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Effects of land-use intensity on arthropod diversity and community structure in grassland

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"The worst thing that can happen [...] is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes would be for us, they can be repaired within a few generations. The one process [...] that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly that our descendants are least likely to forgive us."

Edward O. Wilson in: *Gaia, an Atlas of Planet Management* 1993

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Zusammenfassung

Die Intensivierung der Landnutzung ist der Hauptgrund für Biodiversitätsverlust in Grasländern der gemäßigten Breiten. Der Verlust an Diversität bedroht wichtige Ökosystemdienstleistungen, welche von Arthropodengemeinschaften der Kulturlandschaft bereitgestellt werden. Die Effekte einzelner Nutzungskomponenten (z.B. Mahd oder Beweidung) auf die Vielfalt von Arthropoden sind zwar gut untersucht, jedoch wurden diese meist nur für eine Komponente und unter experimentellen Bedingungen getestet. Studien unter reellen Bedingungen, welche eine Bandbreite an Nutzungsintensitäten abdecken und eine große Anzahl an Arthropodengruppen berücksichtigen, sind jedoch selten. Die vorliegende Arbeit untersucht den Einfluss von Grünlandnutzung auf fünf Arthropodengruppen (Insekten und Spinnen) für drei Regionen in Deutschland.

Im ersten Manuskript wird der gemeinsame Effekt von Mahd, Düngung und Beweidung auf die Vielfalt von pflanzenfressenden (herbivoren) und räuberischen (karnivoren) Arthropoden untersucht. Zusätzlich zum Gesamteffekt werden die indirekten Effekte durch eine Veränderungen in der Vielfalt oder Menge der verfügbaren Ressourcen betrachtet. Intensive Landnutzung verringert die Anzahl herbivorer Arten durch einen Verlust an Pflanzenvielfalt. Im Gegensatz dazu wird die Artenzahl der karnivoren Arthropoden durch einen Rückgang in der Gesamtbiomasse der Herbivoren verursacht, das heißt durch eine Verringerung der verfügbaren Ressourcen.

Im zweiten Manuskript wird der Effekt von Landnutzung auf die Struktur der Arthropodengemeinschaft untersucht, insbesondere ob häufige oder seltene Arten stärker von Landnutzung betroffen sind. Die untersuchten Gemeinschaften zeigen eine typische Gemeinschaftsstruktur mit einigen wenigen sehr häufigen Arten und sehr viel mehr seltenen Arten. Die relative Häufigkeit der häufigsten Art steigt mit zunehmender Düngungsintensität, während häufigere Mahden und intensivere Beweidung die Anzahl der seltenen Arten reduzieren. Beide Mechanismen führen insgesamt zu einer größeren Ungleichverteilung innerhalb der Gemeinschaft mit steigender Nutzungsintensität. Seltene Arten, welche eine geringere Häufigkeit aufweisen und bei intensiverer Landnutzung verloren gehen, wurden außerdem auf weniger als 10% aller untersuchten Flächen gefunden.

Zusammenfassung

Folglich kann ein Verlust dieser Arten auf einzelnen Flächen zu einem Verlust der Art in einer ganzen Region führen.

Eine Änderung in der Artenzusammensetzung kann zu einer Änderung der funktionellen Diversität führen, wenn bestimmt Merkmale einzelne Arten anfälliger für eine Zunahme der Landnutzungsitensität machen. Dies wurde im dritten Manuskript für fünf Merkmale getestet, welche für alle Arten der fünf untersuchten Arthropodengruppen erfasst worden waren. Mit zunehmender Nutzungsintensität nimmt die mittlere Körpergröße in der Gemeinschaft ab und die mittlere Ausbreitungsfähigkeit zu. Des Weiteren nimmt die relative Häufigkeit spezialisierter Herbivoren ab und die relative Häufigkeit von Strauch- oder Baumbewohnenden Arten sinkt. Veränderungen in der mittleren Ausprägung von morphometrischen Maßen in Wanzen (Heteroptera) zeigen zusätzliche Merkmale auf, welche auch in anderen Gruppen durch Landnutzung betroffen sein könnten. Außerdem zeigen diese Veränderungen, dass Beweidung einen gegenteiligen Effekt zu Mahd oder Düngung auf funktionelle Merkmale haben kann.

Im vierten Manuskript wird der Effekt von Landnutzungsintensität auf die Stabilität der Gemeinschaft getestet. Insbesondere werden indirekte Effekte durch eine Veränderung der Asynchronie zwischen Arten, der Artenvielfalt und der Gesamtzahl der Individuen betrachtet. Die Stabilität der Arthropodengemeinschaft ist im Grünland niedriger als im Wald und die Intensität der Nutzung reduziert die Stabilität im Grünland zusätzlich. Der Effekt von Nutzungsintensität wird hauptsächlich durch eine Veränderung in der Asynchronie verursacht. Ähnlich zum ersten Manuskript sind die Wirkungsmechanismen für herbivore und karnivore Arthropoden unterschiedlich. Während eine intensivere Nutzung die Asynchronie (und dadurch auch die Stabilität) von Herbivoren erhöht, wirkt sie sich negativ auf die Stabilität von karnivoren Arthropoden aus, da deren Diversität mit intensiverer Nutzung abnimmt.

Ergänzend zu den ersten vier Manuskripten, welche die Auswirkungen aktueller Grünlandnutzung auf die Vielfalt der Arthropoden untersuchen, beschäftigt sich das letzte Manuskript mit den möglichen Auswirkungen einer Erhöhung der minimalen Nutzungsintensität. Basierend auf den Häufigkeiten der einzelnen Arten entlang des Nutzungsgradienten werden zwei alternative Nutzungsszenarien („Schutz durch Nutzung" oder intensive Bewirtschaftung neben Schutzgebieten) verglichen. Die meisten Arten profitieren demnach von einer intensiven Bewirtschaftung auf möglichst kleiner Fläche, während die verbleibende Fläche extensiv bewirtschaftet wird. Die Anzahl der Arten welche in sehr geringen Häufigkeiten vorkommen zeigt, dass etwa die Hälfte der Arten lokal auszusterben droht wenn die Nutzungsintensität auf die Hälfte der maximalen beobachteten Intensität ansteigt. Wie schon im zweiten Manuskript gezeigt, sind seltene Arten stärker betroffen.

Unter Verwendung eines umfangreichen Arthropodendatensatzes und basierend auf einer großräumigen und langzeitlichen Forschungsplattform, liefert die vorliegende Arbeit neue Erkenntnisse über die Mechanismen von Biodiversitätsverlusten durch intensive Landnutzung. Diese Dissertation zeigt, dass die Effekte von Landnutzung unter realen Bedingungen komplex sind und von den untersuchten taxonomischen und funktionellen Gruppen abhängen. Auf der anderen Seite zeigt sie, dass merkmalsbasierte Untersuchungen an Arthropoden zusätzliche Erkenntnisse über die Wirkungsmechanismen von Landnutzungs-Intensivierung bringen. Basierend auf den Ergebnissen der einzelnen Untersuchungen werden mögliche Ansätze zum Schutz der Arthropodenvielfalt in landwirtschaftlich genutztem Grünland aufgezeigt.

Summary

Land-use intensity is the main driver of biodiversity loss in temperate grasslands. This reduction in diversity threatens important ecosystem services, which are provided by arthropod communities in the cultural landscape. While effects of different management practices (e.g. mowing or grazing) on arthropod species richness are well-documented, those practices are often tested independently and under experimental conditions. Studies under real-world scenarios, which include a range of land-use intensities and consider a wide range of arthropod groups, are however largely missing. This thesis evaluates the effects of grassland management on five arthropod groups across three regions in Germany.

In the first manuscript, the combined effects of mowing, fertilization and grazing intensity on the diversity of herbivorous and carnivorous arthropods are assessed. Additionally to the overall effect, the indirect effects through changes in resource diversity and availability are evaluated. It is shown that intensive land use decreases the species richness of herbivorous arthropods through a reduction of plant species richness. On the other hand, species richness of carnivorous arthropods is affected through a decrease in overall herbivore biomass, i.e. the amount of available resources.

The second manuscript explores the effect of land-use intensity on the arthropod community structure, i.e. whether dominant or rare species are more strongly affected. The studied arthropod communities show the typical abundance structure with a few very abundant and many rare species. The relative abundance of the most dominant species increases with increasing fertilization intensity while increasing mowing and grazing intensity reduces the number of rare species in the community. Both mechanisms lead to an increase in community unevenness with increasing overall land-use intensity. Rare species – which have a lower relative abundance or get lost under intensive land-use intensity – are also found on less than 10% of all plots per region. Hence, a loss of those species on some plots, through an intensification of management, can potentially lead to loss of the species in a larger area.

A change in community composition can lead to a change in the functional diversity of the

community if certain traits make some species more susceptible to increases in land-use intensity. This is tested in the third manuscript for five functional traits which have been collected for the five studied arthropod groups. Average body size decreases and average dispersal ability increases with land-use intensity. Furthermore, the relative abundance of specialist herbivores and of species which use other habitats than the main vegetation layer decreases. Changes in average morphometric traits of Heteroptera reveal additional traits which might be affected in other arthropod groups as well and show that grazing has opposite effects on some traits compared to mowing or fertilization.

In the fourth manuscript, the effect of land-use intensity on community stability is tested. In particular, the indirect effects of land-use intensity through changes in asynchrony between species, diversity and overall abundance are assessed. Arthropod community stability is lower in grasslands compared to forests, and grassland land-use intensity further reduces stability mainly through effects on asynchrony. Similarly to the first manuscript, differences in the mechanisms at play are found between herbivores and predators. While asynchrony in herbivores increases with land-use intensity (and hence increases stability), predator stability is negatively affected by land-use intensity through a decrease in diversity.

In addition to the first four manuscripts which evaluate the effect of current land-use intensity on arthropod diversity, the last manuscript evaluates the potential consequences of an increase in the minimal land-use intensity for arthropod diversity. Based on the abundances of single species across the range of land-use intensities, two alternative conservation scenarios are compared (i.e. land sharing and land sparing). Most species are identified as profiting from land sparing, which means intensive management on parts of an area while the remaining area is extensively managed for conservation. Counting the number of species with very low abundances reveals that about half of all species would be prone to extinction if land-use intensity were to increase to half the currently observed maximum land-use intensity. Confirming the results from the second manuscript, rare species are even more threatened.

Building on a comprehensive arthropod dataset from a large-scale and long-term research platform, this thesis provides new insights into the mechanisms of diversity loss through land-use intensification. It shows that land-use effects in real-world ecosystems are complex and depend on the taxonomic and functional group under consideration. But it also shows the potential of trait analyses in arthropods to explain the mechanisms behind diversity loss through land-use intensification. Based on the results gained in the different manuscripts, possible approaches for arthropod conservation in managed grasslands are illustrated.

