (host plants within one plant family), (3) moderate generalists (host plants recorded from two to four families), and (4) wide generalists (host plants in five or more families). We also categorized all species related to their host plant type as ‘grass’, ‘herb’ and ‘other’; the category ‘other’ includes plant species that are not directly affected by land-use intensity in the grassland like trees and shrubs (for detailed information of references, see Supplementary Material S3.1)

Data analysis

To investigate whether the individual traits are unimodal, bimodal or multimodal, we examined the distribution of wing data for each of the 20 most frequent species, representative for our data. For example, a bimodal distribution may indicate a sexual dimorphism; sex was not determined in most species. None of the species showed an indication for bi- or multimodality. Therefore, we did not consider separate groups per species for our analyses (see Supplementary Material S4.1).

In preparation for the following analyses, we excluded all species that were trapped in the grasslands but do not typically occur in this habitat during its larval stages (283 of 461 species). We assume that only those species that feed as caterpillars on herbs or grasses that regularly occur on meadows and pastures, can be directly affected by local land-use activities. We also excluded all moth species with less than five individuals, resulting in a total of 67 species for the analyses.

For each species, we analysed the linear correlation between each of the three main traits (body mass, wing area, wing loading) and the land-use intensity of the grassland in which the individual was collected. The resulting correlation coefficient (r) and its significance describes the species' trait response to land use, e.g. see the example of *Crambus perlellus* in Fig. 4.2a. We additionally calculated the abundance-weighted mean land-use intensity of each species as its land-use niche optimum (χ_W) (Fig. 4.2b) (see Chisté *et al.* 2016). Afterwards, we plotted *r* against χ_W across all species to investigate the relationship between the trait responses to land use and the overall land-use response. For each relationship, a one-sample t-test, weighted by the number of plots where the species occurred, was used to find an overall trend across all species.

We additionally calculated the mean values and the coefficient of variation (CV; standard deviation divided by the mean) for the traits to analyse how intraspecific variation and size correspond to the species' diet breath. Please note that the coefficient of variation is, in contrast to standard deviation (SD), mathematically independent with the mean value (see Supplementary Material S4.1 for the same analysis using SD, which shows similar results than using the mean values). For this analysis, we used a linear model weighted by the number of individuals per species. For simplicity, we used the host specificity rank from 1 to 4 (see *Host specificity* above) as an explanatory variable in this linear model. We finally analysed the correlation between the mean values and coefficient of variation of the traits and the land-use niche optimum to combine both analysis.

Normal distribution and variance homogeneity were tested using Shapiro-Wilk test and Bartlett test. The statistical and graphical analysis was performed using software R (R Core Team 2014) using the packages diptest (Mächler 2015), weights (Pasek 2016) and SDMTools (VanDerWal *et al.* 2014).

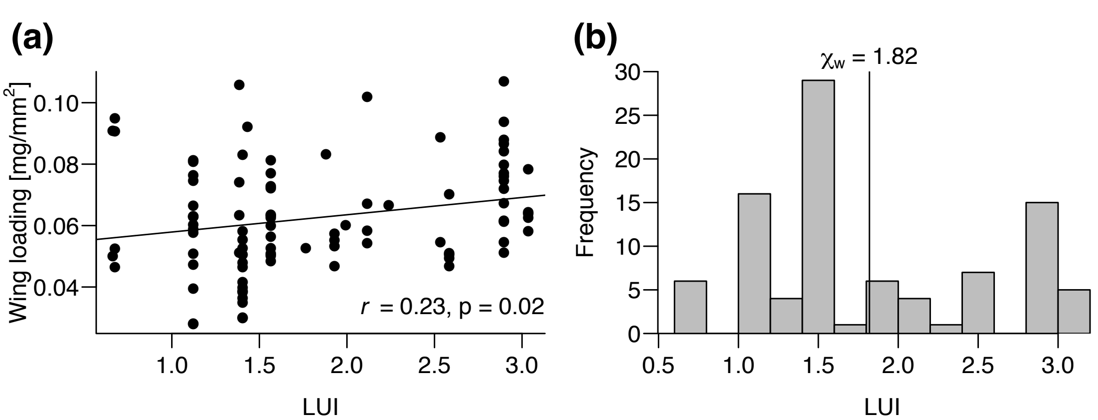


Fig. 4.2: One example of trait variation within a species (*Crambus perlellus*) and its response to land-use intensity. (a) In this case, wing loading significantly increases with the compound land-use intensity (LUI), described by the positive r. (b) This species occurs in many sites along the entire gradient of LUI, but varies in abundance. The abundance-weighted mean LUI of *C. perlellus* – its LUI-niche optimum χ_W – is 1.82.

Results

Among the 67 species considered (2091 individuals; mean 32.7 individuals per species), 30 species showed a significant intraspecific positive or negative response in at least one of the morphological traits (body mass, wing area or wing loading) to land-use intensity (either the aggregate LUI or its components). Body mass (21 positive and 7 negative correlations) and wing loading (21 positive, 10 negative) mostly increased with land-use intensity. In contrast, responses of wing area (13 positive, 13 negative) were balanced (Tab. 4.1, Fig. 4.3). *Agriphila straminella*, *Apamea lithoxylaea* and *Crambus perlellus* showed the most positive and *Agrotis cinerea*, *Mythimna pallens* and *Spilosoma lubricipeda* showed the most negative responses. Across all species, no consistent relationship between the species' land-use niche (χ_W) and their trait responses was found (Fig. 4.3). In case of wing area, a significant correlation between the coefficient of variation based on fertilisation of the traits and the fertilised niche optimum appeared across all species ($r = 0.25$, $p = 0.049$). But this case was, however the only significant trend (body mass – LUI: $p = 0.516$; body mass – grazing: $p = 0.104$; body mass – mowing $p = 0.284$; body mass – fertilisation $p = 0.648$; wing area – LUI: $p = 0.405$; wing area – grazing: $p = 0.181$; wing area – mowing $p = 0.103$; wing loading – LUI: $p = 0.97$; wing loading – grazing: $p = 0.481$; wing loading – mowing $p = 0.673$; wing loading – fertilisation $p = 0.623$; see Fig 4.3 a-l).

Tab. 4.1 (next page): Results of the correlation between morphology and occurrence of each species. + indicates a significant morphological increase with increasing land-use intensity, - indicates an significant decrease and 0 indicates no significant relation. Single lined species show a similar pattern between LUI and the component fertilization. Double lined species show an additional pattern between body mass and wing loading. Host-plant specialisation is classified as (1) narrow specialists (host plants within one plant genus), (2) moderate specialists (host plants within one plant family), (3) moderate generalists (host plants recorded from two to four families), and (4) wide generalists (host plants in five or more families).

		Wing loading				Body mass				Wing area				Host-plant	Host plants		
Species	Family	LUI	G	M	F	LUI	G	M	F	LUI	G	M	F	specialisation	Grass	Herbs	Other
Agriphila straminella	Crambidae	+	0	+	+	+	0	+	+	0	0	0	0	2	✓		
Agriphila tristella	Crambidae	0	0	0	0	+	+	+	0	0	0	0	0	2	✓		
Agrotis cinerea	Noctuidae	-	0	-	-	0	0	-	-	0	0	0	0	3		✓	
Agrotis exclamationis	Noctuidae	+	0	0	+	+	0	0	+	0	0	0	0	4		✓	
Apamea lithoxylaea	Noctuidae	+	0	0	+	+	0	+	+	0	0	+	0	1	✓		
Apamea monoglypha	Noctuidae	0	0	0	0	0	0	0	0	0	0	0	+	2	✓		
Axylia putris	Noctuidae	+	0	0	+	0	0	0	0	0	0	0	0	3	✓	✓	
Celypha rufana	Tortricidae	0	0	0	0	+	0	0	+	0	0	0	0	2		✓	
Chiasmia clathrata	Geometridae	0	0	0	0	0	0	0	0	+	-	+	+	3		✓	
Chrysoteuchia culmella	Crambidae	0	+	0	-	0	+	-	0	0	0	0	0	2	✓		
Cnephasia stephensiana	Tortricidae	0	0	0	0	0	0	0	0	-	+	-	-	4		✓	✓
Crambus perlellus	Crambidae	+	0	0	+	+	0	0	+	+	0	0	+	2	✓		
Crambus pratellus	Crambidae	+	0	0	0	0	0	0	0	0	0	0	0	1	✓		
Deltote bankiana	Noctuidae	0	0	0	0	+	0	0	+	+	0	0	+	3	✓		
Diaphora mendica	Erebidae	0	0	0	0	0	0	0	0	-	0	0	-	4		✓	✓
Hada plebeja	Noctuidae	0	+	0	0	0	0	0	0	0	0	0	0	2		✓	
Lathronympha strigana	Tortricidae	0	0	0	0	0	0	0	0	0	0	0	-	1		✓	
Melanchra persicariae	Noctuidae	0	0	0	0	0	0	0	0	-	0	-	0	4		✓	✓
Mythimna pallens	Noctuidae	0	+	-	0	0	+	-	-	0	0	0	-	2	✓		
Ochropleura plecta	Noctuidae	0	0	0	0	0	0	0	0	+	0	0	0	4	✓	✓	
Oncocera semirubella	Pyralidae	+	0	0	+	0	0	0	0	-	0	0	-	2		✓	
Perizoma alchemillata	Geometridae	0	-	0	0	0	-	0	0	0	0	0	0	2		✓	
Phragmatobia fuliginosa	Erebidae	0	+	0	0	0	0	0	0	0	0	0	0	4		✓	✓
Plutella xylostella	Plutellidae	0	0	0	0	+	0	0	0	0	0	0	0	2		✓	
Pyrausta despicata	Crambidae	0	0	0	0	0	-	0	0	0	0	0	0	2		✓	
Pyrausta purpuralis	Crambidae	0	0	0	0	0	0	0	0	+	+	0	0	2		✓	
Scotopteryx chenopodiata	Geometridae	0	0	0	0	0	+	0	0	0	+	-	0	2		✓	
Spilosoma lubricipeda	Erebidae	-	0	0	0	-	0	0	-	0	0	0	-	4		✓	
Stenoptilia pterodactyla	Pterophoridae	0	0	0	0	0	-	0	0	0	0	0	0	1		✓	
Thalpophila matura	Noctuidae	+	0	+	+	0	0	0	0	0	0	0	0	2	✓		

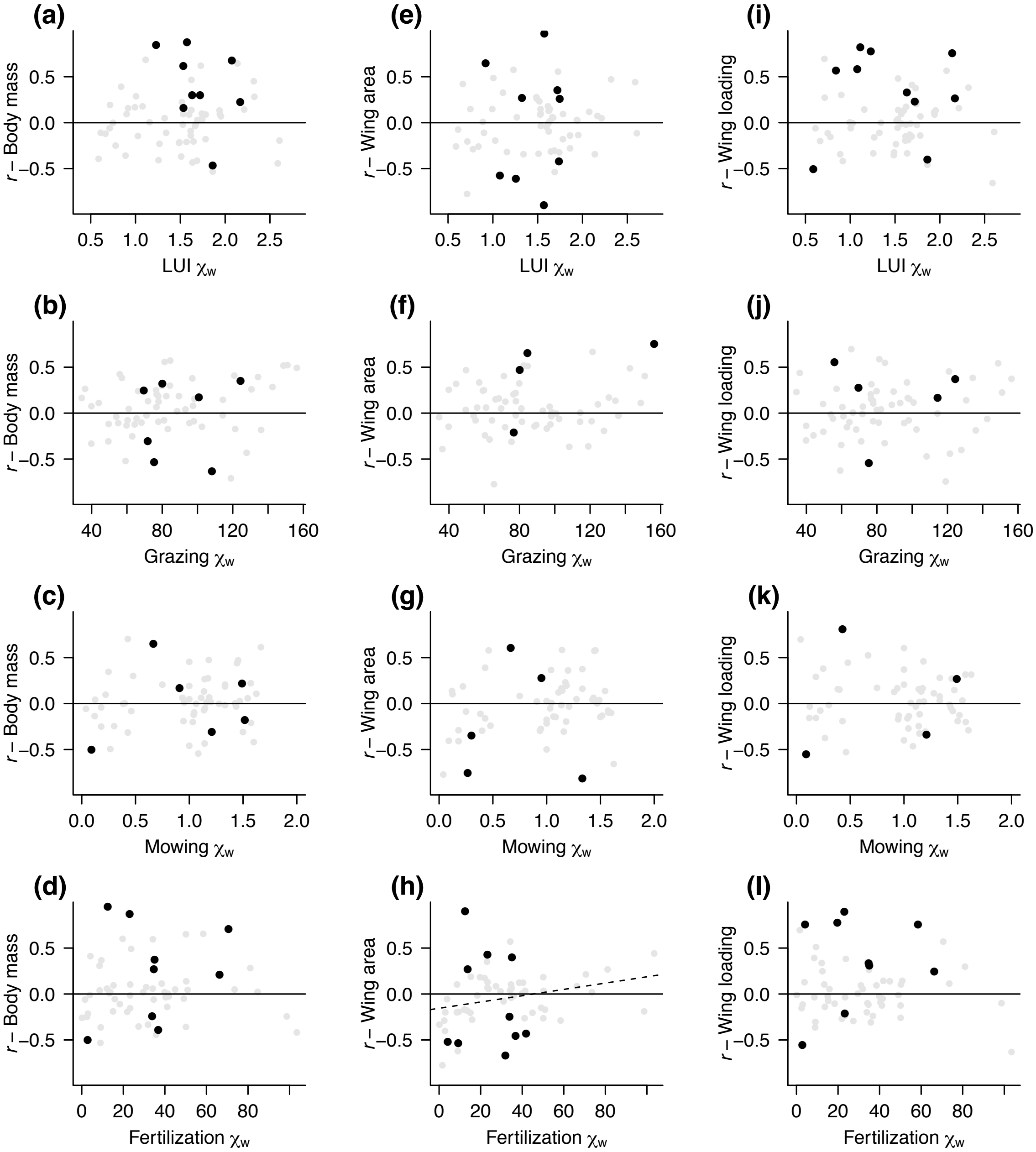


Fig. 4.3: Correlation between the species' morphological trait responses to land-use intensity (*r*) versus their land-use optimum (χ_W) across all 67 moth species. Black circles depict species with significant trait responses, which were not significant in species displayed by grey circles.

