ZENTRUM
FÜR BIODIVERSITÄT UND NACHHALTIGE LANDNUTZUNG
SEKTION
BIODIVERSITÄT, ÖKOLOGIE UND NATURSCHUTZ

– CENTRE OF BIODIVERSITY AND SUSTAINABLE LAND USE –

SECTION: BIODIVERSITY, ECOLOGY AND NATURE CONSERVATION

Plant-herbivore-predator communities and grassland management intensity

—

Implications for biodiversity conservation practices on local and landscape scales

Dissertation zur Erlangung des Doktorgrades der
Mathematisch-Naturwissenschaftlichen Fakultäten der
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vorgelegt von

Dipl.-Biol.

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Tag der mündlichen Prüfung: 19. März 2012

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Deutsche Zusammenfassung

Das schnelle Wachstum der Weltbevölkerung ist verbunden mit steigendem Bedarf an Energie, Nahrung und Agrarprodukten, wodurch sich der Druck auf Ökosysteme weltweit erhöht. Die damit einhergehende Zerstörung und Modifizierung von terrestrischen Ökosystemen sind einer der Hauptgründe für den Klimawandel und werden begleitet von einem dramatischen Verlust an biologischer Diversität. Wir benötigen effektive Managementstrategien um ein Gleichgewicht zwischen Artenschutz und landwirtschaftlicher Produktion zu schaffen.

In dieser Arbeit untersuchen wir, wie sich direkte und indirekte Effekte von Landnutzungsintensivierung in Graslandökosystemen dreier Regionen Deutschlands auf die Diversität und Abundanz von pflanzenfressenden und räuberischen Insektengemeinschaften auswirken. Wir evaluieren den Einfluß von Landschaftsstruktur, und –zusammensetzung auf die Ausbreitung (spillover) von Schädlingspopulationen aus Anbauflächen auf Grasländer und die möglichen Folgen für den Fruchtansatz von Wildpflanzen. Abschließend geben wir Vorschläge für Maßnahmen zum Schutz von Biodiversität auf lokalen und landschaftsweiten Skalen.

Kapitel 1 stellt die einzelnen Themengebiete dieser Arbeit vor. In **Kapitel 2** zeigen wir in einem großräumigen Experiment in drei Regionen Deutschlands entlang eines 600 km Nord-Süd Gradienten, wie Landnutzungsintensivierung die Diversität und Abundanz von herbivoren Insektengesellschaften reduziert. Mahdhäufigkeit wirkte sich negativ auf Vegetationshöhe und Pflanzendiversität aus und war ein Schlüsselfaktor für den Diversitätsrückgang von pflanzenfressenden Insekten. Räuber waren nicht direkt von Landnutzung beeinflusst, jedoch von der Artenvielfalt an Herbivoren abhängig. Das experimentelle Einrichten einer kleinen Brachfläche erhöhte innerhalb eines kurzen Zeitraums die Herbivorendiversität, was folglich zu einem Anstieg der Predatorendiversität entlang der Nahrungskette führte. Interessanterweise stieg die Effizienz dieser Schutzmaßnahme mit dem Grad an landwirtschaftlicher Intensivierung und insbesondere mit der Mahdhäufigkeit. Es zeigte sich, dass das Einrichten von einjährigen Brachen auf zuvor intensiv bewirtschafteten Grasländern eine einfache und wirksame Methode zum Schutz und Erhalt von Habitatheterogenität und Artenvielfalt darstellt.

Kapitel 3 zeigt den Zusammenhang zwischen Graslandmanagement, Pflanzenhöhe und Besiedlungserfolg von spezialisierten Stängel-minierenden Insekten an Gräsern. In dieser Untersuchung war die Pflanzenhöhe eine Folge von kontinuierlichem Management, einjährigem Managementauschluß, oder einer mehrjährigen Stilllegung von Subplots auf Wiesen und Weiden. Wir zeigen, dass eine managementbedingte Verkürzung der Grashalme die Abundanz von herbivoren Insekten reduzierte. Besonders auf den Flächen mit durchgehendem Management kam es zu einer deutlich höheren Überlappung der artspezifischen Befallshöhen, was möglicherweise auch die räumliche Einnischung für gleichzeitig vorkommende Arten begrenzt. Eine mittlere Halmlänge auf den mehrjährig stillgelegten Bereichen von über 1 m war der Schwellenwert für den Besiedlungserfolg von zwei von drei Arten. Grasrandstreifen, ausgeschlossen von Beweidung und Mahd für mindestens zwei Jahre, haben einen hohen Wert für Stängel-minierende Insektengemeinschaften und könnten geeignete Habitate für die Wiederbesiedelung von Grasinseln auf bewirtschafteten Flächen darstellen.