Chapter 1

Introduction

"The use of land to yield goods and services represents the most substantial human alteration of the Earth system."   [Vitousek et al., 1997]

Within the last centuries of its existence on earth, humanity has radically shaped the face of our planet through industrialization, globalization, climate change and land-use intensification. These changes have led to substantial transformations of both the land surface and the oceans [Vitousek et al., 1997] and resulted in a decrease of biological diversity which exceeds the extinction rates in fossil records [Barnosky et al., 2011]. The loss of natural ecosystems and their biodiversity poses a threat to human well-being [Millennium Ecosystem Assessment, 2005] as the provisioning of services and goods strongly depends on a high and stable level of biodiversity [Cardinale et al., 2012; Hooper et al., 2005]. Facing the trade-off between a growing demand for food and other agricultural products and the long-term availability of ecosystem services, we need to understand how human activities affect biodiversity currently and in the future. One major requirement for the development of predictive models and recommendations for policy-makers is *"the understanding of the fundamental ecological processes that link biodiversity, ecosystem functions and services"* [Cardinale et al., 2012]. The Millennium Ecosystem Assessment [2005] reports five major direct drivers of biodiversity loss: habitat change, climate change, invasive alien species, overexploitation, and pollution. Of those five drivers, habitat change (i.e. conversion of natural habitats or intensifying management) had very high or high impact on biodiversity for nine of thirteen biomes considered (Millennium Ecosystem Assessment 2005, p. 9). Land-use intensification was also estimated to have the biggest impact on biodiversity within the next 100 years across ecosystem types [Sala et al., 2000].

1.1 Arthropods – diversity and function

Of about 1.75 million described species worldwide, 963,000 belong to Mandibulata (insects and myriapods) and 75,000 belong to Chelicerata (spiders and others), which makes arthropods (insects and spiders) by far the most species-rich group of organisms on the planet [Groombridge and Jenkins, 2002]. While the greatest number of insect species has been found in tropical forests, insects are also found with high species numbers in systems with a high plant diversity because many insects are specialists on single plant species or genera [Stork, 2009].

In temperate grasslands –which exhibit the highest small-scale diversity of plants [Wilson et al., 2012]– an average of 34 species of herbivorous insects were found per grass species [Tscharntke and Greiler, 1995]. Together with specialized pollinators, parasites and predators, herbivorous arthropods account for most of the biodiversity in temperate grasslands. Given that they exploit a wide range of niches, arthropods are not only the most species-rich but also the most functionally diverse group of organisms [Wilson, 1992] and contribute to the provisioning of ecosystem services in all categories developed by the Millennium Ecosystem Assessment [2005]:

Supporting services are services which support the provisioning of other services and traditionally focus on primary production. Prather et al. [2013] argue that arthropods contribute to primary production through pollination, seed dispersal and habitat formation and hence consider these to be supporting services by arthropods. One direct effect of arthropods on primary production is herbivory, which reduces plant biomass but can also increase plant productivity through increased nutrient cycling. Belovsky and Slade [2000] showed that herbivory by grasshoppers increased plant biomass by speeding up nitrogen cycling. In forests, saproxylic beetles affect dead wood decay and provide a number of related ecosystem services [Ulyshen, 2013]. Pollination by insects ensures or increases production for 43 of 87 studied global food crops [Klein et al., 2007]. Most common seed dispersers are ants, which are essential for the seed dispersal of myrmecochorous plants [Giladi, 2006] but other arthropods were also found to contribute to seed dispersal [e.g. dung beetles, Nichols et al., 2008].

Provisioning services are services which are obtained from the ecosystem in the form of goods for use by humans. Arthropods contribute not only indirectly to the supply of goods through pollination (see previous point) but also directly. They contribute substantially to diets in tropical and subtropical countries [DeFoliart, 1999] and honey-bees produce honey which is widely used in food-production or for health

products and cosmetics [Krell, 1996]. Other goods provided by arthropods include silk, biochemicals (e.g. birth-control hormones) or pharmaceuticals (e.g. anti-venoms) [Prather et al., 2013].

Regulating services maintain and regulate ecosystem processes such as food web stability or pest control. Arthropods contribute to food web stability either as predators and parasites [Lafferty et al., 2006] or as resources for higher trophic levels [cf. Baxter et al., 2005]. Arthropod parasites and predators also play an important role in pest control [Hajek, 2004; Nyffeler and Sunderland, 2003].

Cultural services are services which are not provided in the form of goods or products but are of non-material nature. Arthropods indirectly affect and enrich recreational activities such as ecotourism [Huntly et al., 2005] and other outdoor activities; and they inspire a variety of arts, including design and the movie industry [Prather et al., 2013].

1.2   Importance of grasslands

Grasslands are the largest ecosystem on earth, covering about 40% of earth's landmass, excluding Greenland and Antarctica, and can be defined as vegetation dominated by grasses with little or no tree cover [FAO, 2005]. In Europe, about 184 million ha of land are currently used as permanent grasslands, comprising 34.7% of all agriculturally used land [Smit et al., 2008]. Besides provisioning of fodder for livestock, grasslands provide important services to water management (by regulating water run-off or improvement of water quality), carbon sequestration, biofuel production or recreation [Carlier et al., 2009; Hönigová et al., 2012; Hopkins and Holz, 2006]. The value of the services provided by grasslands depends on the level of biodiversity found on it. More diverse grasslands provide more services and services are more stable and hence more reliable in species-rich grasslands [Cardinale et al., 2012; Hopkins and Holz, 2006].

The diversity in grasslands, and with it all benefits for humanity, is threatened by global changes, i.e. climate change, intensification of management, nitrogen deposition, invasive species and others [Millennium Ecosystem Assessment, 2005]. Among the drivers of decreasing biodiversity, land-use intensification is estimated to be the most important for grasslands [Sala et al., 2000]. In a global-scale study, Newbold et al. [2015] showed that species richness is on average 20% lower in intensively managed pastures compared to extensively used pastures and estimated that changes in land use have led to a reduction of local species richness by on average 13.6% between 1500 and 2005. Similar numbers

were found by Murphy and Romanuk [2014], who found that land-use changes led to an average reduction in species richness by 24.8%. While intensification of land use has been identified as the main driver of biodiversity loss in temperate grasslands [Carlier et al., 2009; Hopkins and Wilkins, 2006; Tscharntke and Greiler, 1995], abandonment of grasslands can have an equally strong effect on diversity [Uchida and Ushimaru, 2014].

To understand why diversity in grasslands is being threatened by both land-use intensification and abandonment, it is useful to look at the history of grassland management. In Central Europe, the conversion of forests to grasslands and the management of grasslands has a century-old tradition [Hejcman et al., 2013; Kapfer, 2010; Poschlod and WallisDeVries, 2002; Poschlod et al., 2005]: The existence of naturally occurring steppe and other grassland habitats in Central Europe can be proven even before the early Neolithic (5500 BC), but those grasslands were fragmented within the mainly forested landscape and kept open through browsing of large wild grazers (e.g. wild horses, aurochs or bison). The first form of 'regulated' grazing evolved during the Middle Ages (around 1000 to 1250 BC) from an originally 'unregulated' pasture system, in which livestock was grazing in forests and fallow arable land. The first 'regulated' grazing system led to the establishment of permanent pastures and to the first meadows, which were used to produce fodder for the winter. These meadows were mown only once at the peak of plant production and additionally used as pastures in spring and autumn. Meadows became regularly fertilized when a second hay harvest became common in the late Middle Ages. This system of pastures in combination with meadows which were grazed for a short time in spring and autumn and mown once or twice a year persisted until about 1850.

Between 1770 and 1850, the first major change in grassland management happened when keeping livestock in sheds for the better part of the year was introduced. Especially the 'privatization' of grasslands after the revolution of 1848 led to a more intensive management on meadows with a reduction of early and late grazing. At the beginning of the 20th century, the fertilized meadow, which was mown twice a year and sometimes grazed in autumn, was the common form of grasslands management. Despite the described changes, the system of mostly grazed grasslands at a maximum of two hay harvests a year persisted for over 1000 years and can be considered important for the development of species-rich grassland communities. The second major change in grassland management happened between 1960 and 1970. The 'industrialization' of agriculture led to a large-scale intensification of meadows through drainage, intensive fertilization and other measures which allow for up to five or more hay harvests per year. On the other hand, increasing import of agricultural products led to another dramatic land-use change. As the management of grasslands which are poor in nutrients but have a high species richness

(e.g. calcareous and sandy grasslands) became less profitable, those habitats were either abandoned or converted into agricultural areas or forests.

The loss of biodiversity in grasslands through both intensification and abandonment led to the successive introduction of policies which aim at increasing biodiversity and landscape conservation within the agricultural context [EU, 2005; Hopkins and Holz, 2006]. Policies introduced by the European Union led to the implementation of different national agri-environmental programs which aim for an increase in agricultural biodiversity [Kleijn and Sutherland, 2003]. However, the effectiveness of those programs for biodiversity on arable land has been questioned [Kleijn and Sutherland, 2003; Kleijn et al., 2006], which was mainly attributed to a lack of baseline data.

1.3   Effects of land use on grassland arthropods

In order to alleviate the negative effects of land-use intensification on biodiversity, we need a thorough understanding of how different levels and types of land use affect diversity. In Central Europe, grazing and mowing are the main management activities in grasslands [Allen et al., 2011; Hejcman et al., 2013] and define the three grassland types used throughout this thesis: meadow, pasture and mown pasture. Meadows are only mown, pastures are only grazed and mown pastures are both mown and grazed. To improve productivity, all three grassland types can be fertilized to varying degrees with organic or mineral fertilizers. Other management activities to improve grassland productivity include herbicide application, sowing, drainage or ploughing, but those are only rarely studied as they are applied infrequently. Accordingly, this thesis focuses only on effects of mowing, grazing and fertilization or any combination of those.

Effects of land-use intensity are well-studied for some grassland arthropod groups but not for others. A literature search for 'arthropod OR insect OR spider' together with either 'mow*', 'cut*', 'fertiliz*', 'graz*','land use' or 'manage*' in the ISI Web of Knowledge database (accessed in April 2015) revealed 7 reviews with a focus on grasslands (Table 1). The reviews show a small bias towards effects of grazing and no review was found which considered only the effect of fertilization on grassland arthropods. Among the studies cited in those reviews, the majority considered only one taxonomic group (e.g. Lepidoptera or Hemiptera). Three main areas of interest become apparent from the cited studies: (1) pollinators such as wild bees or butterflies, because they provide an important service to humans and because they are often target species in conservation schemes; (2) herbivores such as Hemiptera, because they have a close trophic link to the plant community and can be important pests; (3) predators (Araneae and Coleoptera), because they are important

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Table 1 Reviews on the effect of land use on grassland arthropods and the number of studies included therein which consider one or several of the listed taxa.

	Tscharntke and Greiler [1995]	Wilson et al. [1999]	Bell et al. [2001]	Swengel [2001]	Jones and Leather [2012]	Scohier and Dumont [2012]	Joern and Laws [2013]
Mowing	Y	Y	Y	Y			
Grazing	Y	Y	Y	Y	Y	Y	
Fertilization	Y	Y	Y	Y		Y	Y
Araneae	-	3	10	3	-	4	5
Coleoptera	1	11	-	2	8	6	4
Diptera	-	13	-	-	-	-	-
Hemiptera	7	16	-	1	2	5	4
Hymenoptera	3	1	-	-	-	-	1
Lepidoptera	-	5	-	15	11	2	4
Orthoptera	3	6	-	2	-	3	6
several taxa	11	-	6	12	4	3	10

Y=Review covers this land-use type

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for pest control. However, studies including more than one taxonomic order or trophic group are rare, mainly because species determination is laborious and requires expert knowledge in some groups. There also seems to exist a trade-off between the number of arthropod groups studied and the complexity of management considered.