Moth species differed strongly in their trait responses to land-use intensity (Fig. 4.3). Wing loading significantly increased The results for body mass were similar: with increasing LUI eight species significantly increased in eight species and decreased in two species with increasing land-use intensity (LUI). and one species decreased its body mass. Regarding wing area, five species showed a significant positive trend and four species a negative trend with LUI (Tab. 4.1). Land-use effects were mostly driven by fertilization, since effects found for LUI were mostly supported by fertilization intensity in all three traits, rarely by mowing and but least by variation in grazing intensity. In most cases, only one of the three traits was affected, but in five species parallel trends of wing loading and body mass and in one species of wing loading and wing area occurred (Fig. 4.3, Tab. 4.1; see Supplementary Material S4.1 for detailed results of all species).

The mean values of all three morphological traits were strongly related to the species' host-plant specificity: body mass, wing area and wing loading were significantly higher for generalists compared to specialists (body mass: $R^2 = 0.21$, $p < 0.0001$; wing area: $R^2 = 0.257$, $p < 0.0001$; wing loading: $R^2 = 0.318$, $p < 0.0001$). In contrast, the intraspecific variability of body mass did not change significantly with host-plant specialisation ($R^2 = 0.011$, $p = 0.403$), nor the variability of wing loading ($R^2 = 0.001$, $p = 0.994$), while host-plant generalists had a slightly lower variability for wing area ($R^2 = 0.067$, $p = 0.0433$) (Fig. 4.4). In general, trait variability was similar for body mass (coefficient of variation CV: 0.26 ± 0.09, mean ± sd, $n = 67$ spp.) and wing loading (CV: 0.25 ± 0.1) and marginally smaller for wing area (CV: 0.15 ± 0.07) (See Fig. 4.4 d-e).

Correlating morphological traits to each other, they showed strong relations, as wing loading was calculated using body mass and wing area (body mass – wing area: $r = 0.86$, $p < 0.0001$; body mass – wing loading: $r = 0.91$, $p < 0.0001$; wing area – wing loading: $r = 0.73$, $p < 0.0001$)

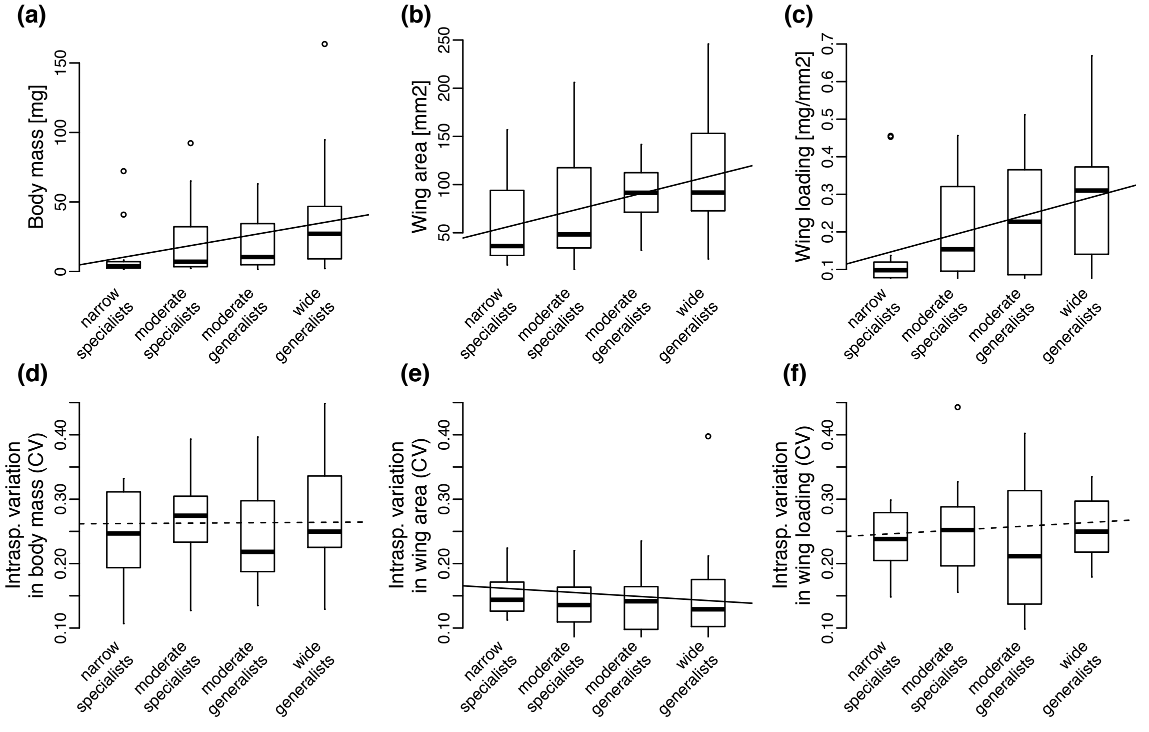


Fig. 4.4: The average body mass, wing area and wing loading (a,b,c) and its intraspecific variation (d,e,f) in relation to host plant specialisation.

Discussion

Variation in the three selected morphological traits – body mass, wing area and wing loading – has potential consequences for the mobility of individual insects (Turlure *et al.* 2016). For several species, such trait variability may occur in responses to land use as a relevant environmental filter. Most notably, body mass and wing loading of more species increased with higher land-use intensity, than decreased. In contrast wing area was similarly affected in both directions. These trends were most pronounced for fertilization and weaker for the other land use components mowing and grazing. Nevertheless, we found no correlation between the response of the morphological traits to land-use intensity and the preferred land-use intensity, where the species existed. The size of all traits degreased with the degree of host plant specialisation across species, whereas it's intraspecific variations were less affected.

Fertilisation and mowing are often coupled, but still have different effects on ecosystems. The application of fertilizers leads to an increase of plant biomass (Crawley *et al.* 2005; Simons *et al.* 2014; Socher *et al.* 2012) and also nutrient concentrations in plant tissue (Klaus *et al.* 2013; Oelmann *et al.* 2009), suggesting that herbivores profit from fertilisation in general. In contrast, aboveground biomass gets removed via mowing, which additionally leads to removal of nutrients (Oelmann *et al.* 2009). Due to increasing biomass and nutrients, moths can increase their body mass during the larval stage. Nevertheless fertilization has only an indirect effect on moth body mass and thus wing loading, during its direct effect on host plants. To understand the mechanism, it is important to consider the type of host plant and the feeding niche of the affected species: Five of seven species that profit from fertilization by a larger body mass are either generalists or grass-feeding species. Only *Spilosoma lubricipeda* is feeding on a variety of herbs and had a negative effect of fertilization on body mass. Fertilization also leads to a shift in the plant composition to grass species (Socher *et al.* 2013), and grass-feeding herbivores and generalists may tolerate or even benefit from fertilization, whereas specialised herb feeders may have negative responses (chapter 3). Indeed, all those species that showed a decreasing wing area with fertilization were specialists on herbs. Whereas fertilization had the strongest effect, relatively few species responded to the intensification of mowing or grazing. Weaker patterns of the land-use components grazing and mowing can also be masked by the strong contingency between mowing and fertilization, or the alternative, contrasting management of meadows (mowing, fertilization) and pastures (grazing) within the Biodiversity-Exploratories (Blüthgen *et al.* 2016).

In contrast to our results, we assumed that moths are more abundant in more intensively used grasslands that are able to change their morphological traits with increasing land-use intensity to modify their flight performance. We are aware that the occurrence of Lepidoptera in grassland sites is depended by a variety of other biotic and abiotic factors, like plant diversity, fragmentation or temperature (De Crop *et al.* 2012; Filz *et al.* 2013; Pellissier *et al.* 2012). In this context the results does not necessarily disprove our hypothesis, but the effect is at least masked by other stronger impacts.

Moreover, morphological traits across species were related to their dietary specialization. The positive correlation between body size and diet breath supports previous findings. Body mass, wing area and wing loading are coupled with the degree of distribution and also generalists are more widespread and abundant than specialists (Brown 1984; Nieminen *et al.* 1999). This pattern is basically observed for other species of lepidopteran (Beck and Kitching 2007; Davis *et al.* 2013; Lindstrom *et al.* 1994; Loder *et al.* 1998), but also for other insects (Brändle *et al.* 2000; Novotny and Basset 1999). Species having a broader feeding niche breath increase their ability to find suitable host plants and thus increase the chance to colonise in new habitats. In contrast, the relationship between intraspecific phenotypic variation, e.g. in body mass, and diet breath has rarely been studied. However, our results do not confirm this hypothesis, and showed that generalists were not more variable in body size than specialists.

Conclusion

Our study suggests that trait variation in several moth species is related to land-use intensity in grasslands, and particularly the application of fertilizers may contribute to an increase in body mass and wing area within species. However, these intraspecific responses to land use did not consistently explain the species' occurrence along the gradient across all species. Generally, environmental filtering effects at the community level and concomitant changes in trait composition across species seem to be more pronounced than trends within species. For instance, the losses of host plant specialists contribute to the decline in moth diversity along the land-use gradient in the same grassland sites (chapter 3). Here, body size was interspecifically independent by land use. Classen *et al.* (2017) showed similar patterns comparing intra- and interspecific body size variation in total depended by elevation. Considering body size associated traits (e.g. glossa length), however, similar interspecific and intraspecific trends appeared. Beyond these changes in species composition, however, intraspecific variation may additionally contribute to the variation across species in land-use responses, particularly where generalised species increase in fitness-related traits with increasing eutrophication or other land-use practices.

Acknowledgements

We thank Ulrike Schmolke and Javier Rodrigo Gomez Jolli for weighting and measuring the individuals and the managers of the three Exploratories, Swen Renner, Sonja Gockel, Kerstin Wiesner, and Martin Gorke for their work in maintaining the plot and project infrastructure; Simone Pfeiffer and Christiane Fischer giving support through the central office, Michael Owonibi for managing the central data base, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. The work has been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (BL 960/2-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

Abstract

Water loss represents an important risk for arthropods, and their responses to avoid desiccation include improved cuticular lipid layers and reduced respiration. In general, species can adapt to their specific local conditions either by desiccation resistance or desiccation tolerance. As a consequence, species from arid habitat have been shown to possess lower water loss rates than species from mesic environments.

Even if studies in this framework are of great importance, methods to measure water loss of arthropods are still complex and time consuming. We thus developed a simple flow-through system, henceforth termed evaporimeter. The device can measure small arthropods, but also plant parts or soil samples and it facilitates to measure water loss of ten samples in less than 30 minutes. Synthetic air with 0 % relative humidity is directed into the evaporimeter and flows through a chamber including the sample, whereas a subsequent air humidity sensor measures the water amount enriched by the sample. With this method, together with an established microrespirometer, we measured water loss and metabolic rate of 557 individuals from two grassland and one forest site in a single region.

Water loss rate and metabolic rate were higher in the grassland sites compared to a forest. Also within a site, the microhabitat plays an important role, and individuals living in or directly on the ground showed lower water loss rates than individuals on the vegetation. As expected due to a stronger cuticular protection, water loss rate was correlated with metabolic rate only for specimen from grasslands.

The relative contribution of cuticular and respiratory water loss varies across species from different climatic conditions. Due to a stronger reduction of cuticular transpiration in species from arid environments, respiratory losses become increasingly relevant, confirmed by a positive correlation between metabolic rate and water loss in such species. Two previous studies showed this relationship via meta analysis on a global scale and for a small number of individuals in a desert ecosystem, but more studies are needed to examine the generality of these trends. Our approach based on an effective evaporimeter confirmed these results for grassland versus forest on a local scale and highlight the relevance of variation in macro- and microhabitat conditions for climatic responses of arthropods.

CHAPTER 5

An efficient method to measure water loss in arthropods: desiccation adaptation hypothesis re-examined

Jule Mangels, Nico Blüthgen

Introduction

Water availability is one of the most important abiotic factors affecting physiological performance in animals and plants. The concentration of body water needs to be within tolerable limits to ensure optimal functioning.

For arthropods, the majority of water loss happens through the cuticular surface, but also via respiratory transpiration (Hadley 1994). The relationship between respiratory transpiration to total water loss, however, depends strongly on the activity of an organism (Harrison and Roberts 2000). Insects can limit desiccation either by behavioural responses, e.g. migration to cooler or wetter microhabitats or by physiological regulation (Chown *et al.* 2011). Physiologic regulation is usually performed either by desiccation resistance or desiccation tolerance (Hadley 1994). Resistant species can have more water in their cellular tissue (Hadley 1994) or show changes in their cuticular lipid composition (Gibbs 1998) to decrease cuticular transpiration. Additionally closing the spiracles temporally and performing discontinuous gas exchange can contribute to a reduced respiratory transpiration. The limit of desiccation tolerance can vary between different groups, and some arthropods, such as larvae of the chironomid *Polypedilum vanderplanki*, do even tolerate nearly complete desiccation (Alpert 2005).