Kapitel 4 stellt die Ergebnisse eines Grasland Phytometer Experiments vor, das skalenabhängige Spillover-Effekte von Rapsglanzkäfern (*Brassicogethes aeneus*) auf Grasländer misst. Ausserdem wurde der Fruchtansatz von Insektizid behandelten und unbehandelten Ackersenf (*Sinapis arvensis*) Pflanzen infolge von Fraßschäden aufgenommen. Das Experiment wurde auf 20 Graslandplots durchgeführt, die aufgrund ihrer unterschiedlichen Anteile an Rapsflächen innerhalb acht konzentrischer Kreise (Radius 250 bis 2000 m) um ihre Plotmittelpunkte ausgesucht wurden. Wie unsere Ergebnisse zeigen, beeinflusst die schwankende Ressourcenverfügbarkeit auf den Anbauflächen die Ausbreitung von Rapsschädlingen auf unterschiedlichen räumlichen Skalen. Ackersenf in der direkten Umgebung (250 m) von Rapsflächen war zuerst und am stärksten von Schädlingsbefall betroffen, da der Fraßschaden mit der Distanz zu den Rapsfeldern abnahm. Daher sollte eine minimale Distanz von 250 m zu großflächigen Rapsmonokulturen die negativen Effekte von Kulturpflanzenschädlingen auf Wildpflanzen (aus derselben Familie) in Grasländern reduzieren.

Zusammengenommen zeigen die in dieser Arbeit vorgestellten Ergebnisse, dass die Intensivierung von Landnutzung die Diversität und Abundanz von

Insektengemeinschaften in Grasländern sowohl über direkte als auch indirekte Effekte herabsetzt. In allen Regionen waren die Mahdhäufigkeiten ausschlaggebend für den Verlust an Biodiversität. Die Ausbreitung von Kulturschädlingen auf Grasländer steigt mit dem Anteil von Rapsflächen in direkter Umgebung an und kann den Fruchtansatz bei Wildpflanzen reduzieren. Daher sollte eine minimale Distanz zwischen Monokulturen und besonders artenreichen Habitaten (z.B. Kalkmagerasen) eingehalten werden. Des Weiteren zeigen wir, dass kleinräumig eingerichtete Sukzessionsinseln (Brachen) effektive Refugien für die Diversität von Herbivoren und Prädatoren sind. Da die Effizienz dieser Maßnahme mit (i) Landnutzungsintensität und (ii) Dauer ansteigt, erwarten wir den größten Nutzen einer Flächenstillegung auf intensiv bewirtschafteten Grasländern.

English Summary

The rapid growth of the human population and the concomitant demands for fuel, food and agricultural products put increasing pressures on ecosystems around the world. This has become a major driver of global environmental change, resulting in the destruction or modification of natural terrestrial ecosystems, often followed up by dramatic losses in biological diversity. Effective management strategies are needed, balancing biodiversity conservation and agricultural production.

In this thesis, we analyse the direct and indirect influences of local land use intensification on diversity and abundance patterns of herbivore and predator insect communities in natural grassland ecosystems across three different regions in Germany. We assess landscape composition and configuration effects on pest insects spilling over from crop fields to grasslands, affecting fruit set of wild plants. Finally, we conclude with suggestions for biodiversity conservation practices on local and landscape scales.