The first review on grassland diversity and management by Tscharntke and Greiler [1995] focused on grasses and their closely associated herbivorous arthropods, but they also developed hypotheses for other arthropod groups. Given that their focus of interest was herbivores, they concluded that grassland management affects arthropods through changes in the plant community, i.e. their host plants. Accordingly, they found that moderate grazing supports arthropod diversity as it increases the diversity of the plant community. They emphasize that a homogeneous and simplified plant community through cutting supports a less diverse herbivore community and should also affect other arthropod groups which depend on complex structures within the vegetation. While they expect that fertilization increases the abundance of herbivores through an increase in plant biomass and better palatability of grasses, they emphasize that fertilization is negatively correlated with plant diversity and consequently also arthropod diversity.

Four years later, Wilson et al. [1999] reviewed the changes in food resources (plants and invertebrates) of birds through intensified agriculture. They found that the effects of grassland management are strongly dependent on the arthropod group under consideration and that effects can be detrimental, neutral or beneficial for abundance or diversity. For example, they list negative effects of cutting for Araneae, Orthoptera, Heteroptera and Lepidoptera, but neutral or positive effects for the abundance of some Hymenoptera and Hemiptera as well as for Diptera and Coleoptera. Regarding fertilization and grazing, they emphasize that effects on arthropod diversity are mediated by changes in vegetation composition and structure, i.e. a homogeneous plant community reduces arthropod diversity. Both a review on the implications of grassland management on spider diversity [Bell et al., 2001] and a review on the effects of fire in comparison with other management activities [Swengel, 2001] followed up on the conclusion that a heterogeneous vegetation supports higher arthropod diversity. Both reviews promote grassland management which varies not only in the intensity and choice of management activities between years but also in space, e.g. by leaving patches or strips within the grassland unmanaged.

While consistent effects on arthropod diversity were found for fertilization and cutting [Jones and Leather, 2012], findings on the effects of grazing were highly heterogeneous, not least because effects of grazing on the plant community depend on various factors including the type of livestock [Rook et al., 2004]. In the following years, a number of studies were conducted to test for effects of grazing in different contexts or on selected

arthropod groups. For example, Batáry et al. [2007] compared the effect of grazing intensity and landscape complexity on beetles and found that grazing intensity affected mainly specialist beetles. Similarly, Sjödin et al. [2008] found that pollinating beetles and hoverflies were affected by grazing intensity while bees and butterflies reacted to landscape diversity but not to grazing intensity. Differences in the effect of grazing between different arthropod groups were also found by Dennis et al. [2007], who observed higher numbers of Araneae, Hemiptera and Coleoptera under less-intensive grazing but no change in the diversity of some Diptera and juvenile Lepidoptera. Following on the frequent observation that grazing effects on arthropods are mediated by the plant community, Woodcock et al. [2009] related grazing effects on arthropods to the architecture of the plant community and found sward architecture to be the main driver of arthropod diversity (for both herbivores and predators). The importance of a heterogeneous vegetation structure was also highlighted by Zhu et al. [2012] who found vegetation structure to be more important than plant diversity for promoting arthropod diversity in grazed grasslands.

Reviewing studies on the effects of sheep grazing, Scohier and Dumont [2012] concluded that low grazing intensity is beneficial for the diversity of Orthoptera, Hemiptera, Coleoptera and Lepidoptera and the abundance of Araneae. However, Joern and Laws [2013] emphasized that a number of the studies they reviewed found hump-shaped relationships between grazing intensity and arthropod diversity and that results heavily depend on the taxon or species considered, as well as on the time frame of the study and site-specific factors. They also highlight that arthropod diversity is affected through a number of different mechanisms, which themselves are affected by the type and combination of management activities. In their conclusion, they emphasize the need for *"linking comparative studies of grassland arthropod diversity with long-term experiments aimed at teasing apart specific ecological mechanisms"* [Joern and Laws, 2013].

1.4   Aims and Questions

The overall aim of this work is to understand how land-use intensity affects different aspects of diversity and community structure in grassland arthropods. With a better knowledge of the mechanisms behind the loss of biodiversity we can make better recommendations for its preservation in managed grasslands. The first step towards this overall aim is to understand how the combination of different land-use activities in grasslands affects arthropod species richness and how those effects are mediated by the plant community. The second step is to evaluate if dominant or rare species react more strongly to

land-use intensity and how this affects the overall community structure. Both a decrease in diversity and changes in the community structure could lead to a shift in the functional composition of the arthropod community, which is tested in the third step. Long-term stability of a community is often an aim of conservation, hence it is crucial to understand how land-use intensity affects the variability of a community over time. Finally, the potential effects of two conservation strategies (land sharing and land sparing) under the scenario of increasing land-use intensity are tested.

Specific questions within this work are:

   i Are indirect effects of land-use intensity on arthropod diversity mediated through changes in resource diversity or resource abundance?

  ii How does land-use intensity affect the abundance structure within the arthropod community?

 iii Does land-use intensity lead to a change in average functional traits for the whole arthropod community?

 iv By which mechanism does average land-use intensity affect the inter-annual variability of the arthropod community?

  v Do grassland arthropod species potentially profit from land sharing or land sparing?

Chapter 2

Study system and methods

One common drawback of experimental studies on land-use effects in grasslands is the experimental design which often compares unmanaged sites with only one or two levels of land-use intensity or only includes one type of management. For example, Báldi et al. [2013] analyzed the effects of grazing on a large dataset including plants, birds and eight arthropod orders sampled in Hungary, but the studied grasslands were subject to only two grazing intensities which were also both within the range of acceptable grazing intensities under the Hungarian agri-environmental scheme. While this study certainly allows comparisons between many groups, it is difficult to transfer the results to grasslands which do not fall within the studied range of grazing intensity. All data used in this thesis has been sampled within the *Biodiversity Exploratories* project –a platform for observational, comparative and experimental studies on the impact of land-use intensity on biodiversity and ecosystem services– which covers a wide range of land-use intensities with the studied plots.

2.1   The Biodiversity Exploratories

The *Biodiversity Exploratories* project for large-scale and long-term biodiversity research (www.biodiversity-exploratories.de) was established in 2006 [Fischer et al., 2010a]. The aim of the project is to understand the effect of land-use intensity on biodiversity and ecosystem services across levels of organisms under real-world scenarios. The three study regions (called exploratories) are the UNESCO Biosphere Reserve Schorfheide-Chorin, the national park Hainich with its surroundings and the UNESCO Biosphere Reserve Schwäbische Alb (Figure 1). With their different geographical characteristics (Table 2), the three study regions are representative for large parts of Germany. They were further chosen because the two habitats of interest (forests and grasslands) occur on similar
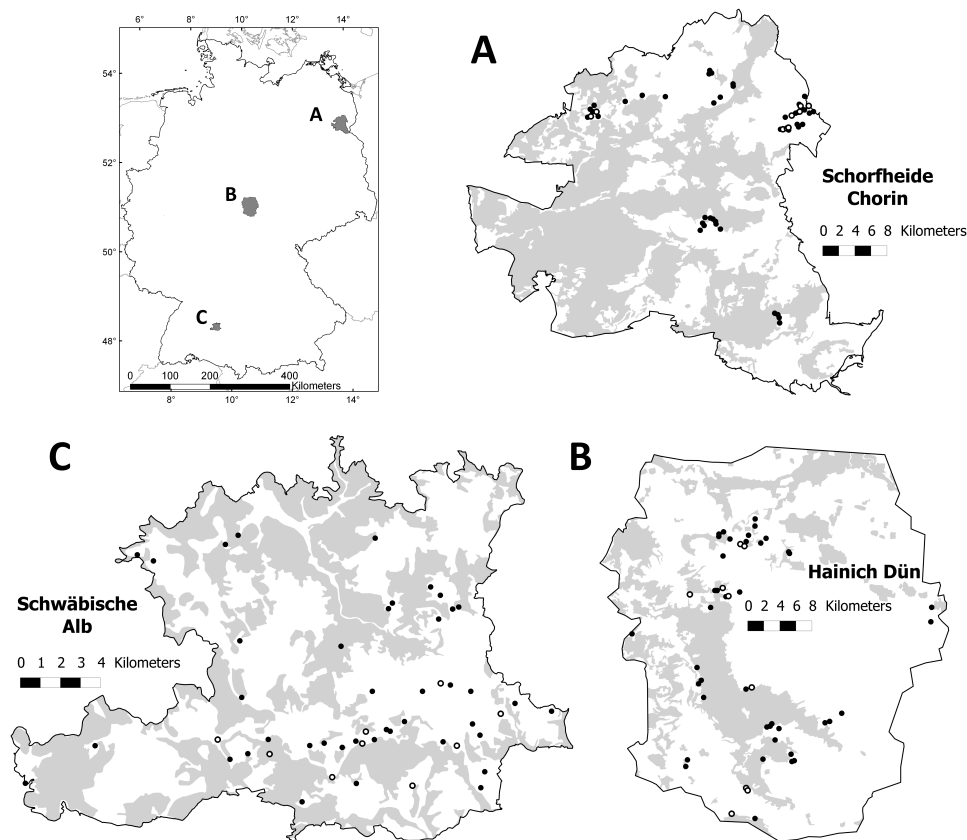
Fig. 1 Overview of the three study regions and the location of the experimental plots (black dots) and the 'very intensive plots' (white dots). Grey areas in the small maps show forest, white areas show open habitats. Small maps by courtesy of Steffen Boch and Eric Heinze.

bedrocks and elevations within each region and because the land use reflects both the risk of abandonment and intensification for grasslands and various management types in forests [Fischer et al., 2010b]. The jointly used study plots were selected in a hierarchical design. Within both grasslands and forests in each region, 500 grid plots were selected for initial soil and plant diversity inventories and assessment of management. From those grid plots, 50 experimental plots (EPs) were chosen in both grasslands and forests by a stratified random sampling to cover the range of observed land-use intensity and soil depth. From those experimental plots, 9 'very intensive' plots (VIPs) were selected for studies which are too labor-intensive to be conducted on all experimental plots [Fischer et al., 2010a].

As this thesis is focused on land-use effects in grasslands, only the grassland plots are described in more detail. The experimental plots in grasslands are 50 x 50 m in size and located at a distance of at least 30 m from the nearest forest edge. Each experimental plot is equipped with a monitoring unit, which measures temperature, humidity and

Table 2 Main characteristics of the three study regions within the *Biodiversity Exploratories* from Fischer et al. [2010a]. Annual averages are given for temperature and precipitation.

	Schorfheide-Chorin	Hainich-Dün	Schwäbische Alb
Location	NE Germany	Central Germany	SW Germany
	53°02'N 13°83'E	51°20'N 10°41'E	48°43'N 9°37'E
Size	˜1300 km^2	˜1300 km^2	˜422 km^2
Geology	Young glacial landscape	Calcareous bedrock	Calcareous bedrock with karst phenomena
Altitude a.s.l.	3-140 m	285-550 m	460-860 m
Temperature	8-8.5 °C	6.5-8 °C	6-7 °C
Precipitation	500-600 mm	500-800 mm	700-1000 mm
Population density	23 km^{-1}	116 km^{-1}	258 km^{-1}

soil moisture. These monitoring units are fenced to prevent damage by livestock or other animals, but the remaining plot area is not fenced or otherwise separated from the surrounding. Hence, the experiments on the plots do not interfere with the management, which is applied on the plots in the same way as on the surrounding grassland [Fischer et al., 2010a].