Species from arid environments are more tolerant against desiccation and have lower rates of water loss after correction for body size variation (Addo-Bediako *et al.* 2001). Thus, the desiccation adaptation hypothesis argues that costs of desiccation resistance strategies needs to be balanced with the benefit in a particular environment. Zachariassen *et al.* (1987) analysed differences in the water loss rate and respiratory rate between Coleoptera from arid and mesic environments in east Africa and the relationship between both factors depended by the environment. Addo-Bediako *et al.* (2001) repeated the analysis with a variety of taxa in a meta-analysis on a global scale. Arid species showed general lower rates than mesic species, but a significant positive relationship only occurred for arid species (Zachariassen *et al.* 1987; see also: Addo-Bediako, Chown & Gaston 2001). The authors argue that respiratory transpiration in xeric species contributes a higher proportion to water losses; cuticular transpiration in such species is more limited e.g. via an increased lipid layer. Zachariassen’s study compiled 71 individuals from 24 species collected in two years; Addo-Bediako’s analysis comprised 180 species (76 published studies). Both used data on a large geographic scale, whereas other studies showed also differences of water resistance on smaller scales (Chown 2001). For example, thermal tolerance of dung beetles increased with increasing elevation in southern Africa (Gaston and Chown 1999), or canopy ants showed higher desiccation resistance than understory ants in a central American rainforest (Bujan *et al.* 2016).

In this study, we re-analyse the trends reported by Zachariassen *et al.* (1987) and Addo-Bediako *el al.* (2001) on a local scale. We investigate the relationship between total water loss and respiration rate for species in different macrohabitats (a forest site, a moist and a dry grassland site) within a single region. We predict that grassland species also show a significant positive relationship between water-loss rate and respiratory rate, whereas species from the forest do not show those patterns. We additionally considered the microhabitat and differed between epigeal arthropods and vegetation associated arthropods, because epigeal communities should be more protected against desiccation.

A variety of methods were developed to measure the water-loss rate directly via cuticular transpiration, e.g. gravimetric methods, radioisotopic tracers as well as *in vivo* and *in vitro* methods (Hadley 1994). Most of the methods are time-consuming and it is problematic to measure a variety or individuals in a short period, e.g. when only a single individual can be measured at one time. In general, one of the main hypotheses is that the amount of respiratory and cuticular transpiration and its differences between species is in strong relation of the habitat, where the species occur. To understand these mechanisms, it is important to consider and compare those physiologic traits of several individuals and species. Thus, we developed a simple flow-through system (hereafter evaporimeter) using electronic moisture sensing to measure water loss of invertebrates (based on Louw and Hadley 1985; Nicolson and Louw 1982 who developed the system with one chamber). The structure of the evaporimeter is simple but effective, and it is possible to measure water loss rate of 10 individuals in 30 minutes. Additionally the evaporimeter enables to demonstrate discontinuous gas exchange. Combining this method with an existing method to measure the metabolic rate (Scheu 1992) facilitate the opportunity to measure water loss and metabolism up to 60 individuals in 24 hours.

Material and Methods

Study area and sampling design

Arthropods were collected in three macrohabitats, a forest site (8°68’02’’ E, 49°85’79’’ N) a moist grassland (8°67’82’’ E, 49°85’81’’ N,) and a dry grassland (8°63’51’’ E, 49°84’59’’ N) in the surroundings of Darmstadt in 2016. The forest site represents a common mixed forest dominated by *Fagus sylvatica* and *Tilia spec*. Here the most abundant species in the herb layer were *Luzula luzuloides*, *Dryopteris carthusiana*, *Dactylis polygama* and *Galium odoratum*. The moist grassland was mainly dominated by *Holcus lanatus*, *Agrostis capillaris*, *Plantago lanceolata* and *Juncus acutiflorus* and was mostly covered by the vegetation cover (6 % open ground). In contrast, the dry grassland had 41 % open ground and was dominated by *Hypnum cupressiforme*, *Carex hirta*, *Euphorbia cyparissias* and *Vulpia myuros*.

In total, we measured water loss rate of 557 individual arthropods and metabolic rate of 305 individuals; 298 species overlapped in both measurements. These individuals were assigned to 10 different orders (Araneae, Auchenorrhyncha, Chordeumatida, Coleoptera, Dermaptera, Diptera, Heteroptera, Lepidoptera, Orthoptera, Pseudoscorpiones).

Arthropods were collected in two sampling rounds with pitfall traps, insect nets and beat sheets. The first survey started in the end of June, and each macrohabitat was sampled for one week (27th of June - moist grassland, 04th of July - forest, 11th of July - dry grassland). During a second survey, sampling sites were sampled in a different order (08th of August - dry grassland, 15th of August - moist grassland, 22th of August - forest). Sampling with three different methods allowed differing the microhabitats of epigeal specimen (pitfall traps) and vegetation related specimen (insect nets, beating trays). Arthropods were kept in vials in which they received water supply with moistened tissues, were kept separately at 10 °C in a climate chamber and were measured within two days after collection in the field.

Evaporimeter

Water loss rate of each arthropod was measured with a custom-made evaporimeter, incorporated into an incubator to regulate the temperature. The evaporimeter enables to measure water loss of samples such as soil, seeds, leaf parts or small animals. Synthetic air

(Air Liquide®) with 0 % relative humidity was directed into the system with an airflow of 200 ml min^{-1}. This air flowed through a copper tube, which was bent in several loops in the incubator to receive the temperature of the inside of the incubator (in our case 25 °C). The dry air then flowed in a distributer, where a temperature sensor and a humidity sensor (Honeywell GmbH®) monitored the condition. From here, the air was distributed among 10 different tubes, each with a connected glass chamber (Peco Laborbedarf GmbH®, Griesheim). The airflow of each chamber was regulated separately at 20 ml min^{-1}. In each chamber, a sample could be placed. At the end of each chamber, a humidity sensor was installed, which was separated by gauze from the main volume of the chamber to prevent samples from drifting or insects from crawling into the following tube. Hence, the water enrichment measured in the humidity sensor (compared to the humidity sensor at the distributor) represented the water loss of the sample. Finally, the enriched air was lead out of the incubator through flowmeters (Profimess GmbH®, Bremerhaven) to monitor the airflow in each chamber (Fig. 5.1).

It was necessary to avoid plastic and rubber materials that absorbed water from the surrounding air to keep the air humidity as low as possible. Because we needed flexible elements in the evaporimeter to simplify handling when exchanging samples, however, we used rubber hoses as adapters between the distributor and the chambers; all ten rubber hoses had the same length of 18 cm. Due to these rubber hoses, it was not possible to maintain 0 % relative humidity with the chosen airflow. Before each measurement we started the evaporimeter without any specimen until the relative air humidity reached 2.5 % in each chamber (control). We then subtracted the control value from the relative humidity value

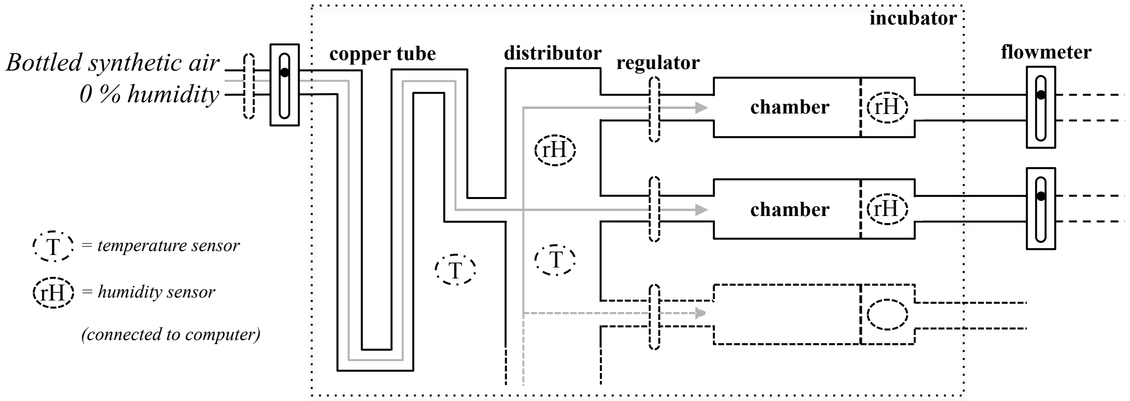


Fig. 5.1: Graphical sketch of the evaporimeter (not to scale). Dry air is first tempered in a copper tube, leading into a distributor. From here it flows through ten independent chambers, each including a biological sample or specimen. A subsequent humidity sensor measures the enriched air humidity caused by the specimen. See main text for a detailed description.

including a sample to obtain the air humidity emitted by the specimen.

All sensors send data every 0.33 seconds to a computer program. The program output included the relative humidity (*rH*), e.g. the percentage of the actual amount of water vapour in the air to the amount it can hold when saturated expressed. To quantify the absolute water loss of the sample per hour, we needed the absolute humidity (*aH*). We first calculated the saturation vapour pressure (E_W) of water using the Magnus-formula giving the temperature in °C (*T*):

$$E_W \ = \ 6.1078 \cdot 10^{7.5 \cdot T/(237.7+T)}$$

The saturation vapour pressure describes the pressure at which water in air is balanced between solid, liquid and gaseous phases and increases exponentially with the temperature. Since E_W cannot be calculated exactly, the Magnus-formula is only an approximation of the true E_W. We then calculated the actual vapour pressure (*E*) by the following equation:

$$E = rH/100 \cdot \ E_W$$

Using the universal gas constant (R_u) and the molecular weight of water vapour (m_W) we could calculate the absolute humidity (*aH*):

$$aH = \ 10^5 \cdot m_W/R_u \cdot E/(273.15 + t)$$

Finally we obtained the desired water loss (L_W) per hour [mg h^{-1}], using *aH* and the adjusted airflow (*af*):

$$L_W = aH \cdot af$$

Arthropods were kept in the evaporimeter until the air humidity was constant, which last not longer than 30 minutes.

Respirometer

Following the measurements in the evaporimeter, the individuals were again kept separately with water supply before being used in the respirometer (6 – 24 hours after the evaporimeter measurement). To measure the oxygen consumption (hereafter: metabolic rate) per individual we used an automated electrolytic microrespirometer (based on Scheu 1992). The apparatus included a pressure detector that compared the pressure between a control chamber and the chamber including the sample. Beside the sample, the last mentioned chamber additionally included potassium hydroxide (KOH) that absorbed the produced carbon dioxide of the sample. This process leaded to a pressure gradient between the two chambers. A third electrolytic chamber including a platinum (Pt) electrode and copper sulphate ($CuSO_4$) solution was directly connected with the sample chamber. In case of a pressure gradient the pressure detector sent a 10 mA pulse lasting for 1 second to the electrode, which liberated 0.83 µg Oxygen (Fig. 5.2). The chambers could be submerged in temperature conditioned water basins to regulate the temperature during the measurements. The whole system was connected to amplifier units and a computer program that made it possible to control up to 30 respirometers simultaneously.

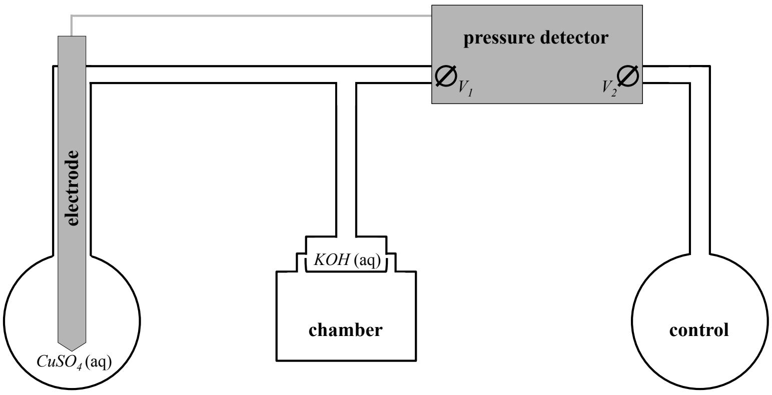
The measurements last either 7 hours during the day (9 am – 4 pm) or 16 hours during the night (5 pm – 9 am). The length of a measurement did not influence the results, because we used only a constant cut-out of the measurement.

After the measurements, the dry weight (as body mass) of all individuals was determined (Mettler Toledo XS3DU; accuracy ±0.001 mg). See Supplementary Material S5.1 for further information (e.g. calibration techniques, R-scripts, pictures) of the evaporimeter and the respirometer.

Data analysis

The small size of insects makes them particularly vulnerable to dehydration, given their higher surface-area-to-volume ratio. The surface area increases with the 2/3 power of volume or body mass, which also predicts their water loss rates, and metabolic rate roughly increases body mass to the power of 3/4 (Brown *et al.* 2004). To account for such isometric

Fig. 5.2: Graphical sketch of the respirometer (not to scale). Each chamber includes the specimen and some potassium hydroxide (KOH), which absorbs the produced carbon dioxide. The pressure detector compares pressure differences between the sample and a control and sends an impulse to the electrode if necessary. This process produces oxygen for the sample and balances the pressure difference. See main text for a detailed description.



scaling effects, we transformed body mass either with the power term 3/4 for water loss rate accorded linear regressions or with the power term 2/3 for metabolic rate accorded linear regressions. Additionally, body mass and response variables (water loss and metabolic rate) were log transformed.