Chapter 1 gives an overview of the topics covered in this thesis. In **Chapter 2**, we use the framework of a large-scale and multi-site experiment, located in three regions of Germany along a 600-km north-south gradient, to show that local land use intensification reduces diversity and abundance of the herbivore community consistently across all study regions. Mowing frequency, affecting vegetation height and local plant species richness, excelled as key predictor of declines in herbivore diversity. Predators were bottom-up controlled via herbivore diversity and not directly influenced by management intensification. Experimentally established short-term and small-scale succession enhanced herbivore diversity, which in turn increased predator diversity via bottom-up effects. Interestingly, efficiency of this conservation practice increased with land use intensity, in particular with mowing frequency. Temporarily allowing successional subplots on intensively used grasslands appeared to be a low cost but high benefit conservation measure introducing and sustaining habitat heterogeneity and insect diversity despite of ever changing land use practices and environmental conditions.

Chapter 3 relates management-induced reduction in host plant height to colonization success of specialized grass-shoot miners. In this study, changes in host

grass heights resulted from experimentally excluding subplots from management (1-year set aside) or of an *a priori* selection of continuously managed and already abandoned (≥2-year set-aside) grassland patches. We show that abundances of herbivores are negatively affected by a management–induced reduction in host shoot length over time. Especially on continuously managed grasslands, overlaps in attack heights between species increased, potentially narrowing spatial niche width for co-occurring species. Mean grass shoot length above 1 m in the abandoned areas was a threshold, boosting colonization success for two out of three species. We conclude that implementation of small grassy strips e.g. located at grassland edges, excluded from grazing and mowing for at least two years should be highly effective in supporting a diverse and abundant insect community and may provide suitable refuges from which stem-borers can re-colonize sward islets on managed grasslands.

Chapter 4 presents a grassland phytometer experiment that quantifies scale dependent crop-noncrop spillover of rape pollen beetles (*Brassicogethes aeneus*) and fruit set of insecticide-treated and untreated wild mustard plants (*Sinapis arvensis*) as a consequence of herbivore damage. We used a set of 20 grassland plots along a gradient of increasing proportion of oilseed rape (OSR) within eight circles (with 250 to 2000 m radius) around the centre of each plot. Our results show that pest insect spillover from crop fields is triggered by pulsing availability of mass-flowering crops at different spatial scales. Mustard in the direct neighbourhood of cropland (250 m) suffered first from increased herbivore spillover since damage increased with decreasing distance from crop fields after mass-flowering peak of crops. Thus, a minimum distance of 250 m between large crop monocultures and wild plants (of the same family) in grasslands may reduce potentially negative herbivore spillover effects.

Taken together, the results presented in this thesis provide evidence that land use intensification reduces diversity and abundance of insect communities in grasslands via direct and indirect effects. Mowing frequency excelled as a key driver of herbivore diversity decline in all three regions. Pest insect spillover across the crop-noncrop interface increases with higher proportions of crop fields at small spatial scales and can reduce fruit set in wild plants, suggesting to keep a minimum distance between crop monocultures and habitats when high biodiversity (e.g. on

calcareous grasslands) needs to be protected. We further show that even small and easily set up successional islets on meadows and pastures can serve as important refuges for the diversity of herbivores and associated predators. Since the efficiency of this conservation practice increases with (i) land use intensity and (ii) duration, we expect the highest benefit of long-term grassland set-asides on intensively managed grasslands.

CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

Biodiversity and ecosystem functioning in the face of a changing world

Global human population is growing rapidly, lately exceeding the seven billion mark, and projected to increase to 9.2 billion by the year 2050 (Population Reference Bureau 2006). Society's concomitant increasing demand for fuel, food and agricultural products (Tilman et al. 2002) puts pressure on ecosystems around the world and became a major driver of global environmental change (Tilman et al. 2001a). This nexus has led to increasing destruction ("land clearing") or modification of natural terrestrial ecosystems. Nowadays, more than half of the earth's surface is covered with agricultural fields, managed forests and grasslands or urban areas (Gaston & Spicer 2004), a development followed up by dramatic declines in biological diversity (Sala et al. 2000).

The human need for maintaining biodiversity is often driven by ethical and aesthetical reasons and finds expression in increasing "ecotourism" across Earth's most diverse regions like Neotropical rain forests. Apart from that, preserving single species and associated genetic diversity can have a direct value when it comes to scientific interest, e.g. for species taxonomists or as resource for the challenges in future genetic engineering of pest resistant plant varieties. However, the Earth will retain its most striking feature, its biodiversity, only if we realize the extent to which we use biodiversity (Tillmann 2000).