The main types of land use on the grassland plots are mowing, grazing and fertilization and range from unfertilized and extensively grazed sheep pastures over fertilized and mown cattle pastures to highly fertilized three-cut meadows or cattle pastures. Type and intensity of land use are assessed yearly by interviews conducted with farmers and land-owners. Mowing intensity is recorded as the number of mowing events; fertilization intensity is calculated as the amount of nitrogen applied per hectare through organic (slurry or manure) or mineral fertilizers; grazing intensity is transferred from the number of grazing animals (standardized as livestock units) per hectare and the duration of the grazing period(s) [Fischer et al., 2010a]. The resulting values for mowing (number of cuts), fertilization (kg N/ha) and grazing (livestock-unit*days/ha) per experimental plot are standardized by the mean of the respective region and then summed into an index of overall land-use intensity (LUI). The LUI is then square-root transformed to achieve more evenly distributed values [Blüthgen et al., 2012]. The resulting values of LUI range between 0.5 and 3.5 (Figure 2). Depending on the dataset used for each analysis (one year or several years), the average LUI over a different number of years was used. In general, the two years prior to data sampling and the year of data sampling were considered (e.g. the average LUI over the years 2006-2008 was used for the analysis of the arthropod data sampled in 2008).
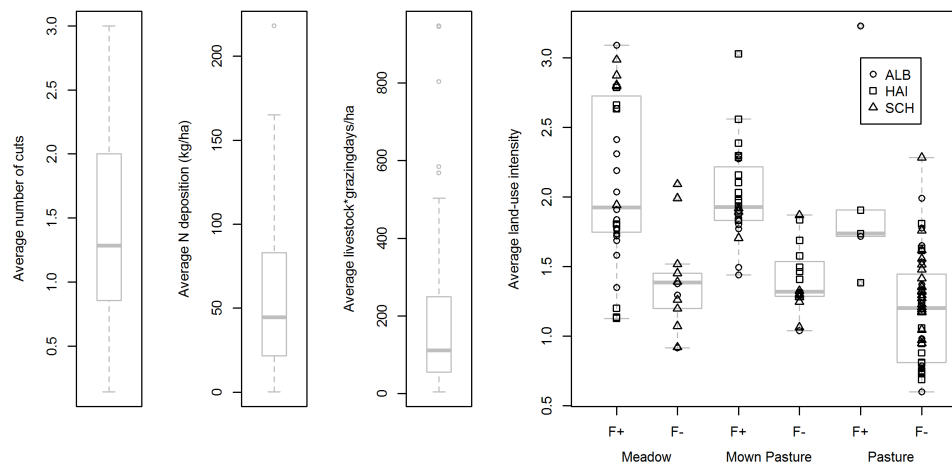
Fig. 2 Average mowing, fertilization, grazing and combined land-use intensity over the years 2006 to 2012. Combined land-use intensity is calculated as the square-rooted sum of standardized mowing, fertilization and grazing [Blüthgen et al., 2012]. ALB: Schwäbische Alb; HAI: Hainich-Dün; SCH: Schorfheide-Chorin. F+ = fertilized; F- = unfertilized.

2.2 Arthropod sampling

The focus of this thesis is on vegetation-dwelling arthropods excluding the typical polli-nator groups (i.e. Hymenoptera & Lepidoptera) as these are studied by another project within the *Biodiversity Exploratories.* Arthropods were sampled by sweep-netting with a round sweep net of 30 cm diameter. Sampling was conducted on a transect of 150 m along three of the plot borders by performing 60 double-sweeps (one double-sweep is defined as moving the net from the left to the right and back perpendicular to the walking direction) through the vegetation at about 5 cm above the ground. All caught animals were transferred into 70% ethanol and stored therein until they were sorted in the lab-oratory. Sampling was conducted two times each year between 2008 and 2012, once in early (June/July) and once in late summer (August/September) on all 150 experimental plots. Sampling in all three regions was conducted within several days per region and a maximum of two weeks across regions during favorable weather conditions (no rain, temperature above 15 °C). The arthropod samples were sorted into taxonomic groups (on order level for most groups and on family level for some Coleoptera) and target groups were sent to taxonomic experts for identification to species level. Araneae, Hemiptera (Auchenorrhyncha and Heteroptera), Coleoptera and Orthoptera were selected as target taxa because of their numerical dominance in the studied grasslands. Only adult indi-viduals were used for the analyses because identification of juveniles is often difficult. Furthermore, specimen which could not be identified to species level were excluded.

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2.3   Trait collection

Despite functional traits (or just 'traits') being *"a rich source of additional evidence that can supplement, test or even replace evidence from studies based on taxonomic composition"* [Fountain-Jones et al., 2015], they have been widely used for plants and vertebrates but only rarely for invertebrates. In this thesis, a trait database is used which includes trait information based on literature and expert knowledge for all species in the five target taxa [Gossner et al., 2015a]. The database includes information on body size, dispersal ability, feeding mode, specialization and stratum use (Table 3).

Body size   was collected from literature sources as the averaged body length (mm) over males and females. For some analyses, body size was standardized within each target group by dividing by the group's mean length.

Dispersal ability   was defined in five levels between zero (very low dispersal ability) and one (very high dispersal ability). The classification of dispersal ability was based on different information in the five target groups. For Hemiptera and most Coleoptera, the level of wing dimorphism between males and females was used. For other Coleoptera, dispersal ability was based on descriptions of flying ability. Species of Araneae were assigned to the five dispersal groups by taking into account activity ranges and dispersal strategies (e.g. ballooning and migration). For Orthoptera, dispersal ability was estimated on the basis of the size of the hind wings (alae), the occurrence of macropterous forms and studies of individual movement and colonization dynamics.

Feeding mode   includes herbivores, carnivores, detritivores, fungivores and omnivores. Both the larval and adult stage were considered for the classification, hence assigning a specific feeding mode only if both stages use the same resource (e.g. plants). All species which use more than one resource (plants, animals, fungi, decaying plants or dead animals) to similar extent across larval and adult stages were classified as omnivores.

Specialization   was only assigned within herbivores and defined by the number of genera or major plant lineages a species feeds on. Monophages were classified as species feeding on only one plant genus, oligophages as species feeding on one higher plant lineage and polyphages as species feeding on more than one higher plant lineage.

Stratum use   was defined by the main vegetation layer (or vertical stratum) in which the species was usually observed and included ground- and soil-dwelling species,

Table 3 Species richness, abundance and trait overview for the five target taxa sampled from 2008 to 2012. Specialization is only determined for herbivores.

		Araneae	Auchenorrhyncha	Coleoptera	Heteroptera	Orthoptera
No. species		148	138	574	163	32
Total abundance		2,890	60,697	21,021	28,912	1,477
Body size	Mean	4.48	4.04	4.20	5.60	17.63
	Min	1.25	2.00	0.31	2.00	9.00
	Max	12.50	9.70	14.50	13.50	35.00
Dispersal ability	Mean	0.77	0.77	0.94	0.83	0.48
Feeding mode		all predators	all herbivores	302 herbivores, 113 predators, 159 others[a]	112 herbivores, 21 predators, 20 omnivore	20 herbivores, 1 predators, 11 omnivore
Specialisation			53 mono-, 59 oligo- & 26 polyphag	131 mono-, 131 oligo- & 109 polyphag	26 mono-, 66 oligo- & 51 polyphag	8 oligo- & 23 polyphag
Stratum use		40 ground, 16 herb-layer, 30 tree-layer, 62 indifferent	119 herb-layer, 6 tree-layer, 13 indifferent	158 ground, 303 herb-layer, 51 tree-layer, 62 indifferent	23 ground, 91 herb-layer, 14 tree-layer, 35 indifferent	1 ground, 29 herb-layer, 2 tree-layer

a = 22 detritivore, 28 fungivore, 109 omnivore

herb-layer species, shrub- and tree-layer species and others (species without clear preference or species linked to water bodies). As for feeding mode, information on both larvae and adults was combined.

In Manuscript 1, information on body size was used to estimate each species' biomass and calculate the overall arthropod biomass of herbivores and predators on each experimental plot. Biomass was estimated with the general power function developed by Rogers et al. [1977]:

$$biomass[mg] = 0.305 * L^{2.62}$$

with L being the body length (mm) of a species. Overall biomass per plot was then calculated by multiplying each species' abundance with its biomass.

In Manuscript 3, the trait expression of the whole arthropod community on each experimental plot was analyzed. For all numeric traits, community weighted means (CWM, weighted by the relative abundance of each species) were calculated. For categorical traits, the relative abundance of all species which exhibit the most commonly found trait characteristic (i.e. herbivores for feeding mode, monophages for specialisation and herb-layer species for stratum use) was calculated. The analysis of literature-based traits in Manuscript 3 was complemented by morphometric traits which had been measured on Heteroptera [Gossner et al., 2015b]. For each Heteroptera species sampled between 2008 and 2012, at least one male and one female specimen and at least one brachypterous and one macropterous specimen (for species with known wing dimorphism) was measured. Nine morphometric traits were derived from the 23 measurements taken: Body volume was calculated from body length, width and thickness following Siemann et al. [1999]. Body shape was calculated by dividing body length by body width. Leg length, wing length, rostrum length, and antenna length were defined relative to body length. Hind femur and front femur shape were calculated by dividing their length by their width. Eye width was defined relative to head width.

2.4   Statistical analyses

The five main questions of this thesis are answered by using different methodological approaches. Manuscripts 1 & 4 focus on the mechanisms by which land-use intensity affects arthropod diversity and stability, respectively. Structural equation models are used in both manuscripts because relative effects of different variables can be compared and indirect effects can be estimated with this method. In Manuscript 2, species-abundance-distribution models are used to estimate the effect of land-use intensity on community

structure. Generalized linear models are used in Manuscript 3 to test the effect of land-use intensity on average traits. In Manuscript 4, the structural equation model includes a measure of community stability which is based on the 'portfolio effect'. In Manuscript 5, the potential effect of two alternative conservation strategies (land sharing vs. land sparing) is tested. Some of the used methods are explained in more detail in the following.

2.4.1 Structural Equation Models

In both Manuscripts 1 & 4, structural equation models are used following a confirmatory approach in which a single model is defined and tested against the data [Grace, 2006]. In Manuscript 1, two models are defined and compared, one based on the 'Resource Heterogeneity hypothesis' [Strong et al., 1984] and one on the 'More Individuals hypothesis' [Srivastava and Lawton, 1998]. The 'Resource Heterogeneity hypothesis' predicts that more diverse resources provide more niches for a greater number of specialized species at higher trophic levels. Its representation includes paths from land-use intensity to plant diversity and biomass as well as paths from plant diversity and biomass to arthropod diversity. The 'More Individuals hypothesis' proposes that diversity of consumers increases when resource quantity increases. Its representation additionally includes arthropod biomass which is affected by plant biomass and affects arthropod diversity. In Manuscript 4, the tested model includes an effect of land-use intensity on arthropod diversity, abundance and asynchrony which in turn affect the measured 'portfolio effect' (for a description of the concept behind the 'portfolio effect' see Section 2.4.3.)