Tukey's post hoc tests following linear mixed effect models were used to analyse the effect on responses (i.e. water loss and metabolic rate). Here, we used body mass, macrohabitat (forest, grassland) and microhabitat (ground dwelling, above ground) as independent fixed effects and taxonomic order as a random effect:

lmer(log(water loss [g/h]) ~ log(body mass [g] ^(2/3)) + macro + micro + (1|order))

lmer(log(metabolic rate [J/h]) ~ log(body mass [g] ^(3/4)) + macro + micro + (1|order))

We calculated the correlation between water loss versus metabolic rate after accounting for body mass and order, hence between the residuals of the same model but without macrohabitat and microhabitat as independent fixed effects.

All analysis were performed using R (R Core Team 2014), including the packages lmerTest (Kuznetsova *et al.* 2014), and multcomp (Hothorn *et al.* 2008).

Results

Across 557 individuals from 11 different orders, body mass had a positive effect on water loss rate ($F_{\mathrm{df}=1} = 140.03$, $p < 0.0001$). Macrohabitat ($F_{df=2} = 8.04$, $p = 0.0004$) had a significant effect, and specimen from the forest site had a higher water loss rate than those from the moist meadow ($p = 0.02$) and the dry meadow ($p < 0.001$), whereas both meadows were relatively similar ($p = 0.154$). The microhabitat also showed a significant effect, since water loss was higher for epigeal species than for those that were associated to the vegetation ($F_{df=1} = 109.12, p < 0.0001$) (Fig. 5.3 a-b).

The metabolic rate also increased with body mass ($F = 145.67$, $p < 0.0001$) and differed across macrohabitats ($F = 9.55$, $p < 0.0001$), but not across microhabitats ($F = 2.74$, $p = 0.1$). It was higher for specimen from the forest than from the moist meadow ($p = 0.01$) and dry meadow ($p < 0.001$), respectively. Specimen from both meadows were more similar ($p = 0.06$) (Fig. 5.3 c-d).

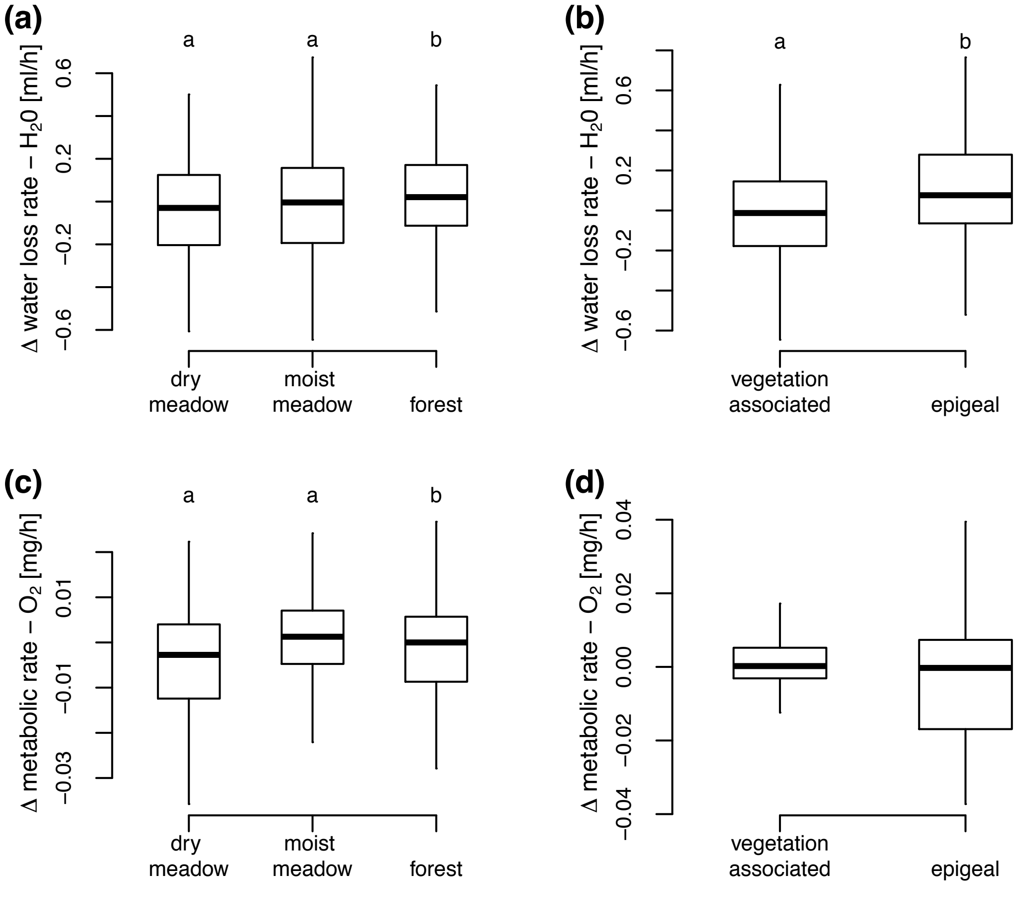


Fig. 5.3: Differences of water loss (a,b) and metabolic rate (c,d) based on macrohabitat (moist and dry meadow) and microhabitat (vegetation associated or epigeal).

The correlation between the residuals of the water loss rate and the residuals of the metabolic rate was significant in the moist meadow ($r = 0.39$, $p < 0.0001$) and in the dry meadow ($r = 0.29$, $p = 0.006$), but not in the forest ($r = 0.07$, $p = 0.48$). Additionally a significant correlation appeared for species associated to the vegetation ($r = 0.34$, $p < 0.0001$), but not for epigeal species ($r = 0.04$, $p = 0.74$; Fig. 5.4).

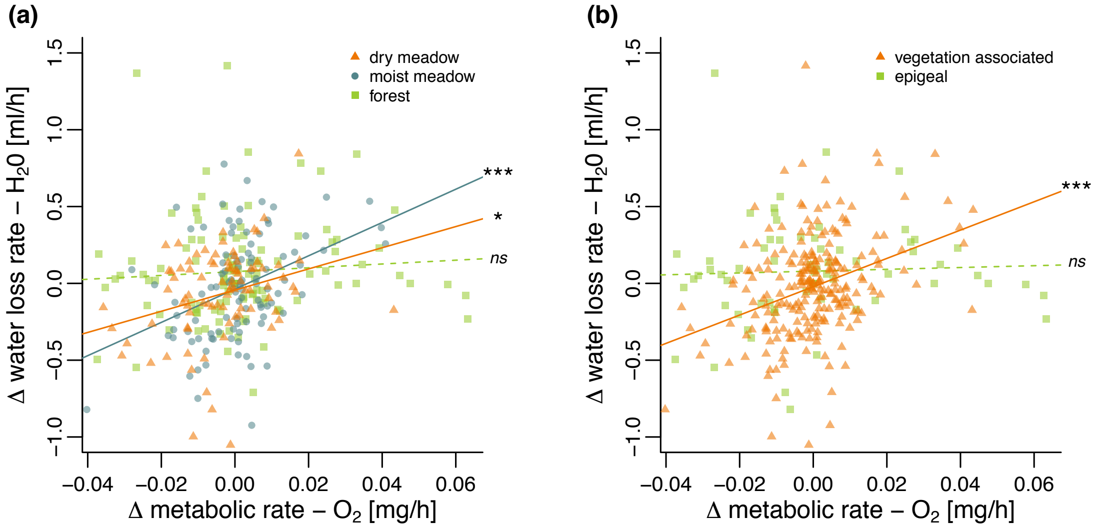


Fig.5. 4: Correlation between water loss and metabolic rate based on macrohabitat forest, moist and dry grassland (a) and vegetation associated or epigeal microhabitat (b).

Discussion

Our results from a single region were consistent with the desiccation hypothesis previously tested at larger scale for arid versus mesic habitats (Addo-Bediako et al 2001, Zachariassen et al 1987): both water loss and metabolic rates were lower in species from two grasslands than from a forest. The differentiation even occurred similar in microhabitats, i.e. the stratum in which the specimen were collected: vegetation associated specimen had lower water loss than epigeal specimen, but the metabolic rate did not differ. We additionally showed that a significant correlation between both rates only appeared for species in dry macro- and microhabitats, consistent with the global analyses (Addo-Bediako et al 2001, Zachariassen et al 1987). Addo-Ediako *et al.* tested the hypothesis on a global scale based on 76 published papers and Zachariassen *et al.* collected and analysed 71 individuals in two years. In contrast, we developed and simplified an evaporimeter to measure water loss of 10 individuals simultaneously. Using this method, we were able to collect and measure water loss and metabolic rate of 557 individuals within six weeks. As studies about functional diversity and also physiological traits became more relevant (Hooper *et al.* 2000), the evaporimeter gives the opportunity to provide much larger datasets on several taxa and thus to understand the mechanisms and the relationship between climate conditions within an ecosystem and its including organisms.

Species can adapt to local conditions including strategies to avoid desiccation, as long as such investments are balanced with benefits of the environment (Bujan *et al.* 2016). Grassland sites are usually more exposed to dry weather conditions than forest sites. The average air temperature in grasslands is about 1 °C warmer and has more pronounced diurnal temperature range including maximum at midday than in forests (Morecroft *et al.* 1998). Also within the site, microclimatic conditions additionally differ between species that live inside the soil or epigeal on the ground, protected by the vegetation layer, versus species that live more exposed on the vegetation. As a consequence, species from open environments should be more adapted to warmer, drier conditions. In doing so, their physiological processes are lower compared to species from less exposed environments.

The relation between cuticular and respiratory transpiration is contentious and varies across species, although the majority of total water loss generally occurs via cuticular transpiration (Chown 2002). Water loss in arid species is reduced mainly by a stronger protection against cuticular transpiration; the remaining respiratory transpiration becoming more relevant.

Thus as the proportional cuticular transpiration decreases, the effect of respiratory transpiration on total water loss becomes stronger.

In general, physiological traits vary with body mass (Brown *et al.* 2004). This study also confirmed that both, water loss and metabolic rates increased significantly with body mass. As a consequence, the correlation between water loss and metabolic rate may simply be a consequence of their parallel body mass relationships (Addo-Bediako *et al.* 2001). However, both processes are still coupled, because a higher metabolism rate leads to an increasing transpiratory water loss (Hadley 1994).

Conclusions

In the actual context of the global climatic warming, the number of studies investigating the responses of different organisms to weather conditions recently increased. We developed a simple method to measure water loss of several individuals simultaneously in a short period, allowing for an efficient assessment of responses of populations and/or communities, which is important to understand the consequences of changes in temperature or drought for ecosystems. Based on this method we were able to show that species from xeric versus mesic habitats within the same region and even microhabitats show a similar differentiation than species from arid and mesic habitats at a global scale.

Acknowledgements

We want to thank the workshop of the biological department at the TU Darmstadt; Karl Schuller took a great part by developing the evaporimeter, Manuel Camargo wrote the software program, and Udo Pelger and Tobias Wohlfromm mainly build the evaporimeter. We additionally want to thank Jennifer Godeck for collecting arthropods and performing the measurements and Christian Storm for providing site information. Part of this work has been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (BL 960 2-1).

Abstract

Global warming is predicted to have a strong effect on the fitness of ectotherms such as insects. Due to an exponentially increasing metabolic rate, growth rates of developing larval stages of insects increase strongly under warmer conditions, but also their mortality. However, such thermal reaction norms – and corresponding risks – are likely to vary across species, partly mirroring the environmental conditions in the species' natural range and habitat. Besides their geographic distribution, another key aspect that varies across species is their feeding niche, e.g. the host plant specialisation of herbivorous insects. Narrow specialization represents a further risk against land use or disturbance, and if resource specialization is coupled with a reduced thermal tolerance, both risks could be non-independent and additive. Here we compared the thermal responses of 30 different species of moths (Lepidoptera) raised in climatic chambers under three regimes (average summer day, 4°C and 8°C warming), henceforth termed 'thermal treatments'. Across species, we confirmed a decreasing survival rate, faster larval development and higher pupal mass in warmer thermal treatments. Treatments also had an effect on respiration rate and water loss rate at 25°C; both rates increased with the thermal treatment at which specimen were grown. All thermal responses varied significantly across species. Host plant generalists were better adapted to higher temperatures than specialists, suggesting that resource specialization and thermal responses are coupled – and together increase a species' risk to global change.

CHAPTER 6

Thermal reaction norms of moth species and their host plant specialisation: specialists face a dual risk

Jule Mangels, Nico Blüthgen

Introduction

The performance of insects depends on a variety of biotic and abiotic factors, such as food quality, photoperiod and humidity (Berggren *et al.* 2009; Gotthard 2008; Jang *et al.* 2015). But since insects are ectotherms, temperature has a direct effect on their growth and development rate, final body mass, fitness and mortality (Bale *et al.* 2002). Apart from direct effects, temperature indirectly affects adult performance since the juvenile growth provides the fundament for later stages including reproductive fitness during the adult phase for most organisms (Abrams *et al.* 1996). Our understanding of such thermal reaction norms becomes increasingly relevant in the light of global warming, given the predicted increase in mean temperature up to 4.8 °C as well as increased climatic variation (IPCC 2014).

The niche breath of a species characterises its degree of specialisation and is defined as the extent of a resources or environmental conditions it can appropriate, including the range of temperatures (Gaston *et al.* 1997). The thermal niche is described as the temperature range in which a species is able to perform; these and the species' thermal responses (its temperature-dependent reaction norms) are species-specific. For example, the variation in pollinator activity in grasslands is largely explained by temperature with an optimum at 24.3°C, and it varies across species (Kühsel and Blüthgen 2015), and the number of moths attracted to light increases with temperatures at night (Jonason *et al.* 2014). Thermal reaction norms not only include activity or consumption, but also developmental rates as well as physiological processes such as respiration and water loss, both of which are related to metabolism and performance of insects but also represent critical constraints for thermal niches (Chown *et al.* 2011; Gillooly *et al.* 2001). Ectotherms from the temperate zone often have a broad thermal niche and may benefit physiologically from warmer conditions if they are not too extreme, whereas species from tropical climates may be less tolerant to further increases in their temperature conditions (Deutsch *et al.* 2008). Species differ in their responses, depending on their origin, and those adapted to cooler conditions may face a higher risk of extinction. Range shifts towards the poles or higher altitudes are expected, but will vary across species depending on their thermal niche and dispersal abilities (Regniere *et al.* 2012).

Under their optimal and predictable conditions, environmental or resource specialists may outperform generalists, because physiological plasticity that provides individual generalists with an opportunity to respond to variable environments can be associated with increasing energetic costs (the ‘jack-of-all-trades is master of none’ hypothesis; Levins 1968). As a consequence of their narrow tolerance, however, specialists tend to be stronger negatively affected by disturbance than generalists (Gaston *et al.* 1997). For example, the amount of specialistic lepidopteran degreases with the degree of land-use intensity (Börschig *et al.* 2013, chapter 3). The degree of specialisation can vary across different life-history traits and niche dimensions. For example, species that are able to capitalize a broader variety of resources tend to be more widespread (Brown 1984; Slatyer *et al.* 2013). Nevertheless, the relationship between the degree of specialisation in any niche dimension versus the specialization in another dimension has been rarely investigated. This is particularly important for variation in resource specificity versus sensitivity to warmer temperatures across species – two factors that may impose species-specific risks to habitat disturbance, land use and climatic change.

The relationship between time of development of ectotherms and temperature is well documented in a variety of publications (reviewed in Bale *et al.* 2002). Most studies only focused on a single or very few species, however, and did not include comparisons of life-history traits. In this study we will focus on the effect of temperature across many species of Lepidoptera that vary in their degree of host plant specialisation. We hypothesise that generalised species are also more tolerant against warmer conditions and thus possibly against climate warming. We thus examined the larval growth, pupal mass and mortality for 30 species of moths in climatic chambers with average temperature regimes of typical summer months in Central Europe (including diurnal variation) and compared their performance against conditions increased by 4°C and by 8°C. In addition, to examine the physiological responses in more detail, we tested respiration and water loss for a subset of the species raised under these three conditions.

Material and Methods

Study areas and moth sampling

In the framework of the German Biodiversity Exploratories Project (http://www.biodiversity-exploratories.de) we collected female moths in grassland in in three different regions of Germany: the Biosphere Reserve ‘Schorfheide-Chorin’ (13°23’27’’-14°08’53’’ E / 52°47’25’’-53°13’26’’ N), the National Park ‘Hainich-Dün’ and its surroundings (10°10’24’’-10°46’45’’ E / 50°56’14’’-51°22’43’’ N), and the Biosphere Reserve ‘Schwäbische Alb’ (09°10’49’’-09°35’54’’ E / 48°20’28’’-48°32’02’’ N) in 2014. For further information of the Biodiversity Exploratories see Fischer *et al.* 2010. In 2015, we additionally caught moths in a grassland site in northern ‘Odenwald’ (08°77’31’’ E, 49°83’66’’ N) and in a forest site southeast of Darmstadt (8°69’62’’ E, 49°86’10’’ N).

In the Biodiversity-Exploratories, moths were collected once a month between May and August in Hainich and Alb and in June and July in Schorfheide (n=26). The observation at the grassland site in Odenwald last twice a month and in the forest three times a week from Mid-April until Mid-July.

For the sampling in the Biodiversity-Exploratories and the grassland site, a battery powered (12 V) portable light trap, consisting of a super actinic and a black light tube (230 V, 2 x 20 W, bioform®) with a twilight sensor, surrounded by a gauze cylinder (height: 180 cm; diameter: 70 cm) was used. The twilight sensor facilitated the onset of the light-traps right after sunset. In the Biodiversity-Exploratories, every observation comprised two sampling rounds (first round 20 minutes, second round 15 minutes) were moths were collected manually. Here, the mean illumination for the plots lasts 225.1 minutes. At the grassland site in Odenwald, the light trap was observed two hours after sunset and last till no new moth appeared within 15 minutes.

The observations in the forest 2015 were made using an automatic battery powered (12 V) portable light-trap considering of a super actinic light tube (15 W, bioform®), an interbred acrylic glass, a twilight sensor and a collecting bag. Moths were collected on the next morning from the collecting bag.

Growth-related reaction norms

Only female moths were kept and feed with a honey-water mixture until they laid eggs. Both were kept at 15 °C in a climate chamber. One day after hatching, larvae were separated in three different vivaria (each with 12 – 35 larvae depending on the species) that were prepared with paper towels and leaves from species-specific host plants stuck in water-soaked floral foam (see Supplementary Material S6.1 for list of host plant species). These vivaria were placed into three different thermal treatments, where larvae were kept until pupation. The first treatment had a mean temperature of 17.7 °C (min = 12.5 °C, max = 23 °C, humidity = 60 %, day/night = 10/14 hours, '*control*'), which represents the average summer temperature in Germany between 2003 and 2013 (source: Rahlf 2015). In the second treatment, larvae were kept at 21.4 °C mean temperature (min = 15 °C, max = 28 °C, humidity = 60 %, day/night = 10/14 hours, '*+ 4 °C*') and in the third treatment at 25.3 °C mean temperature (min = 18 °C, max = 33 °C, humidity = 60 %, day/night = 10/14 hours, '*+ 8 °C*'). Each vivarium was monitored at least after three days, depending on the host plant quality and number and size of larvae. Vivaria were cleaned; host plant leaves renewed and living larvae were counted. In case of pupation, pupae were removed and weighted (Mettler Toledo XS3DU) at the next day. For logistical reasons it was not possible to focus on both, the development based on single individuals and on various species.

As growth rate reaction norms, we thus used survival rate, pupal mass and growth rate from 2014 and 2015. In 2015 we additionally measured physiological reactions norms, namely respiration and water loss of the larvae.

Physiological reaction norms

To quantify respiration rates, an automated electrolytic microrespirometer was used (Scheu 1992). Here, the individual is kept in a chamber containing KOH, which absorbs the produced carbon dioxide. This process leads to a pressure loss in the chamber. If the pressure decreases to a certain level, a pressure detector sends a signal to a Pt electrode in an electrolytic chamber including $CuSO_4$ solution, which liberates 0.83 µg oxygen. Both chambers are connected to each other and the pressure difference will be balanced. A computer records the number of impulses that are needed to keep the pressure balanced, whereas the amount of oxygen that is used can be calculated (see chapter 5 for a detailed description of the respirometer).

To measure the water loss of the individuals, we used an evaporimeter. Air with 0 % humidity flows through a chamber including the individual. A humidity sensor after the sensor measures the relative humidity of the air, which is enriched by the individual. Afterwards the absolute water loss can be calculated using the relative humidity and the airflow per hour (see chapter 5 for a detailed description of the evaporimeter).

Both measurements were performed using an environmental temperature of 25 °C. All individuals were weighted before the measurement started (Mettler Toledo XS3DU; accuracy ±0.001 mg).

Feeding niche

To analyse how the development was affected within the degree of specialisation, we categorized the larval feeding niche in four ranks: (1) narrow specialists (host plants within one plant genus), (2) moderate specialists (host plants within one plant family), (3) moderate generalists (host plants recorded from two to four families), and (4) wide generalists (host plants in five or more families) (see Supplementary Material S6.1 for feeding niche per species; for detailed information and references, see chapter 3).

Data analysis

Effects of thermal conditions on survival rate (5, 20 and 40 days after hatching), time of development from egg hatching to pupae, pupal mass and growth rate (pupal mass divided by development time), water loss rate and respiration were assessed by linear mixed-effect models with treatment as fixed effect and clutch identity as random effect, followed by a Tukey post-hoc test. For water loss rate and respiration the body weight was also included as a random effect in the model. For better allometric scaling, the body weight was log transformed and multiplied by the ¾ exponent. First, we performed the analysis for all individuals. For the second step, we executed the same model, but for each feeding niche category separately (not for water loss rate and respiration). We did not use feeding niche as an explanatory because the distribution of clutches within each category was unbalanced. In some cases larvae did not develop until pupation. For this reason we decided to analyse the survival rate at three different times: at beginning, the middle and the end of development.

For a phylogenetic analysis, we used Pearson's correlation for the larval development and pupal weight, followed by an ANOVA with pupae weight as predictor and larval development and family as explanatory.

All analysis were performed in R (R Core Team 2014, Version 3.1.2) using the packages lme4 (Bates *et al.* 2014) and multcomp (Hothorn *et al.* 2008).

Results

The study was performed with 30 different moth species (17 Noctuidae and 8 Geometridae, 4 Erebidae, 1 Nolidae), represented by a total of 63 egg clutches for which subsets of eggs were distributed among temperature treatments. Water loss rate of 213 individuals (11 species, 12 clutches) and respiration rate of 326 individuals (9 species, 12 clutches) was measured. Species differed in all reaction norms. The survival rate differed significantly among species ($F = 3.7$ after 5 days, $F = 5.5$ after 20 days and $F = 4.0$ after 40 days, all $p < 0.0001$; Tab. 6.1).

Species also differed in developmental time, pupal weight and growth rate, but more importantly in their thermal responses, i.e. the interaction term between each parameter and the thermal treatment (larval development $F = 95.1$, $p < 0.0001$; interaction $F = 2.4$, $p = 0.001$; pupal weight $F = 96.1$, $p < 0.0001$; interaction $F = 2.2$, $p = 0.002$; growth rate $F = 73.4$, $p < 0.0001$; interaction $F = 2.6$, $p = 0.001$; Tab. 6.2).

Tab. 6.1: Median values of the survival rate 5, 20 and 40 days after hatching per species (Ere = Erebidae, Geo = Geometridae, Noc = Noctuidae, Nol = Nolidae).

		Survival rate (5 days)			Survival rate (20 days)			Survival rate (40 days)		
Species	Family	*control*	*+ 4°C*	*+ 8°C*	*control*	*+ 4°C*	*+ 8°C*	*control*	*+ 4°C*	*+ 8°C*
Acronicta rumicis	Noc	1	1	0.97	1	0.94	0.46	0.35	0.2	0
Agrotis exclamationis	Noc	1	0.95	0.93	0.74	0.76	0.75	0.39	0.43	0.46
Autographa gamma	Noc	1	1	1	0.79	0.05	0.24	0.26	0	0
Autographa pulchrina	Noc	1	1	0.79	1	0.93	0.57	0.92	0.71	0.29
Axylia putris	Noc	0.77	0.57	0.6	0.6	0.49	0.34	0.49	0.26	0.11
Calliteara pudibunda	Ere	1	1	1	0.85	0.81	0.73	0.73	0.69	0.54
Campaea margaritaria	Geom	1	0.91	0.91	0.66	0.37	0.01	0.05	0	0
Catarhoe cuculata	Geom	1	1	0.18	0.67	0.13	0.00	NA	NA	NA
Ceramica pisi	Noc	0.8	0.57	0.71	0.6	0.00	0.29	0.17	0	0.14
Charanyca trigrammica	Noc	0.63	0.49	0.66	0.23	0.17	0.57	0	0.09	0.2
Colocasia coryli	Noc	1	1	1	0.79	0.63	0.53	0.73	0.23	0.47
Eilema griseola	Ere	1	0.82	0.85	0.93	0.65	0.38	0.93	0.59	0.38
Epirrhoe alternata	Geom	1	0.75	0.35	0.45	0.15	0.2	NA	NA	NA
Euplexia lucipara	Noc	1	1	1	0.58	0.1	0.33	0.58	0.11	0.17
Hada plebeja	Noc	1	0.71	0.4	0.77	0.49	0.31	0.03	0.06	0
Hoplodrina spec.	Noc	0.74	1	0.83	0.36	0.23	0.05	0.15	0.16	0.02
Hypomecis roboraria	Geom	0.75	0.31	0.56	0.69	0.31	0.44	0.63	0.31	0.44
Idaea deversaria	Geom	0.75	0.81	0.44	0.38	0.38	0.31	0.38	0.38	0.31
Lacanobia oleracea	Noc	1	0.91	1	0.26	0.00	0.09	0.06	0	0
Macdunnoughia confusa	Noc	0.82	0.7	0.52	0.55	0.20	0.11	0.22	0.03	0
Miltochrista miniata	Noc	1	1	1	0.89	0.89	0.84	0.46	0.35	0.38

		Survival rate (5 days)			Survival rate (20 days)			Survival rate (40 days)		
Species	Family	*control*	*+ 4°C*	*+ 8°C*	*control*	*+ 4°C*	*+ 8°C*	*control*	*+ 4°C*	*+ 8°C*
Ochropleura plecta	Noc	0.83	0.67	0.58	0.75	0.65	0.30	0.65	0.18	0.15
Phlogophora meticulosa	Noc	1	1	0.71	0.80	0.43	0.22	0.61	0.34	0.01
Phragmatobia fuliginosa	Noc	0.99	0.97	1	0.89	0.87	0.71	0.67	0.6	0.54
Pseudoips prasinana	Nol	1	1	0.95	0.87	0.92	0.68	0.71	0.45	0.22
Scotopteryx chenopodiata	Geom	1	1	0.67	0.53	0.24	0.28	0.53	0	0.22
Spilosoma lubricipeda	Ere	0.94	0.79	1	0.74	0.79	0.79	0.66	0.23	0.06
Spilosoma lutea	Ere	1	1	0.8	0.71	0.51	0.77	0.34	0.14	0.23
Xanthorhoe montanata	Geom	1	1	1	0.82	0.88	0.82	0.82	0.81	0.28
Xestia c-nigrum	Noc	1	0.4	0.46	0.58	0.26	0.06	0.23	0.03	0