Structural equation models are fitted by a Maximum Likelihood method based on the observed and expected covariance matrices. The model fit is estimated from a Chi^2 test with the p-value indicating whether the two covariance matrices are significantly different from each other (p<0.05, bad model fit) or not (p>0.05, good model fit) [Grace, 2006, p. 128f]. Following Grace and Bollen [2008], land-use intensity –which is defined by the three components mowing, fertilization and grazing– can be defined either as a latent variable or as a composite variable. In Manuscript 1, land-use intensity is defined as a latent variable to reflect that the three land-use components are manifestations of the farmers management decision. In Manuscript 4, land-use intensity is defined as a composite variable to allow for the effect of the three land-use components to be tested independently from each other. Based on the estimates for each path coefficient in the model, the combined effect of direct and indirect paths can be calculated. This is done by multiplying the path coefficients within each possible pathway between two variables (e.g. land-use intensity and the response variable) and then summing the products of all possible pathways.

2.4.2 Species-abundance distributions

In Manuscript 2, three parameters are used to analyze the effect of land-use intensity on the communities' abundance structure, which is represented by species-abundance distributions (SADs). SADs are calculated by ranking all species in a community based on their abundance and plotting the species' abundances against the species' ranks (beginning with the most abundant species up to the least abundant species). Different parameters can then be used to describe the shape of the SAD. The first parameter 'decay rate' describes the overall shape of the distribution and is derived from the niche-preemption model:

$$n_i = NCr(1-r)^{i-1} \text{ with } C = [1-(1-r)S]^{-1}$$

in which the expected abundance n of a species i is defined by the total number of individuals N of all species, the estimated decay rate r per rank and by a constant factor C [Magurran, 2011; Tokeshi, 1993]. The second parameter d represents dominance and is calculated as the number of individuals of the species that is most abundant (N_1) divided by the total abundance of all species in the community (N) [May, 1975]. The third parameter –Fisher's α– represents rarity and is derived from fitting Fisher's log-series model [Fisher et al., 1943] to the species-abundance distributions.

2.4.3 Portfolio analysis

In Manuscript 4, a concept originally developed in the financial sector [Markowitz, 1952] –the 'portfolio effect'– is adapted to test the effect of land-use intensity on community stability. The portfolio effect describes the phenomenon that the variability in a portfolio of objects (e.g. variability in the market value of stocks) is reduced if a) the set is larger (i.e. more stocks are included) or b) the single objects vary asynchronously. In ecology, the objects are single species which vary in their abundance between time steps (e.g. years), and the portfolio is the distinct community formed by those species. The portfolio effect is then defined as the difference between the average variability of the single species and the variability of the community. Following Hautier et al. [2014], the strength of the portfolio effect is positively affected by diversity, asynchrony and total abundance of the community.

To compare the relative contribution of those three variables to the portfolio effect and to estimate the indirect effect of land-use intensity via changes in those variables, structural equation modeling is used (see Section 2.4.1). One difficulty in this approach is the selection of an appropriate measure of asynchrony. Asynchrony can be generally described

by the standardized temporal correlation coefficient between all species in a community [Loreau and de Mazancourt, 2008]. To overcome some conceptual problems with different definitions of asynchrony [Thibaut and Connolly, 2013], both asynchrony and diversity are weighted by the relative total abundance of species. Diversity is defined as $\exp H'$, the exponential form of Shannon's diversity index [Jost, 2006] and asynchrony η_w is defined following Gross et al. [2014]. The original asynchrony η in Gross et al. [2014] is calculated as the mean correlation coefficient r between the abundances A of each species i versus the abundance of the rest of the community (all A_j except i) :

$$\eta = \frac{1}{S}\sum_{i}^{S} r(A_i, \sum_{j \neq i}^{S} A_j)$$

with S as the total number of species. The weighted asynchrony η_w, which gives a higher influence to the asynchrony between two dominant species in contrast to the asynchrony of two rare species, is calculated as:

$$\eta_w = \sum_{i}^{S} [p_i r(A_i, \sum_{j \neq i}^{S} A_j)]$$

with p_i as the relative total abundance over all years of species i. The resulting index ranges from -1 (perfect asynchrony) to $+1$ (perfect synchrony).

2.4.4 Land sparing vs. land sharing

The challenge of meeting both the food demand of an increasing human population [Godfray et al., 2010] and conservation targets for biodiversity in agricultural landscapes has sparked a debate over the best strategy to achieve both [Fischer et al., 2014; Tscharntke et al., 2012]. The two main approaches discussed are 'land sharing' and 'land sparing'. The land sharing approach advocates extensive production on all of the available area in a region (e.g. all agricultural fields) whereas the land sparing approach advocates intensive production on a part of the available area (management intensity should be as high as possible to reduce the required area to a minimum) while leaving the remaining area unmanaged (i.e. by preserving or restoring natural habitat) [Green et al., 2005; Phalan et al., 2011]. However, these scenarios are not directly applicable to grassland-dominated cultural landscapes, as extensive land use is required to maintain grassland diversity (see Section 1.3). In Manuscript 5, the scenarios of land sparing and land sharing are therefore adapted to managed grasslands:

Land sharing corresponds to a minimal use of all grasslands by increasing land use on extensively used grasslands and decreasing land use on intensively used grasslands.

Land sparing corresponds to an increase of land use on the now moderately used grasslands and no change on extensively used grasslands.

The consequences of those two strategies for arthropod diversity are then assessed based on the optimal strategy for each individual species. The optimal strategy is assigned following the method developed by Green et al. [2005], which uses a fitted model of abundance over the land-use intensity gradient. The shape of this fitted abundance curve determines the optimal strategy of a species. A species profits from land sharing if its abundance curve is concave, i.e. the fitted abundance declines slowly with increasing land-use intensity such that under moderate land-use intensity the abundance is only slightly lower than at the lowest land-use intensity. In contrast, species which profit from land sparing have a convex abundance curve and their fitted abundance declines quickly with increasing land-use intensity, i.e. their estimated abundance is much lower under moderate land-use intensity than at lowest land-use intensity.

Chapter 3

Manuscript overview

This thesis contains five manuscripts, for which a brief summary, the publication status and the contribution of the authors is given.

Resource-mediated indirect effects of grassland management on arthropod diversity

Nadja K. Simons, Martin M. Gossner, Thomas M. Lewinsohn, Steffen Boch, Markus Lange, Jörg Müller, Esther Pašalić, Stephanie A. Socher, Manfred Türke, Markus Fischer and Wolfgang W. Weisser

This manuscript investigates the indirect effects of grassland land-use intensity on arthropod diversity. In semi-natural grasslands, land-use activities such as mowing, grazing and fertilization affect the diversity of plants and arthropods, but the combined effects of different drivers and the chain of effects are largely unknown. In this study we used structural equation modelling to analyse how the arthropod communities in managed grasslands respond to land use and whether these responses are mediated through changes in resource diversity or resource quantity (biomass). Plants were considered resources for herbivores which themselves were considered resources for predators. Plant and arthropod (herbivores and predators) communities were sampled on 141 meadows, pastures and mown pastures within three regions in Germany in 2008 and 2009. Increasing land-use intensity generally increased plant biomass and decreased plant diversity, mainly through increasing fertilization. Herbivore diversity decreased together with plant diversity but showed no response to changes in plant biomass. Hence, land-use effects on herbivore diversity were mediated through resource diversity rather than quantity. Land-use effects on predator diversity were mediated by both herbivore diversity (resource diversity) and herbivore quantity (herbivore biomass), but indirect effects through resource quantity were stronger. Our findings highlight the importance of assessing both direct and indirect effects of land-use intensity and mode on different trophic levels. In addition to the overall effects, there were subtle differences between the different regions, pointing to the importance of regional land-use specificities. Our study underlines the commonly observed strong effect of grassland land use on biodiversity. It also highlights that mechanistic approaches help us to understand how different land-use modes affect biodiversity. The different indirect pathways of land-use effects on herbivores and predators suggest that land-use intensity might also affect other groups within the community differently.

NS, MG, TL & WW conceived and developed the idea for the manuscript and refined the intellectual content and scope. MF & WW were involved in setting up the project. MG, SB, ML, JM, EP, SS and MT conducted and managed data collection in the field. NS, MG

and TL analyzed the data. NS wrote the first manuscript draft. MG & WW commented on all manuscript versions. SB, ML, JM, EP, SS, MT & MF contributed to the writing of the manuscript.

Effect of land-use intensity on arthropod species abundance distributions in grasslands

Nadja K. Simons, Martin M. Gossner, Thomas M. Lewinsohn, Markus Lange, Manfred Türke and Wolfgang W. Weisser

This manuscript evaluates the effect of land-use intensity on the abundance-structure of the arthropod community and compares land-use effects between rare and abundant species. As a rule, communities consist of few abundant and many rare species, which is reflected in the characteristic shape of species abundance distributions (SADs). The processes that shape these SADs have been a longstanding problem for ecological research. Although many studies found strong negative effects of increasing land-use intensity on diversity, few reports consider land-use effects on SADs. Arthropods (insects and spiders) were sampled on 142 grassland plots in three regions in Germany, which were managed with different modes (mowing, fertilisation and/or grazing) and intensities of land use. We analysed the effect of land use on three parameters characterizing the shape of SADs: abundance decay rate (the steepness of the rank abundance curve, represented by the niche-preemption model parameter), dominance (Berger-Parker dominance) and rarity (Fisher's alpha). Furthermore, we tested the core-satellite hypothesis by comparing the species' rank within the SAD to their distribution over the land-use gradient. When data on Araneae, Cicadina, Coleoptera, Heteroptera and Orthoptera were combined, abundance decay rate increased with combined land-use intensity (including all modes). Among the single land-use modes, increasing fertilisation and grazing intensity increased the decay rate of all taxa while increasing mowing frequency significantly affected the decay rate only in interaction with fertilisation. Results of single taxa differed in their details, but all significant interaction effects included fertilisation intensity. Dominance generally increased with increasing fertilisation and rarity decreased with increasing grazing or mowing intensity, despite small differences among taxa and regions. The majority of species found on less than 10% of the plots per region were generally rare (<10 individuals), which is in accordance with the core-satellite hypothesis. We found significant differences in the rarity and dominance of species between plots of low and high intensity for all three land-use modes and for the combined land-use intensity. We conclude that effects of land-use intensity on SADs lead to a stronger dominance of the most abundant species. Furthermore, species which have restricted distributions are more likely to also be rare species in the local SAD and therefore are at high risk of being lost under intensive

land use. It is shown that dominant and rare species show differences in their reaction to land-use modes, which might be a consequence of different functional characteristics.

NS, MG, TL & WW conceived and developed the idea for the manuscript and refined the intellectual content and scope. NS conducted all analyses and wrote the first draft. MG, TL & WW contributed to data analyses and commented on all versions of the manuscript. ML & MT collected data in the field and commented on the final version of the manuscript.

Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient

Nadja K. Simons, Wolfgang W. Weisser and Martin M. Gossner

Under review with Ecology.