Tab. 6.2: Median values of larval development, pupal weight and growth rate per species (Ere = Erebidae, Geo = Geometridae, Noc = Noctuidae, Nol = Nolidae). Species listed in Tab. 6.1 but not here did not reach the pupal stage**.**

		Larval development			Pupal weight			Growth rate		
Species	Family	*control*	*+ 4°C*	*+ 8°C*	*control*	*+ 4°C*	*+ 8°C*	*control*	*+ 4°C*	*+ 8°C*
Acronicta rumicis	Noc	51	34	NA	219.1	171.1	NA	1.37	1.46	NA
Agrotis exclamationis	Noc	63	55	44	304.5	270.6	286.1	1.37	1.42	1.47
Autographa gamma	Noc	26	20	21	186.2	163.7	102.5	1.60	1.69	1.53
Axylia putris	Noc	45	42	36.5	110.3	135.4	117.6	1.22	1.32	1.32
Calliteara pudibunda	Ere	104	97	78	863.1	623.1	678.7	1.46	1.39	1.50
Catarhoe cuculata	Geom	23	NA	NA	43.7	NA	NA	1.20	NA	NA
Ceramica pisi	Noc	NA	NA	39	NA	NA	254.8	NA	NA	1.51
Colocasia coryli	Noc	68.5	NA	42	198.6	NA	218.7	1.25	NA	1.45
Epirrhoe alternata	Geom	35	29	NA	43.8	48.6	NA	1.09	1.15	NA
Euplexia lucipara	Noc	62	NA	NA	132.0	NA	NA	1.15	NA	NA
Hypomecis roboraria	Geom	68	72	NA	174.5	168.0	NA	1.22	1.20	NA
Idaea deversaria	Geom	48	NA	NA	61.3	NA	NA	1.06	NA	NA
Macdunnoughia confusa	Noc	36	25	24	137.5	105.6	91.9	1.38	1.42	1.42
Ochropleura plecta	Noc	44	38	37	163.7	161.2	153.8	1.36	1.41	1.41
Phlogophora meticulosa	Noc	56	NA	NA	354.7	NA	NA	1.46	NA	NA
Phragmatobia fuliginosa	Noc	NA	82	80	NA	124.5	147.8	NA	1.01	1.14
Pseudoips prasinana	Nol	53	40	39.5	262.3	318.2	257.1	1.41	1.55	1.55
Spilosoma lubricipeda	Ere	47	38.5	35	316.1	299.9	263.1	1.50	1.58	1.57
Spilosoma lutea	Ere	66	43	49	131.6	222.8	128.9	1.16	1.41	1.24
Xanthorhoe montanata	Geom	97	101	NA	57.3	50.5	NA	0.89	0.85	NA
Xestia c-nigrum	Noc	NA	79.5	NA	NA	158.2	NA	NA	1.11	NA

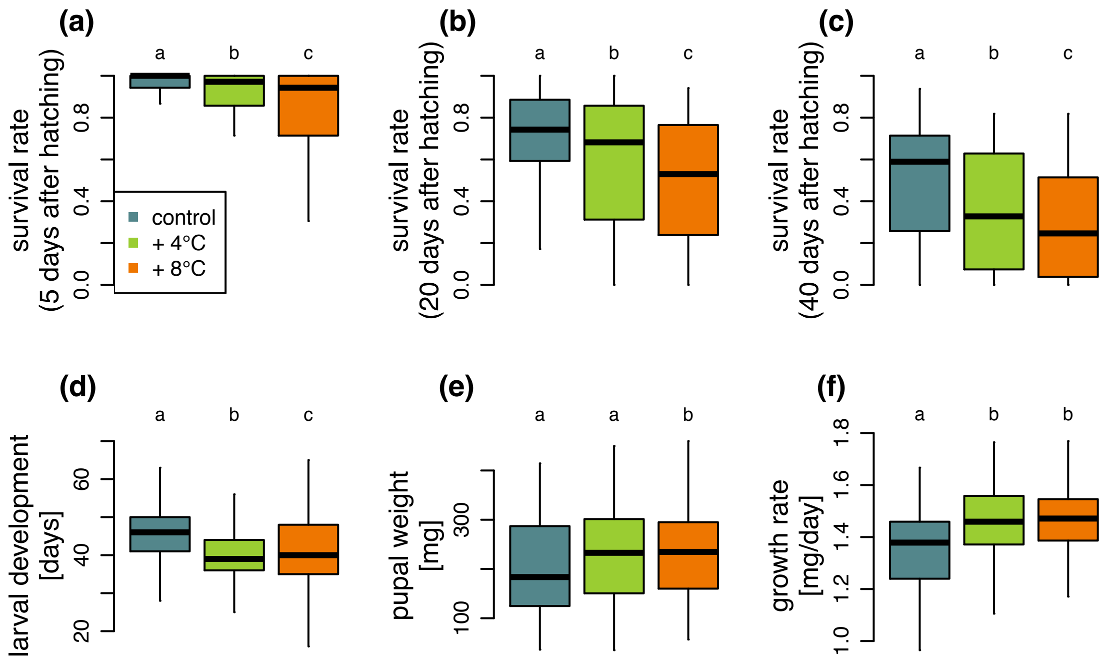


Fig. 6.1: Survival rate 5, 20 and 40 days after hatching (a-c), larval developmental time (d), pupal weight (e) and growth rate (f) in relation to the three thermal treatments: *control* (mean: 17.7 °C, range: 12.5 – 23 °C), *+ 4°C* (21.4 °C, 15 – 28 °C) and *+ 8°C* (25.3 °C, 18 -33 °C). Please note: y-axis shows raw data, while the analysis is based on clutch as random factor.

Independent of the larval stage, survival rate decreased continuously with increasing temperature 5 days after hatching (control / + 4°C: z = -2.58, $p = 0.027$; control / + 8°C: $z = -5.43$, $p < 0.001$; + 4°C / + 8°C: $z = -2.85$, $p = 0.012$) 20 days after hatching (control / + 4°C: z = -4.35, $p < 0.001$; control / + 8°C: z = -7.13, $p < 0.001$; + 4°C / + 8°C: $z = -2.78$, $p = 0.015$) and 40 days after hatching (control / + 4°C: z = -4.86, $p < 0.001$; control / + 8°C: z = -7.62, $p < 0.001$; + 4°C / + 8°C: z = -2.75, $p = 0.017$; Fig. 6.1 a-c). The time of development from hatching until pupation decreased significantly over all thermal treatments (control / + 4°C: z = -12.87, $p < 0.001$; control / + 8°C: $z = -14.18$, $p < 0.001$; + 4°C / + 8°C: z = -3.03, $p = 0.006$). Pupal mass and growth rate increased consistently (albeit not always significant) with increasing temperature (Fig. 6.1 d-f). An increase of 4 °C comparing to the control treatment did not affect pupal mass ($z = 0.41$, $p = 0.91$), but an increase of 8 °C lead to significantly heavier pupae (control / + 8°C: $z = -2.93$, $p = 0.009$; + 4°C / + 8°C: z = -3.44, $p = 0.002$). The growth rate was significantly higher in 4°C and 8°C warmer temperature regimes than in the control (control / + 4°C: $z = 9.49$, $p < 0.0001$; control / + 8°C: $z = 7.63$, $p < 0.0001$; + 4°C / + 8°C: $z = -0.76$, $p = 0.73$).

Water loss in the control treatment differed significantly to the + 4°C treatment ($z = 2.39$, $p = 0.044$) and the + 8°C treatment (z = 2.43, $p = 0.039$), whereas the warmer thermal

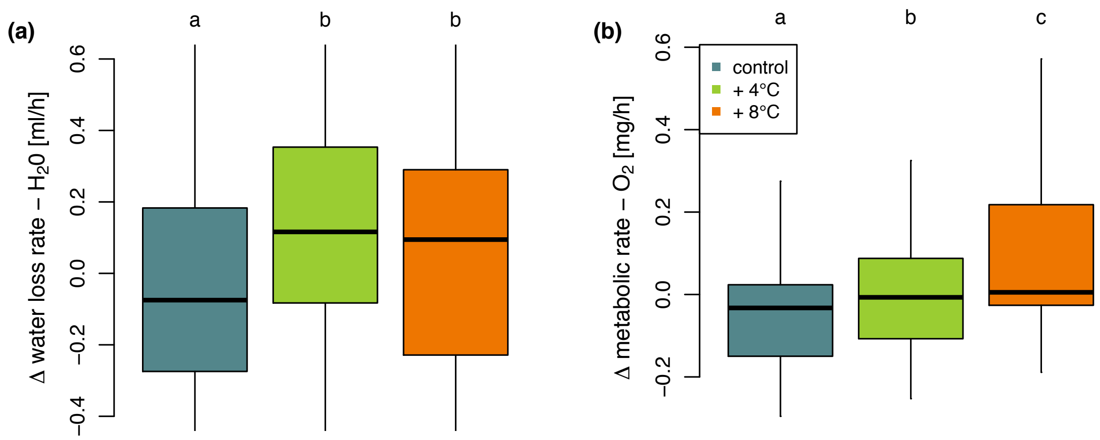


Fig. 6.2: Water loss rate (H_2O ml/hour) and respiration rate (O_2 mg/hour) in relation to the climate treatment *control*, *+ 4°C* and *+ 8°C*. Please note: y-axis shows the residuals of body weight and clutch, whereas they were used as random factors in the analysis.

treatments did not differ significantly among themselves ($z = 0.2$, $p = 0.97$). In contrast respiration rate was different in all treatments (control / + 4°C: $z = 3.19$, $p = 0.004$; control / + 8°C: $z = 6.63$, $p < 0.001$; + 4°C / + 8°C: $z = 3.87$, $p < 0.001$; Fig. 6.2).

The comparison across different host specialisation categories showed variable effects of thermal treatments, mainly a more negative impact of warmer conditions in climate chambers to host specialists than generalists (Fig. 6.3). After the first five days of development, specialists showed a stronger mortality increment with increasing temperature than generalists. This difference became weaker over time and was not significant after 40 days of development (Fig. 6.3 a-c). None of the narrow and moderate specialists developed until pupation in the warmest treatment. Time of development declined with increasing temperature for all niche levels, but the effect was not significant in all groups (Fig. 6.3 d). Moderate generalists were heaviest and showed the strongest growth rate in the + 4°C treatment. The trend reversed for + 8°C, whereas it still increased continuously for wide generalists with increasing temperature (Fig. 6.3 e-f, see Supplementary Material S6.1 for the result of the statistical analysis, and S6.2 for effects of temperature on survival rate, larval development, pupal weight and growth rate based on species level). It was not possible to compare physiological reaction norms across different host plant specialisation types, because too few specialists survived and most measured species were generalists.

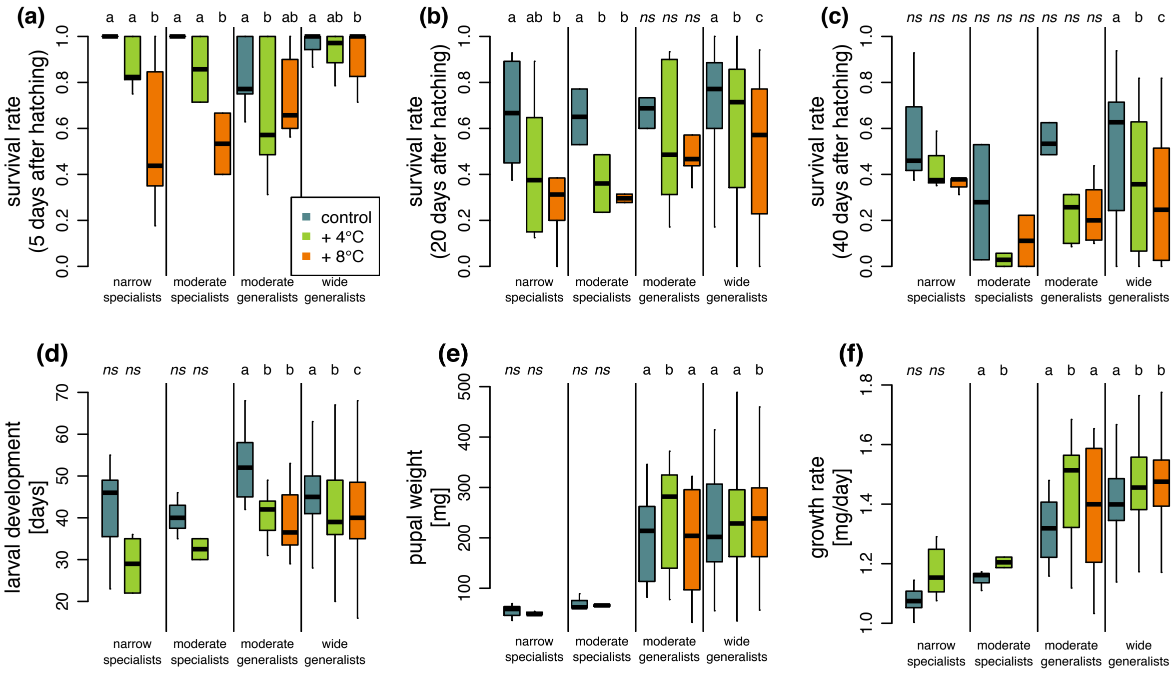


Fig. 6.3: Survival rate 5, 20 and 40 days after hatching (a-c), larval developmental time (d), pupal weight (e) and growth rate (f) in relation to the climate treatment *control*, *+ 4°C* and *+ 8°C* within each host-plant category. Please note: y-axis shows raw data, while the analysis is based on clutch as random factor.