This manuscript evaluates if the sensitivity of species towards land-use intensity can be explained by the functional traits those species exhibit. Intensification of land use reduces biodiversity but may also shift the trait composition of communities. Understanding how land use affects single traits and community trait composition helps to understand why some species are more affected by land use than others. Trait-based analyses are common for plants, but rare for arthropods. We collected literature-based traits for nearly 1000 arthropod (insect and spider) species to test how land-use intensity (including mowing, fertilization and grazing) across 124 grasslands in three regions of Germany affects community weighted mean traits in the whole community and in single taxa. We additionally measured morphometric traits for more than 150 Heteroptera species and tested whether they are affected by land-use intensity. Community average body size decreased and community average dispersal ability increased from low to high land-use intensity. Furthermore, the relative abundance of herbivores and of specialists among herbivores decreased and the relative abundance of species using the herb-layer increased with increasing land-use intensity. Community weighted means of the morphometric traits also changed from low to high land-use intensity towards longer and thinner shapes as well as longer appendices (legs, wings, and antenna). While mowing and fertilization intensity had consistent effects with the combined land-use intensity, grazing intensity often had no or the opposite effect on community average traits. We conclude that high land-use intensity acts as an environmental filter selecting for on average smaller, more mobile and less specialized species across taxa. Although trait collection across multiple arthropod taxa is laborious and needs clear trait definitions, it is essential for understanding the functional consequences of biodiversity loss due to land-use intensification.

NS, WW & MG conceived the idea for the manuscript. NS & MG defined the final outline of the manuscript and collected trait information. NS analysed the data and wrote the first manuscript draft. MG & WW commented on all manuscript versions.

Land use impedes the portfolio effect of biodiversity: plant, bird, bat and arthropod stability in forests and grasslands

Nico Blüthgen*, Nadja K. Simons*, Kirsten Jung, Dani Prati, Swen Renner, Markus Fischer, Norbert Hölzel, Valentin H. Klaus, Till Kleinebecker, Marco Tschapka, Wolfgang W. Weisser and Martin M. Gossner   *Both authors contributed equally

In preparation.

This manuscript evaluates how land-use intensity affects inter-annual variability among species and within the whole community. Long-term stability of species communities —and ecosystem functions provided by them-– is fundamental for biodiversity conservation and represents a main target for sustainable ecosystem management. Community stability can be achieved by a higher species diversity as well as higher asynchrony across species. This theory –analogous to 'portfolio effects' in financial markets-– has rarely been tested in real-world terrestrial ecosystems except for grassland plants. Here we investigated for the first time whether habitat conversion and land-use intensity imperil community stability via reduced species density, diversity and asynchrony in a comparison across taxa and habitats of variable land use. We examined the stability of 599 plant, 2008 arthropod, 114 bird and 13 bat species across 300 forest and grassland sites over a period of 5-6 years. Community stabilization by portfolio effects was pronounced, ranging from 27% to 73% reduction of mean species fluctuations across taxa. It was strongest in grassland plants, intermediate in arthropods and birds, and weakest in bats. Forest conversion to managed grassland was associated with a 2 to 2.5-fold higher instability in arthropod and bird communities, respectively, driven by reduced asynchrony. Within forests and grasslands, land-use intensity did not have a pervasive impact on portfolio effects, but indirectly destabilized communities via reduced asynchrony, diversity and abundance as major drivers of stability. Our results highlight that diversity alone insufficiently predicts variation in stability across taxa and sites, habitats and land-use gradients, and that asynchrony is particularly crucial for long-term stabilization and sustainable ecosystem management.

Taking the land sparing/land sharing debate to grasslands in cultural landscapes

Nadja K. Simons and Wolfgang W. Weisser
In preparation.

Meeting both the food demand of a rising human population and conservation targets for biodiversity in agricultural landscapes has sparked a debate on whether both demands should be targeted on the same area of land by extensive management (land sharing) or targeted on separate areas by increasing management intensity on one part and preserving natural habitat on the remaining area (land sparing). This debate is however not directly applicable to landscapes which are dominated by managed grasslands, as those need extensive management in order to maintain biodiversity. We adapt the typical scenarios of land sharing and land sparing to managed grasslands and test their potential impact on arthropod diversity. We used abundance data of 1006 arthropod species sampled on managed grasslands in three regions in Germany which represent a range of land-use intensity. Based on the shape of their abundance curves, species were grouped into 'winners' or 'losers' and it was assessed whether species would profit from land sparing or land sharing. As the optimal approach for a species can depend on the minimal land-use intensity applied, we tested a range of minimal land-use intensities. Most species were losers, i.e. their abundance decreased with increasing land-use intensity and most species were assigned land sparing. Most species had simple convex or concave abundance curves, hence the optimal approach for most species did not depend on the level of minimal land-use intensity. However, the number of species which were not found above a given minimal land-use intensity, or only with a very small number of individuals, increased with increasing minimal land-use intensity. This loss of species reached 50% of all rare species already at an intermediate level of land-use intensity. Our results indicate that intensification of land use in grasslands should be restricted to some areas (land sparing) rather than managing the whole area under moderate land-use intensity (land sharing) in order to protect arthropod diversity. Future studies should use our approach in combination with measurements of grassland productivity to bring the land-sharing/land-sparing debate even further towards applicability for grassland-dominated cultural landscapes.

NS and WW conceived the idea for the manuscript and defined the final outline. NS analysed the data and wrote the first manuscript draft. WW commented on all manuscript versions.

Chapter 4

Discussion

Intensification of land use in order to increase productivity has lead to a decrease of diversity in agricultural systems and further intensification threatens to decrease biodiversity even more [Millennium Ecosystem Assessment, 2005; Sala et al., 2000]. This loss of biodiversity decreases the diversity and amount of ecosystem services provided by the agricultural habitats [Cardinale et al., 2012]. Many of those services are directly or indirectly provided by arthropods [Prather et al., 2013], hence it is crucial to protect their diversity within agricultural systems. In order to achieve this target, a thorough understanding of how land-use intensity affects arthropod diversity is crucial. While our knowledge is already profound for some arthropod groups, others are less often studied and there is still a lack of studies in real-world ecosystems which include a wide range of intensity and variety of land-use practices [Joern and Laws, 2013].

This thesis complements the existing knowledge by providing insights into the effect of land-use intensity for a number of grassland arthropod groups which were sampled on a large number of grasslands in three geographic regions, covering the whole gradient of land-use intensity found within those regions. It shows that land-use intensity affects the diversity of arthropods through changes in their resources and that the pathways differ between herbivores and carnivores (Manuscript 1). Not only the mechanisms by which land-use intensity affects arthropods differ between trophic groups, but also the strength of effects varies depending on the species' traits (Manuscript 3). Different land-use modes (fertilisation, mowing and grazing) affect arthropod diversity and community structure differently (Manuscripts 1, 2, 3 & 4), with fertilisation and mowing being closely related in their effect on arthropods. Land-use intensity affects common and rare species differently, leading to changes in the community structure (Manuscript 2), having implications for possible conservation strategies (Manuscript 5).

4.1   Components of land-use intensity

Of the three land-use components considered in this thesis, mowing has the most immediate and devastating effect on arthropods as it removes the complete vegetation layer and most of the vegetation-dwelling arthropod community [Humbert et al., 2009]. Arthropods can adopt different strategies to compensate for the effects of mowing: they can escape mowing if they are good flyers or have other means of fast dispersal, they can avoid mowing either by moving to the ground or by completing their life-cycle prior to the first mowing event (eggs or nymphs can then survive mowing if they are developing near the ground or in non-grassland habitats), and they can sustain their population by fast recolonization after the mowing event (either through individuals which had escaped the mowing event or by individuals from populations in close-by grasslands [den Boer, 1990]). Mowing also has an indirect effect on arthropods by changing plant diversity and community structure towards a plant community which is dominated by fast-growing and disturbance-tolerant species (mostly grasses) and characterised by a homogeneous canopy structure [Socher et al., 2013; Zechmeister et al., 2003].

The studied arthropod communities show several of those adaptation strategies. Average dispersal ability in the community increases with mowing intensity (Manuscript 3) which indicates an advantage of species which can escape mowing or recolonize the grassland faster after a mowing event. With each additional mowing event within the season, this strategy becomes more advantageous and increases the dominance of good dispersers. A higher mowing intensity also leads to a decrease in average body size within the arthropod community (Manuscript 3), indicating an advantage of species with a short life-cycle which are thus more likely to have reproduced prior to the first mowing event compared to large-bodied species with a longer life-cycle. The indirect effects of mowing on arthropod diversity are mediated by a change in plant diversity rather than a change in plant biomass (Manuscript 1). A shift towards an arthropod community which is adapted to grasses is confirmed by a dominance of grass-specialist Heteroptera (Manuscript 3). The conclusion that mowing requires specific adaptations by arthropods is encouraged by the distribution of species among the managed grasslands as many species were not found on mown plots at all, and those who can tolerate mowing were found both at low and high mowing intensities (Manuscript 2).

Grasslands are fertilized to increase their productivity in terms of plant biomass and hence the amount of fertilizer applied is often correlated with the frequency of mowing (Manuscript 1). Although the application of fertilizer leads to a disturbance of the grassland by an immediate and strong increase of nitrogen, it is often done at the beginning of the year or directly after a mowing event and hence its effects on arthropods are consid-

ered to be rather indirect than direct [Tscharntke and Greiler, 1995; Wilson et al., 1999]. This indirect effect and strong link with mowing intensity can consistently be found on the studied grasslands (Manuscript 1, 2 & 3). The strongest effect of fertilization was found on the arthropod community structure, as a high fertilization intensity increases the effects of mowing and grazing intensity on dominance (Manuscript 2). In contrast to mowing, which clearly separates mowing-tolerant from mowing-intolerant species, irrespective of its intensity, fertilization affects arthropods depending on its intensity. Many species were found on grasslands with low fertilizer input but not on grasslands with high fertilizer input (Manuscript 2).

While fertilization and mowing intensity were positively correlated, grazing intensity was mostly negatively correlated with mowing intensity (Manuscript 1), which reflects the typical management decision made for grasslands: grasslands are either mainly used as pastures (this also includes protected grasslands which are often extensively grazed with sheep) or mainly used as meadows to produce hay or silage. On mown pastures, grazing either happens for an extensive time after a first cut in spring or for a short time late in autumn after the last of several mowing events. While grazing does lead to a disturbance of the vegetation-layer simply through the act of grazing, this disturbance is less intense than mowing and does not affect the whole grassland at once. Hence, arthropods do not need to show high dispersal ability or short life-cycles as required on mown grasslands. One example for different adaptations to mowing and grazing can be found in Heteroptera, which are dominated by species with long wings on grasslands with high mowing intensity but dominated by species with increased jumping ability on grasslands with high grazing intensity (Manuscript 3).

Grazing has a strong indirect effect on the arthropod community as it increases the heterogeneity of the vegetation structure and hence provides a variety of niches [Bell et al., 2001; Tscharntke et al., 2005]. While this positive indirect effect of grazing on arthropods has been found for different arthropod groups, the results presented within this thesis show that effects of grazing strongly depend on its intensity and on the livestock type, resulting in mixed effects of grazing when the range of grazing intensities is variable between years (Manuscript 1). Another indication for the negative effect of high grazing intensity compared to low or moderate grazing intensity is the observation that about a third of all arthropod species does fairly well under low grazing intensity (i.e. they showed intermediate abundance) but are not present under high grazing intensity (Manuscript 2). As grazing intensity is closely related to other land-use components in the studied grasslands, it is difficult to draw clear conclusions on the mechanisms of grazing intensity effects on arthropods. Although a number of studies have experimentally tested the effect

of grazing on arthropod diversity, they were often limited in the range of grazing intensity considered or included only one type of livestock. Future studies are therefore needed which test the effect of grazing on arthropods independent of other land-use activities but over a wide range of intensities and livestock types.

Interacting effects of the three land-use components influence both arthropod diversity and community structure (Manuscripts 1 & 2), indicating that overall land-use intensity is driving changes in the arthropod community more strongly than the single land-use components. For example, any combination of land use which leads to a decrease in plant diversity (highly fertilized pastures, frequently mown pastures or highly fertilized meadows) also lead to a strong increase in dominance among arthropods (Manuscript 2). Hence, a reduction in intensity of any land-use component helps to sustain and protect arthropod diversity in grasslands. Nevertheless, the whole range of land-use intensities should be applied within a region in order to provide habitats for specialist species which are adapted to frequently mown or intensively grazed grasslands.

4.2   Aspects of diversity

Species richness (i.e. the number of taxonomically distinct species) is the most fundamental measure of diversity. It is widely used in the assessment of ecosystem health and as a target for conservation policy [e.g. biodiversity hotspots, Myers et al., 2000] because it is an easy to understand and straightforward measure. The number of species in a community also determines the possible range of other measures of diversity such as the number of interactions between species or the number of functions provided by the community.

Additionally, the species richness of one group or trophic level often determines the species richness of interacting groups or trophic levels. While the number of species determines the possible range of interactions or functions (the potential number of interactions or functions is higher for a community of 100 species than for a community of ten species), it is the species' identity which determines the actual number of interactions or functions exhibited (e.g. generalist herbivores interact with more plant species than specialist herbivores) and it is the species' abundance which influences the strength or frequency of interactions (e.g. more pollinator individuals can visit more flowers). Hence, two communities of identical species richness can be completely different in their community composition, abundance structure and functional diversity. Following this notion, the insights gained from the manuscripts included in this thesis will be discussed with

three aspects of diversity in mind: species richness, abundance structure and functional diversity.

4.2.1 Species richness

There are numerous studies and reviews which find a decrease in arthropod richness with increasing land-use intensity (Table 1) and also many studies which relate this decrease in richness to changes in lower or higher trophic levels [Bell et al., 2001; Dennis et al., 2007; Swengel, 2001; Weiner et al., 2011; Wilson et al., 1999]. In accordance to those studies, I found an indirect effect of land-use intensity on arthropod species richness through changes in their resources (Manuscript 1). This indirect effect is mediated by plant species richness for herbivores, indicating that specialized species lose their resources and cannot fall back on other plant species. The proportion of monophagous species (i.e. species which feed on one single plant genus) among herbivores indeed decreases with increasing land-use intensity (Manuscript 3).

Although increasing land-use intensity clearly leads to a loss of species, this does not mean that extensively used grasslands harbour the complete species pool from which species get lost depending on their tolerance against land-use intensity. In fact, a number of arthropod species can be found only under intermediate or intensive land use and not under low land-use intensities (Manuscript 2) and about 40% of the common species increases in their abundance with increasing land-use intensity (Manuscript 5). Those species which become part of the community under high land-use intensity compensate the loss of other species, which means that more species are lost with increasing land-use intensity as the change in number of species reveals. The loss of species with increasing land-use intensity is especially severe for rare species, with about half of those species not being found after an increase to half of the maximum land-use intensity (Manuscript 5).

4.2.2 Abundance structure

Virtually all communities consist of few very abundant and many less abundant (rare) species, with the rare species being often the main focus of conservation [McGill et al., 2007]. In general, a species can be rare due to three different factors: geographic range, habitat tolerance and population size [Rabinowitz, 1981]. Contrasting the two extremes of each of those three factors (i.e. extensive vs restricted range, broad vs narrow habitat tolerance, large vs small population size) results in *seven types of rarity* (Table 4). With each additional factor being low for a species, this species becomes more rare and the rarest species has a restricted geographic range, narrow habitat tolerance and a small

Discussion

Table 4 Number of arthropod species among the seven forms of rarity defined by Rabinowitz [1981]. Geographic range is based on the number of regions in which a species was found (broad = more than one region); Habitat tolerance is based on the range of land-use intensity a species was found under (narrow = only highest or lowest third of land-use intensity); Population size is based on the total number of individuals sampled between 2008 and 2012 (small = fewer individuals than average=111 individuals). Bold text highlights aspects of rarity.

No. species	Geographic range	Habitat tolerance	Population size	
93	Extensive	Broad	Large	Common
3	**Restricted**	Broad	Large	|
0	Extensive	**Narrow**	Large	|
355	Extensive	Broad	**Small**	|
0	**Restricted**	**Narrow**	Large	|
269	**Restricted**	Broad	**Small**	|
28	Extensive	**Narrow**[a]	**Small**	V
287	**Restricted**	**Narrow**[b]	**Small**	Rare

a = all species only found under lowest land-use intensity
b = 240 species only found under lowest land-use intensity

population size. Within the context of this thesis, geographic range can be defined as the number of regions a species was found in, and habitat tolerance can be defined as the range of land-use intensity under which a species was found (only under low/high land-use intensity or across the whole gradient). The resulting number of species among the *seven types of rarity* is shown in Table 4.

Of the 1035 arthropod species sampled between 2008 and 2012, the majority has a population size smaller than the average over all species. This over-representation of rare species across communities reflects the typical abundance distribution within in a community [McGill et al., 2007]. Among species with a small population size, about two third are found only in one region and about half of those species have a narrow habitat tolerance. Independent of their population size, four groups of species can be identified: species which occur over the whole range of land-use intensity and in more than one region (448 of 1035 species) or in only one region (272 species); species which occur only under low or high land-use intensity and in more than one region (28 species) or in only one region (287 species). The first two groups are very likely not affected by an increase in land-use intensity, provided that their population size is similar across the range of land-use intensities. However, this is not the case for many species, because about half of the common species can be found with less than two individuals per plot across a wide range of land-use intensities (Manuscript 5) and many species which are relatively abundant under low land-use intensity are rare under high land-use intensity (Manuscript 2). Without stable source populations, those species can easily become lost from a grassland through

stochastic effects even without a change in land-use intensity. In contrast to the first two groups, the species in the latter two groups are much more threatened by increasing land-use intensity, because the majority of species with a narrow habitat tolerance were only found under low land-use intensity. Additionally, almost all of the species which are restricted to low land-use intensity were found in only one region (Table 4), suggesting that their occurrence is also restricted by climatic or other abiotic conditions. Future studies should therefore evaluate the geographical distribution of the species among the rarest of the *seven types of rarity* in order to assess whether a species' occurrence within the three studied regions reflects the range of its distribution (i.e. if a species could find suitable conditions in a region given that its requirements for land-use intensity are met). Another dimension of rarity is a species' occurrence over time. A species would be considered common if it were found at each time of observation (e.g. each week over the whole season or each year) and be considered rare if it were only found at some of the observed time points. One famous example is the genus *Magicicada* spec.: Adults from this genus emerge in large numbers after a developmental phase of 13 to 17 years in deciduous forests across the eastern United States [Williams and Simon, 1995]. While the species in this genus have an extensive geographical range, a more or less broad habitat tolerance and large population sizes, they rarely occur as reproducing adults. Due to their wide distribution and large population sizes they are not likely to become extinct even if they would face a strong disturbance (e.g. a wildfire) during their rare occurrence. At the same time, such a coinciding disturbance would affect a rarely occurring species, which is also restricted in its distribution, habitat tolerance and population size, quite differently.
The presence of such rare species within the studied arthropod communities is far from being negligible. In fact, 208 out of the 287 species which fall into the rarest type of rarity (Table 4) were only found in one of six years. The absence of those species in the other five years can have various reasons. Firstly, a small population size decreases the chance of an individual being sampled even though the species is present at all sampling times. Secondly, the species can have a long developmental cycle and hence be present as adults only after a number of years. Or a species' occurrence within the season does not regularly coincide with the sampling dates. Therefore, long-term studies are needed to determine the 'true' rarity of a species and its importance for community stability.

Community stability is essential for the reliable provisioning of ecosystem services [Cardinale et al., 2012; Loreau et al., 2001] and it is hence important to understand how global changes (including land-use intensification) are affecting community stability [Hautier et al., 2014]. In principle, stability increases with a higher asynchrony between species and

with more species in the community (because the probability increases that two species vary asynchronously). An equally important factor is the abundance structure of the community because the overall variability will be strongly determined by the most abundant species, hence measures of asynchrony and diversity should incorporate abundance. Of the many definitions of community stability available [Ives and Carpenter, 2007], the one which was used within this thesis is the 'portfolio effect' (Manuscript 4). The 'portfolio effect' is a measure of the difference between the fluctuation of the whole community and the average fluctuation of the single species in a community [Thibaut and Connolly, 2013].

Asynchrony between species contributes most strongly to the community stability of grassland arthropods, followed by diversity. Interestingly, higher land-use intensity (especially mowing intensity) increases the asynchrony between species and therefore contributes positively to community stability. However, this result is driven by herbivorous species, whereas land-use intensity strongly decreases the diversity of carnivorous species and thereby reduces community stability in predators (Manuscript 4). As unexpected the positive effect of land-use intensity on the stability of the herbivore community might be, as well does it fit with the other results gained within this thesis: As stated before, the most abundant species contribute most strongly to community stability. As an increase in land-use intensity leads to an increased dominance of the most abundant species (Manuscript 2), their influence on community stability becomes stronger. Those species which are the most abundant within and among the communities are also those species which are tolerant to different levels of land-use intensity or even adapted to intensively used grasslands as the different types of rarity (Table 4) and the results in Manuscript 2 show. Most of these species are specialists on grasses (Manuscripts 2 & 3), with large population sizes in intensively used grasslands (Manuscript 1). Predator communities are in contrast more dependent on heterogeneous habitat structures [Bell et al., 2001] which provide more niches and therefore also sustain more even communities [Joern and Laws, 2013]. These contrasting effects of land-use intensity on community stability between different trophic groups emphasizes the need for a differentiated look at the effects of land-use intensity. While it is important to analyse effects for a broad range of groups in order to draw general conclusions, it is equally important to evaluate the effects of land-use intensity for specific groups (either taxonomic or functional).

4.2.3 Functional diversity

The importance of functionally diverse communities for ecosystem stability and the provisioning of ecosystem services is widely recognized. The functional diversity of a community is determined by the diversity of functional traits present within a community. Although the use of functional traits is common for plants, the definition of a functional trait –especially for animals– is still subject to debate. In one influential paper, McGill et al. [2006] called for community ecology to go back to the evaluation of traits and their changes over environmental gradients. They defined traits as any *"well-defined, measurable property of organisms [which] should vary more between than within species and preferably be measured on continuous scales"* [McGill et al., 2006]. Any trait which affects a species' performance is then considered a **functional** trait. Quite similar is the definition by Violle et al. [2007], who defined functional traits as *"any [morpho-physio-phenological] trait which impacts fitness indirectly via its effect on growth, reproduction and survival"* [Violle et al., 2007]. They also defined two additional types of traits, namely **response** traits which *"vary in response to changes in the environmental conditions"* and **effect** traits which *"reflect the effects of a plant on environmental conditions, community or ecosystem properties"* [Violle et al., 2007].