Across species, pupal mass and larval developmental time were generally positively correlated ($r = 0.28$, $p < 0.0001$), particularly for Geometridae, although variation across species was pronounced (Fig. 6.4). The correlation between pupal mass and larval development within the treatments was not affected by the factor family of the species (control: $F = 0.19$, $p = 0.82$; + 4°C: $F = 0.04$, $p = 0.96$; + 8°C: $F = 0.56$, $p = 0.48$).

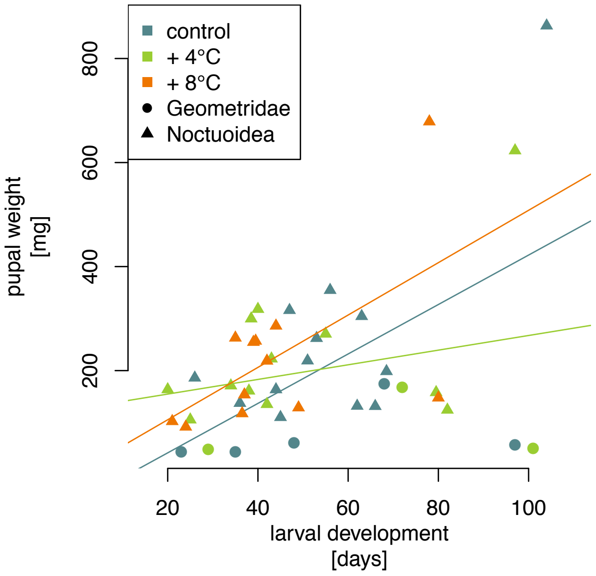


Fig. 6.4: Correlation between larval development and pupal weight of each species' median values in each of the climatic treatments (*control*, *+ 4°C*, *+ 8°C*) and phylogeny (the superfamily Noctuoidea includes Erebidae, Noctuidae and Nolidae).

Discussion

Our results confirmed that high temperatures during the larval development of 30 Lepidoptera species (Erebidae, Geometridae, Noctuidae and Nolidae) were generally associated with a lower survival rate, increased growth rate and higher pupal mass. With warmer conditions the water loss rate and the respiration rate also increased, even if the measurements were performed using a standardized temperature (25 °C). For those species that were host plant specialists, mortality due to warmer temperatures during their particularly sensitive early larval stages was much stronger than for generalists – thermal specialization and host-plant specialization were thus coupled. This effect became less strong during the later stages. Specialists did not manage to pupate in the warmest regime in the climatic chamber representing an actual increase of 8 °C, hence they were unable to complete their life cycle. For moderate generalists, the highest pupae mass and fastest growth rate were reached in the intermediate temperature regime (+4 ℃ warming). Broad generalists, however, showed a general increase of pupa mass and growth rate with increasing temperature. Additionally, we showed that the results did not vary across the families and thus the effect of temperature on morphological traits was independent of the phylogeny.

Increasing growth rate with higher temperature has been confirmed by a variety of studies on caterpillars and other insects (Bale *et al.* 2002; Buse *et al.* 1999; Pimentel *et al.* 2011; Salis *et al.* 2016). In case of unlimited food availability, growth rates of larvae can increase and can substantially reduce the time of development from hatching until pupation. This plasticity suggests that the actual temperature is still below a species-specific thermal optimum. Once temperature exceeds the thermal optimum, however, growth rate may decrease rapidly (Kingsolver and Woods 1997; Kingsolver *et al.* 2006). In addition, we showed a general increase of pupae mass with warmer temperature. This result for a small thermal range of 8 °C is not consistent with previous findings on the correlation between temperature and pupae mass: most studies reported a negative effect on pupae mass for a temperature range between 10 °C and 40 °C (da Silva *et al.* 2012; Kingsolver and Woods 1997; Kingsolver *et al.* 2006). Nevertheless, marginally positive effects (Lindroth *et al.* 1997), inconsistent effects (Higgins *et al.* 2015) or even no effect (Lemoine *et al.* 2015; Schwartzberg *et al.* 2014; Seiter and Kingsolver 2013) were also found for Lepidoptera. Lemoine *et al.* (2014) identified an increase in overall consumption rate with temperature for herbivores between 20 °C and 30 °C. An increase in consumption rate with increasing metabolic requirements is important to compensate demands for development and other physiological processes. The positive correlation up to 30 °C suggests a sufficient plasticity within the investigated climate range. In our study, the mean temperature did not exceed 25 °C despite much warmer conditions at mid-day, hence we assume a decrease of pupal mass for higher temperatures.

Nearly all physiological and biochemical rates of ectotherms increase exponentially with temperature (Brown *et al.* 2004; Kleiber 1932). Nevertheless, most studies analyse this effects by varying the temperature during the measurement, not necessarily the climate regimes in which they grow (DeVries and Appel 2013; Ehnes *et al.* 2011; Rourke and Gibbs 1999). The higher rates for larvae grown under warmer regimes (but measured at standard temperature) indicate a more general, long-lasting thermal response, e.g. potential biochemical reaction, developmental plasticity and higher basal metabolic rate. However, such responses may not mirror short time temperature changes, and specimen may not be able to compensate such fluctuations in the same way. Additionally water loss regulation of arthropods is usually performed either by desiccation resistance or desiccation tolerance (Hadley 1994). Resistance includes a decreasing cuticular transpiration of individuals from warmer conditions, due to changes of cuticular lipid composition of epicuticular waxes (Gibbs 1998). Nevertheless, our results rather suggest a desiccation tolerance. Individuals developing under warmer condition had a higher cuticular transpiration rather than a down-regulation, and obviously tolerate such higher transpiration rates e.g by higher water uptake during consumption.

In our study, host plant specialists were less tolerant to thermal stress than generalists, particularly during the very early larval phases. This pattern supports the hypothesis that generalists are in general more tolerant against climate warming and other global change effects, whereas specialists have a reduced tolerance against disturbances. Due to biotic homogenisation, generalists often replace specialists (McKinney and Lockwood 1999; Olden *et al.* 2004). Correspondingly, the most abundant nocturnal Lepidoptera are often polyphagous, i.e. they are host plant generalists. Because specialists are less commonly trapped, generalists were much more common than specialists in our study (see Supplementary Material S6.1). To better generalize the findings on the relationship between host plant specialisation and thermal tolerance, it is indispensible to investigate the effects of temperature on development particularly for other specialists and relatively rare species in general.

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CHAPTER 7

General discussion

In this thesis, I analysed anthropogenic effects on Arthropod composition and their functional traits. Land-use intensity and climate change have negative effects on Arthropod diversity and abundance. Both drivers act as environmental filters, leading to a shift towards more generalistic species communities. The intraspecific traits variation also differs between specialists and generalists as only generalists show benefits with increasing land use and specialists face a higher risk of distinction with increasing environmental temperature. Morphological (increasing body mass) and physiological (water loss resistance and changings in metabolic rates) processes affect responses to anthropogenic effects and differences between specialists and generalists.

We determined herbivore induced leaf damage in beech forests to analyse the effect of tree species composition and harvesting intensity on herbivore density (**chapter 2**). The next study focused on moths, as a representative taxon for herbivores and pollinators in grassland, to examine how grazing, mowing and fertilisation each affect moth diversity. We additionally analysed composition of life-history traits (**chapter 3**) and intraspecific variation of morphologic traits (**chapter 4**) according to land-use intensity. We developed a new method to measure water loss of several arthropod groups from grassland and forest sites within one region. By combining this method with measurements of the metabolic rate, we showed physiological differences of arthropods according to their environmental conditions (**chapter 5**). Additionally, we kept caterpillars at different climatic conditions to determine the effect of temperature on their survival, development and physiology in the context of their degree of specialisation (**chapter 6**).

Land-use intensity leads to a general loss of Arthropods and a lack of functional traits

Forest ecosystems are influenced anthropogenically, via forest management activities, including hunting, livestock grazing, logging, and reforestation of monocultures (Jactel *et al.* 2009; Milad *et al.* 2011; Wilson 1992). Herbivore density in beech trees correlates with the abundance of their host trees and decreased with harvest intensity (**chapter 2**). This pattern was, however, less pronounced during the vegetation period and was not continuous across three different regions in Germany. In grassland sites of the same regions (**chapter 3)**, the majority of moths preferred extensively used management strategies, as the diversity and abundance decreased with land-use intensification. The most relevant negative component was mowing.

Generalists did benefit from land-use intensity, whereas specialists were less tolerant. In contrast, more species showed an intraspecific increase of wing loading than a decrease, mostly conditioned by fertilisation (**chapter 4**). Increasing wing loading is caused by higher body mass, which also enhances reproduction success in insects as was shown for several taxa (Boggs and Freeman 2005; Knapp and Uhnava 2014). Species that did show these morphological advantages according to land-use intensity in our study had not been more abundant on stronger managed sites than others. Additional interspecific analysis of morphological traits in relation to the host-plant specialisation of the species showed that generalists were larger than specialists.

Today, German forests are mainly extensively and sustainable managed (Höltermann and Oesten 2001), whereas the proportion of intensively managed grasslands as pastures or meadows (in combination with fertilisation) is still increasing (Umweltbundesamt 2015). Disturbance via land-use intensification affects vegetation and Arthropod composition, which could also be shown for several taxa in the framework of the Biodiversity-Exploratories (Birkhofer *et al.* 2017; Chisté *et al.* 2016; Gossner *et al.* 2014a; Gossner *et al.* 2016; Simons *et al.* 2015; Socher *et al.* 2012). As anthropogenic activities in forests and grasslands differ massively, land-use intensity in grasslands has a stronger direct effect on the ecosystem structure. The stronger impact of human activities in grasslands mirrors our results: Comparing the results of **chapter 2** and **chapter 3**, we see a general negative impact of land-use intensification on species composition and functional traits in both ecosystems. But in grasslands land use causes a stronger effect across the season in different regions, and thus the ecological reaction is more pronounced. The study in **chapter 4** shows that some species also benefit of land use. Stronger fertilisation leads to a higher plant biomass production and thus a possible increase of food resources for herbivores, resulting in an intraspecific increase in body mass with land-use intensity. This response, however, appeared only for generalists or grass feeding specialists, which means that land use act as a strong environmental filter and lead to a loss of diversity especially in grasslands.

Temperature effects inter- and intraspecific plasticity

Considering climatic effects, we first analysed interspecific physiological responses to local climatic conditions and then intraspecific morphological and physiological adaptions with increasing temperature. We detected higher transpiration and metabolic rates of arthropods in forests than these from grasslands and that only grassland species show a strong correlation between both rates (**chapter 5**). In general, arid species develop strategies to avoid desiccation (Chown 2001) either during desiccation resistance or desiccation tolerance (Hadley 1994). We suggest that species from arid environments show a stronger reduction of cuticular transpiration and thus respiratory transpiration becomes more relevant in total water loss, which could also be shown on larger geographic scales (Addo-Bediako *et al.* 2001; Zachariassen *et al.* 1987). This process is, however, protracted and related to evolutionary processes. Considering single individuals adapted to warmer conditions short-term (e.g. within one generation), lead to a change of this pattern. The analysis of development and survival of several caterpillar species in different temperature treatments suggests a decreasing mortality rate and an increasing growth rate with warmer conditions (**chapter 6**). Here, individuals in warmer conditions suffer greater stress and their transpiration and metabolism is in general higher. Similar to stronger negative land-use effects on specialists, they face a higher risk of elimination with increasing temperature than generalists. In contrast to the results of **chapter 5**, larvae that have adapted to warmer temperature treatments have higher transpiration and metabolic rates. Short-term temperature depended fluctuations pose a major threat for arthropods and especially specialists are vulnerable to changing climatic conditions.

The results of my studies suggest that, under a scenario of increasing global temperatures and more extreme weather events, environmental filtering will preferentially select for generalist species, whereas the specialists are vulnerable to extinction.

Combining general relationships between anthropogenic drivers and its consequences for human well-being

The main purpose of this thesis is to contribute to the understanding and response of anthropogenic activities on ecosystems processes and –services (Fig. 7.1). Ecosystems are influenced by its occurring species, but no other species has such a massive effect on global environments than humans, and thus the present age is considered as the Anthropocene (Lewis and Maslin 2015). Studies investigate general consequences of anthropogenic drivers on terrestrial and aquatic ecosystems (Halpern *et al.* 2008; Ives and Carpenter 2007; Tilman *et al.* 2012; Winfree *et al.* 2009), being in permanent alteration, due to immigration and emigration of species and by biotic and abiotic factors. The interaction between drivers in an ecosystem and its species is, however, complex and a change in one driver can lead to unpredictable chain reactions in the ecosystem. Additionally, different drivers can affect ecosystems in similar ways and simultaneous changings can reinforce the effect of other drivers.