Although originally developed for plants, the definition of traits *sensu* [Violle et al., 2007] is widely used in studies on the traits of animals (vertebrates as well as invertebrates), but has also been criticised and extended. Instead of comparing resource-centred ecological guilds (i.e. trophic groups) among animals and separating response and effect traits, Blaum et al. [2011] proposed the definition of **core** traits which are *"describing [a] species' dependency on their habitat as well as life history traits that are related to the process of birth, survival and movement"* [Blaum et al., 2011]. The definition of a functional trait as being a trait which affects the performance or survival of a species has recently been criticised as not being useful, especially in the context of ecosystem services: *"All traits within an organism are 'biological', meaning, they are crucial for the fitness and performance of the organism; but not all traits are 'functional', meaning, not all are significantly modulating ecosystem processes"* [Mlambo, 2014]. Other authors are not as harsh in their critique and rather consider the definition of [Violle et al., 2007] not broad enough in the context of arthropods and propose to add *"ecological performance traits or traits quantifying how well an individual survives in an environment"* [Fountain-Jones et al., 2015]. While Fountain-Jones et al. [2015] recognize that ecological performance traits are derived from different individual traits *sensu* Violle et al. [2007], they emphasize that there is still a lack of knowledge on which individual traits influence performance in animals and hence the evaluation of ecological performance traits is useful in order to develop and promote

the use of functional traits in animals.

Despite their different definitions, all authors agree that functional traits have to be linkable to a function, be it the species' reproductive fitness, its ability to respond to changes in the environment or its effect on other components of the ecosystem. In the context of global changes and their effect on community diversity, stability and function, all traits are therefore of interest which determine a species' reaction to a change in the environment, be it that its traits give it the ability to cope with the changes or that they make it especially vulnerable and therefore of special interest to conservation. Given that the evaluation of changes in traits under global change is still in its infancy for animals, any trait which shows variation across communities should be considered as being potentially functional. This consideration closely follows the appeal that the variation of traits across environmental gradients and communities should be returned to the focus of community ecology [McGill et al., 2006].

Two of the traits considered in this thesis (feeding guild and stratum use) are based on ecological guilds which are typically defined based on the resources used by a species [Blaum et al., 2011]. For arthropods which use different food resources (i.e. herbivores and predators), different mechanisms lead to a decrease in diversity under intensive land use. While herbivore diversity decreases with plant diversity, predator diversity decreases because the amount of available resources (biomass of herbivores) decreases (Manuscript 1). This decrease in biomass can either be due to a lower abundance of herbivores of all sizes or due to an unproportional loss of large species. While the decrease in average body size in the whole community under intensive land use suggests a loss of large species, this loss was mainly driven by spiders and rather weak among herbivores (Manuscript 3). Future studies would hence need to disentangle the effects of abundance and body size on higher trophic levels to inform the decision whether conservation should aim towards conserving a high abundance or a specific type of resources for predators. Predators should also be a target for conservation efforts in that they are over-represented among rare species and among species which occur only under low land-use intensity (Manuscript 2).

While the evaluation of herbivores vs predators draws a picture of herbivores being only little affected in their abundance by land-use intensity (Manuscripts 1 & 2), this picture is incomplete if herbivores with different resource requirements are considered together. In fact, the community composition among herbivores changes strongly with land-use intensity. The relative abundance of monophagous herbivores decreases with higher fertilization and grazing intensity (Manuscript 3) which can be attributed to a loss of resource diversity (Manuscript 1). However, higher mowing intensity promotes monophagous

herbivores which are specialists on grasses (Manuscript 2), indicating a complete shift in the herbivore community composition which does not become apparent when herbivores are considered as one group.

This shift in the community composition of herbivores as a reaction to changes in plant community composition is also the crucial mechanism which leads to a decrease in invertebrate herbivory under intensive land use [Gossner et al., 2014]: Increasing land-use intensity increases the dominance of grasses within the plant community (Manuscript 1) which leads to a decrease in herbivore diversity and a shift towards grass-specialists among herbivores (Manuscripts 2 & 3). As herbivory is generally lower on grasses compared to dicotyledons [Gossner et al., 2014], this shift in plant and herbivore community composition leads to an overall lower herbivory. In what way a change in plant quality (e.g. nutrient content) with land-use intensity [e.g. through fertilisation; Klaus et al., 2011] additionally influences herbivory needs however further investigation.

Apart from being grouped based on feeding guilds, arthropods can be grouped based on the resources used for hunting, oviposition, shelter and others. These resources will determine in which part of the habitat a species can be found. In the context of grasslands, this can be the soil or ground (including the litter layer), short vegetation (grasses and dicotyledons) or tall vegetation (shrubs or trees). Due to the limited number of species among the studied arthropods which are not associated to the main vegetation layer –given that the sampling was done by sweep-netting– effects of land-use intensity on stratum use were not profound. However, the proportion of shrub-and tree-associated species decreases with increasing land-use intensity (Manuscript 3), indicating that their presence in grasslands is promoted by shrubs and trees within extensively used grasslands. Many arthropod species switch their main habitat during their development, e.g. larvae of many species in the family Cerambycidae (Coleoptera) develop in dead wood but their adults feed on pollen of plant species which are found in open habitats [Gossner et al., 2015a]. For those species, it is crucial that both habitat types are not too distant from each other. Landscape composition also plays an important role under scenarios of increasing land-use intensity for species with a small dispersal ability. Whenever a management activity (e.g. mowing) disturbs the grassland and the inhabiting arthropods, those species which can distribute faster or over longer distances will have an advantage over other species [den Boer, 1990]. The more frequent such disturbances and recolonization events are on a grassland, the greater this advantage of high dispersal ability should become. In fact, the average dispersal ability among arthropods increases with increasing land-use intensity, especially with mowing intensity (Manuscript 3). This negative effect of inten-

sive land use on species with low dispersal ability can be dampened by an increase in landscape diversity (i.e. its heterogeneity which reduces the average distance between similar habitat types) [Tscharntke et al., 2005]. This effect was found for beetles [Liu et al., 2014] and a range of arthropod groups (Gámez-Virués et al., unpublished data) in our study system. Future studies, which not only consider the potential of active dispersal in a species but also test the actual dispersal activity and dispersal range of species, will further improve our knowledge of the influence of landscape composition on local diversity and community composition.

As reviewed by Fountain-Jones et al. [2015] and shown by many other studies [e.g. Birkhofer et al., 2015; Börschig et al., 2013; Dziock et al., 2011]), the use of ecological groups and functional traits (however they are called or defined) in arthropods has significantly advanced our understanding of the mechanisms in community composition and effects of environmental change. But some challenges still remain in the use of functional traits for arthropods [Fountain-Jones et al., 2015] and future studies should make use of functional traits which are comparable between groups and collected according to a standardized framework. Another way forward in the use of functional traits in animals is the measurement of ecomorphological traits (or morphometric traits) across environmental gradients which follows the original appeal by McGill et al. [2006] to identify important traits by their variability. Measuring morphometric traits across a range of sites is labour-intensive, but initially focusing on one taxonomic group can reveal traits which might be important in other groups as well. For example, the average body volume of Heteroptera species reacts much more strongly to land-use intensity than the average body length, and changes in the average wing length and leg shape in Heteroptera reveal that dispersal over longer distances is important in mown grasslands and that good jumping ability is important under intensive grazing (Manuscript 3).

4.3   Conclusion

Increasing land-use intensity in temperate grasslands reduces the diversity of many organismal groups, including arthropods. I was able to show that this reduction in diversity is not only leading to a reduction in species richness, but also to changes in the community structure and functional composition of arthropods. However, a large-scale reduction of land-use intensity is neither economically feasible, considering growing demands for agricultural products, nor does it protect the diversity of specialized grassland communities. Based on my findings, different management strategies can be expected to maintain or enhance arthropod diversity on managed grasslands: At the local scale of

single grasslands, the exclusion of patches from management (especially from mowing) provides a 'safe haven' for disturbance-intolerant species and species with a long life-cycle. Grazing with intermediate intensity creates a heterogeneous vegetation structure which especially promotes predator abundance and diversity. Herbivores which are specialized on herbs can be protected by sowing additional plant species into species-poor intensive grasslands. Adding shrubs or trees at the margins of grasslands can provide shelter for vegetation-dwelling arthropods as well as crucial habitat for species with different resource requirements during their life-cycle. All those local strategies should however be coordinated within the landscape context to provide benefits for a larger area. An ideal landscape for high arthropod diversity includes a range of land-use intensities, from extensively grazed pastures to grasslands with a high productivity and abundance of grasses. Extensively used grasslands should be close enough or connected to intensively used grasslands to facilitate recolonization by arthropods with low dispersal ability. This landscape-level perspective is especially important as the loss of species with low dispersal ability was not only one of the pronounced changes discovered in my research, but is also found by an increasing number of other studies. In the end, a high arthropod diversity in grasslands will not only improve the ecosystem services provided by the grasslands, but also benefit the diversity of other trophic levels (e.g. birds) and have positive effects for other habitats close to the grasslands (e.g. through pollination or pest control).

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Appendix A

Curriculum Vitae

First name: Nadja Katharina
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Education

Oct 2011–Apr 2015 PhD student at Technische Universität München.

Thesis: Effects of land-use intensity on arthropod diversity and community structure in grassland

Oct 2009–Sep 2011 M.Sc. in Biology at Justus-Liebig Universität Giessen

Thesis: Impact of elevated CO_2 on phenology, community structure and pollinators in a permanent grassland

Oct 2006–Sep 2009 B.Sc. in Biology at Carl-von-Ossietzky Universität Oldenburg

Thesis: Lightfleck-usage by epiphytes and terrestrial plants in a tropical understorey

Publications

- Martin M. Gossner, Nadja K. Simons, Roland Achtziger, Theo Blick, Wolfgang H.O. Dorow, Frank Dziock, Frank Köhler, Wolfgang Rabitsch & Wolfgang W. Weisser (2015): A summary of eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in grasslands in Germany. *Scientific Data* **2**:150013.

- Martin M. Gossner, Nadja K. Simons, Leonhard Höck & Wolfgang W. Weisser (2015): Morphometric measures of Heteroptera sampled in grasslands across three regions of Germany. *Ecology* **96**(4):1154.

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- Nadja K. Simons, Martin M. Gossner, Thomas M. Lewinsohn, Steffen Boch, Markus Lange, Jörg Müller, Esther Pašalić, Stephanie A. Socher, Manfred Türke, Markus Fischer & Wolfgang W. Weisser (2014): Resource-mediated indirect effects of grassland management on arthropod diversity. *PLoS ONE* **9**(9):e107033.

- Nadja K. Simons, Martin M. Gossner & Wolfgang W. Weisser: Land-use intensity and arthropod functional diversity in grasslands. *44th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland.* Hildesheim 09/2014

- Nadja K. Hersacher, Martin M. Gossner, Thomas M. Lewinsohn & Wolfgang W. Weisser : Land-use intensity in semi-natural grasslands indirectly affects arthropod diversity through changes in resource diversity or abundance. *43rd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland.* Potsdam. 09/2013

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