We thus studied direct and indirect effects of anthropogenic activities by analysing land-use intensity and temperature change on arthropod communities and functional traits. We considered several aspects like herbivore density in forests, moth diversity in grassland and also several functional traits of moths like life-history traits (feeding niche breath, voltinism or hibernation), morphological traits (wing area, body weight and wing loading), and

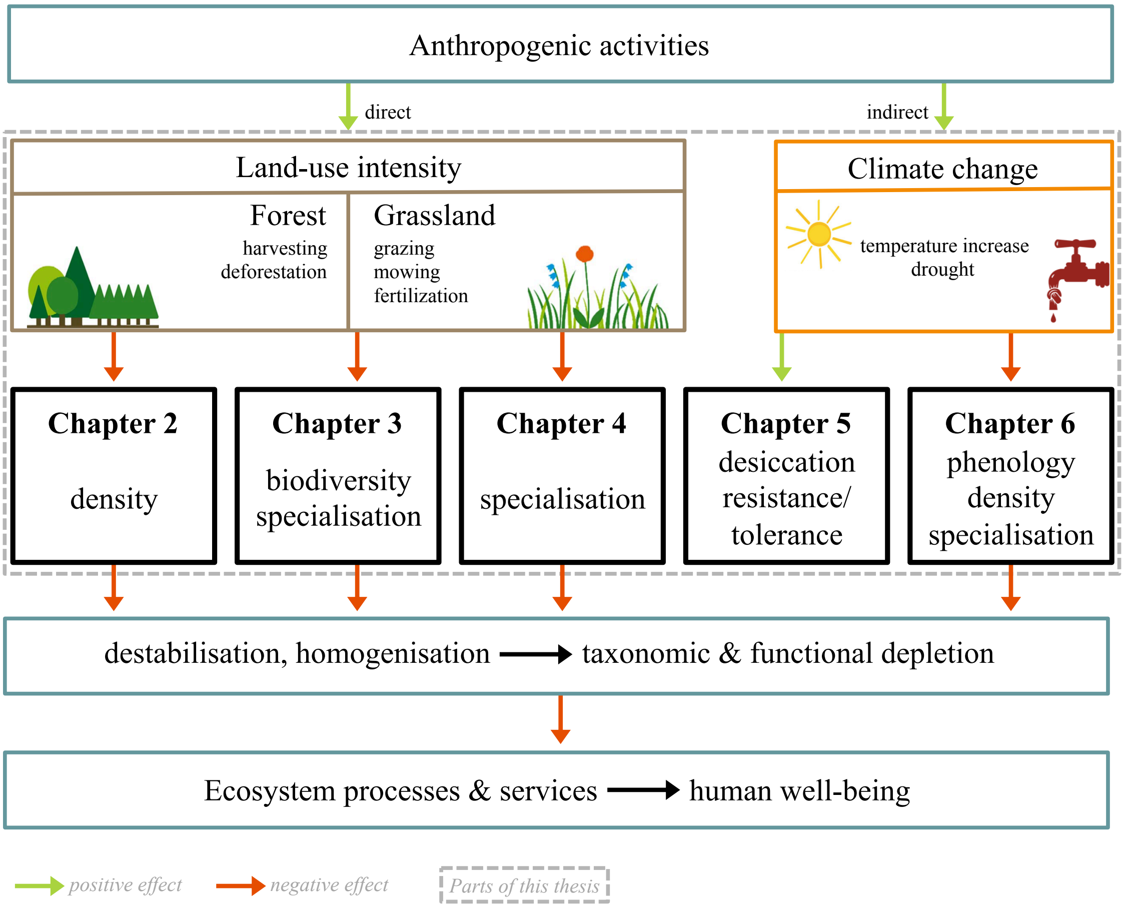

Fig. 7.1: Overview of the main results of this thesis in a general context.

physiological traits (growth rate, water loss rate and metabolism). Our results confirm a general species loss and decreasing density and biodiversity of herbivores and pollinators with increasing land-use intensification (**chapter 2-3**). Arthropods are able to adapt to their local and relatively stable climatic conditions in a long term (**chapter 5**). During the development of single individuals, environmental temperature has, however, negative effects on the survival (**chapter 6**). Especially specialists face a higher risk of extinction: land-use intensity leads to a shift towards more generalistic communities (**chapter 3**), and within these communities mostly generalists show morphological benefits of the higher input of nutrients (**chapter 4**). Negative temperature effects are stronger for specialists, as the survival rate is lower and pupation is constrained (**chapter 6**). Other studies suggest a biodiversity decrease with increasing temperature (Miles *et al.* 2004; Parmesan 2006; Williams *et al.* 2003). Thus this thesis shows similar consequences of land-use intensification and climate change as two different anthropogenic drivers (Fig. 7.2). Especially mutually reinforcing effects of human activities lead to a shift of taxonomic and functional composition towards generalistic communities and a general loss of diversity. Cardinale *et al.* (2012) describes possible consequences of these responses. He predicts that species- and functional-rich communities decrease homogenisation, which leads to stable ecosystem functioning, higher productivity and functional performance of ecosystem processes and services. Human activities can thus have an indirect negative effect on human well-being.

Outlook

Responses of harvesting intensity and beech dominance was mostly analysed on herbivory induced leaf damage (**chapter 2**). Sustainable and effective sampling methods within beech trees should be improved to observe direct effects of land use on beech herbivore communities on the considered scale (see Longino *et al.* 2002 for a selection of methods). As the community changes towards sun exposed canopies (Grimbacher and Stork 2007), leaf samples of the entire vertical stratification should be observed to analyse our hypothesis in a broader scale and to enhance the validity.

Analysing functional traits is a useful method to measure precise relationships between the stability in an ecosystem and its species. The analysis of functional traits yields more information than considering the occurrence of species alone, as these traits include ecological processes like predictions of the performance of a species in an ecosystem as well as the effect of a species on an ecosystem (Violle *et al.* 2007). Compared to previous studies, that only consider species diversity, the study of functional traits is a new field, and to facilitate more research in this direction it is necessary to collect and categorise more data on functional traits. This is supported by our newly developed new method that measures water loss of several samples within a short period (described in detail in **chapter 5**).

Especially the study about temperature-related responses on development and physiological processes in **chapter 6** should be further improved. In this study we compared effects on generalists and specialists, but as specialists are underrepresented in general, specialists need more investigations. The study additionally suggests that the temperature range was still within tolerable limits, as pupae weight increased with temperature. One should investigate absolute limits but also analyse effects of temperature variability. It would also be interesting to analyse differences between different generations, to see how temperature affects reproduction and plasticity of the offspring.

Conclusion

In this thesis, I analysed the effects of the two main anthropogenic disturbances – namely land-use intensity and climate change – on species diversity and functional traits of Arthropods. Functional traits are features or measurable properties that are related to the effect or response of species in an ecosystem. Investigating functional traits yields additional information than taxonomic species composition in an ecosystem alone, as they consider the effect of the species in an ecosystem (e.g. their host-plant specialisation).

The results show that biodiversity and population densities decrease in general with land-use intensification and a rise in temperature. Anthropogenic drivers affect mainly resource specialists negatively, which leads to a prevalence of generalist species. Decreasing biodiversity and a shift towards generalised communities increase functional homogenization of the species community and decrease the stability and functional performance of the ecosystem. The maintenance of high biodiversity, heterogeneity and stability, however, is important to guarantee sufficiently productive ecosystem functioning (biological, geochemical and physical processes) and services (goods provided by ecosystems) that are important for human well-being.

Trait-based ecology is a useful tool to describe, quantify and predict anthropogenic impacts on biodiversity and can be used to indicate the performance of ecosystem functioning and services. Thus, traits can be effective indicators to analyse sustainable land-use management strategies. Knowledge transfer between research and policymaker, stakeholder, and general public is needed to increase the importance of conversation and functional diversity.

CHAPTER 8

Appendix

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Supplementary Material

Supplementary Material is provided on a CD in the end of this thesis.

Chapter 2:

S2.1: Calculated percentage damage of a fictive leaf to support the estimation of damage of sampled leaves and complementary analysis of significant interaction effects between region, beech dominance and harvest intensity.
S2.2: Data summary

Chapter 3:

S3.1: Additional information of land-use intensity and live-history traits, supplementary literature, analysis of co-variance tables for residual model (including figures) and main model.
S3.2: Data table of life-history traits and larval habitat of 460 moth species .
S3.3: Data table of abundances of 447 moth species per region and month.

Chapter 4:

S4.1: Additional information of the intraspecific distribution for the most frequent species and statistical analysis including the correlation between the morphological traits and land-use intensity and abundance-weighted means of the land-use intensity.

Chapter 5:

S5.1: Pictures of the evaporimeter and the respirometer, calibration analysis of the evaporimeter and descriptions for generating data including R-scripts and exemplary datasets.

Chapter 6:

S6.1: Additional information of host plants, number of individuals per clutch and statistical analysis including results of the Tukey-Tests.

S6.2: effects of temperature on survival rate, larval development, pupal weight and growth rate based on species level.

Keywords, Author Contributions and Submissions

J.M.	Jule Mangels	A.H.	Andrea Hilpert
N.B.	Nico Blüthgen	K.M.	Karsten Mody
Ke.F.	Kevin Frank	Ko.F.	Konrad Fiedler
F.G.	Fabrice Grassein	F.S.	Florian D. Scheider

Chapter 2: Tree species composition and harvest intensity affect herbivore density and leaf damage on beech, *Fagus sylvatica*, in different landscape contexts

Jule Mangels, Nico Blüthgen, Kevin Frank, Fabrice Grassein, Andrea Hilpert, Karsten Mody

N.B., K.M. and J.M. conceived and designed the experiments. J.M., K.F., A.H. and F.G. perfomed the experiments. J.M., N.B. and K.M. analysed the data and J.M., K.M., N.B. and F.G. wrote the paper.
This chapter was published in "Plos One" volume 10, Issue 5, May 4th 2015, doi: 10.1371/journal.pone.0126140.
This chapter is rewritten using British English spelling and abbreviations and graphics are adapted to the layout of this thesis.

Chapter 3: Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists

Jule Mangels, Konrad Fiedler, Florian D. Schneider, Nico Blüthgen

Keywords: land-use intensification • life-history traits • Biodiversity Exploratories • functional homogenization • herbivorous insects

J.M. and N.B. conceived and designed the experiments. J.M. performed the experiments. J.M., F.S., N.B. and Ko.F. analysed the data. J.M. and Ko.F. collected the traits and J.M., N.B., F.S. and Ko.F. wrote the paper.
This chapter is conditionally accepted in "Biodiversity and Conservation".

Chapter 4: Intraspecific trait variation and responses to land use: body mass and wing *loading in grassland moth communities*

Jule Mangels, Nico Blüthgen

Keywords: Intraspecific trait variation • land-use intensity • meadows • pastures • host plant specialization • Lepidoptera

J.M. and N.B. conceived and designed the experiments. J.M. performed the experiment. J.M. and N.B. analysed the data and wrote the paper.

This chapter was under review in "Ecology and Evolution" and will be resubmitted.

Chapter 5: An efficient method to measure water loss in arthropods: desiccation adaptation hypothesis re-examined

Jule Mangels, Nico Blüthgen

Keywords: transpiration • metabolism • desiccation • arthropod communities • cuticular water loss

J.M. developed the evaporimeter and analysed the data. J.M. and N.B. conceived and developed the experiments and wrote the paper.

This chapter will be submitted to "Journal of Experimental Biology".

Chapter 6: Thermal reaction norms of moth species and their host plant specialisation: specialists face a dual risk

Jule Mangels, Nico Blüthgen

Lay-summary: *Across 30 species of moths, growth rate and pupal mass increased with temperature at conditions 4°C and 8°C above average summer days, but effects varied across species. Host plant specialists had higher mortality rates at warmer temperatures than generalists during larval development, suggesting an additional threat in a warming world.*

Keywords: thermal niche • host plant specialisation • Lepidoptera • development • adaption • water loss • respiration

J.M. and N.B. conceived and designed the experiments. J.M. analysed the data and J.M. and N.B. wrote the paper.

This chapter will be submitted to "Conservation Physiology".

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Mangels J, Blüthgen N, Frank K, Grassein F, Hilpert A, Mody K (2015) Tree species composition and harvest intensity affect herbivore density and leaf damage on beech, *Fagus sylvatica*, in different landscape contexts. Plos One, 10 (5). doi: 10.1371/journal.pone.0126140

Conference contributions

Mangels J (2016) Diversity and trait composition of moths respond to land-use intensity in grasslands. Talk at the 46th annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ)

Mangels J (2016) Diversity and trait composition of moths respond to land-use intensity in grasslands: generalists replace specialists. Poster at the 13th Annual meeting of the Biodiversity-Exploratories

Mangels J (2015) Grassland moths, their responses to land use and climatic stress. Poster at the 12th Annual meeting of the Biodiversity-Exploratories

Additional contributions

Interview in the corporate video of the Biodiversity-Exploratories (2014)

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Word, Excel, PowerPoint, Programming language R

Voluntary work

I am a member of the Verband christlicher Pfadfinderinnen und Pfadfinder (VCP, the largest protestant scouting organisation in Germany) since 1995. I guided a youth group, headed several projects and courses and planned national and international activities.

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Ehrenwörtliche Erklärung

Ich erkläre hiermit ehrenwörtlich, dass ich die vorliegende Arbeit entsprechend den Regeln guter wissenschaftlicher Praxis selbstständig und ohne unzulässige Hilfe Dritter angefertigt habe.

Sämtliche aus fremden Quellen direkt oder indirekt übernommenen Gedanken sowie sämtliche von Anderen direkt oder indirekt übernommenen Daten, Techniken und Materialien sind als solche kenntlich gemacht. Die Arbeit wurde bisher bei keiner anderen Hochschule zu Prüfungszwecken eingereicht.

Darmstadt, den 23. Juni 2017

....

Hinter jeder Ecke
lauern ein paar Richtungen.

Stanislaw Jerzy Lec