Biodiversity provides services of economic interest to agriculture, such as biomass production (Tilman et al. 2001b), nutrient retention, the regulation of water flows, crop pollination and pest control (Hooper et al. 2005, Kremen 2005), thereby maintaining ecosystem stability and securing resources for food and industrial production (Ehrlich & Ehrlich 1992, Tilman 2000). Local intensification of land use and ongoing fragmentation and destruction of natural or semi-natural habitats on a landscape scale, are considered as the most severe threats to biodiversity (Fahrig 2003, Sala et al. 2000, Foley et al. 2005) and connected to declines in ecosystem services (Kleijn et al. 2009, Vitousek et al. 1997) and functioning (Loreau et al. 2001, Balvanera et al. 2006). Many ecosystem processes that humans rely on are associated not only with component species but particularly with species interactions, such as crop pollination and biological control of herbivores (Kearns et al. 1998, Van der Putten et al. 2004). The importance of conserving these ecosystem processes has been stressed repeatedly (Ehrlich & Ehrlich 1992, Tilman 2000) and effective strategies are urgently needed to balance biodiversity conservation and agricultural production (Fischer et al. 2008).

Herbivores and predators as functional groups

Phytophagous insects comprise one quarter of all existing organisms (Strong et al. 1984, Mayhew 2001) and play a crucial role in shaping ecosystems in interaction with plants (Weisser & Siemann 2004). On the one hand, herbivory as an ecosystem function can reduce plant biomass and productivity (Matson et al. 1997); mass-outbreaks of pest insects like pollen beetles on crop monocultures can even cause serious yield losses of over 80 % on oilseed rape fields (Hansen 2004). On the other hand, increasing (non-pest) herbivore populations can provide resources for higher trophic levels and may positively affect predators (i.e. biocontrol agents) through bottom-up trophic cascades from plants via herbivores to predators (Scherber et al. 2010). However, environmental changes causing shifts in one or both functional groups can cause instability of ecosystem functioning (Chapin et al. 1997).

Land use intensification affecting plant-herbivore-predator communities

Local land use effects

About half of Europe´s farmland is managed as grassland pasture or hay meadow (Minns et al. 2001). Increasing management intensification on grasslands by means of grazing, fertilization and mowing is a key factor influencing biodiversity in grasslands (Plantureux et al. 2005) in various ways. Management practices like intensive grazing and cutting directly affect resource availability for herbivores (Danell & Huss-Danell 1985) by reducing plant biomass and can mechanically harm and kill individuals (Humbert et al. 2010). On the long-term, land use intensification can alter plant species composition (Fédoroff et al. 2005, Dumont et al. 2011) and plant architecture (Danell & Huss-Danell 1985, Price et al. 1987) e.g. by promoting grasses such as cocksfoot (*Dactylis glomerata*) that are able to produce short leaves and flowering shoots (Brock et al. 1996). Management-induced fluctuations in the herbivore guild may further cascade up the food chain and be passed to predator populations. Thus, a deeper understanding of herbivore and predator functional group responses is needed to develop efficient management practices enhancing insect communities in human-dominated landscapes.

Landscape context effects

Grassland habitats are often considered as refuge habitats for insects in agricultural landscapes after crop harvesting (see Rand et al. 2006) and some calcareous grasslands rank among the most species-rich in Central Europe (Poschlod et al. 2002; Van Swaay 2002). The expansion of agricultural areas, e.g. by widespread planting of biofuel crops, reduces habitat diversity at larger spatial scales (Turner 1989, Wrbka et al. 2004) and may affect distribution patterns of highly mobile insects (Rand et al. 2006). Especially in agricultural mosaic landscapes, mobile organisms can use resources across the crop-noncrop interface, thereby influencing patterns of important plant-insect interactions (Kareiva & Wennergren 1995, Hooper et al. 2005) such as pollination (Diekötter et al. 2010) and herbivory (Wrbka et al. 2004). Current studies mainly focus on how mobile organisms like pollinators or predators occurring in managed areas benefit from neighbouring natural habitats (e.g. Rand et al. 2006, Ricketts et al. 2008, Holzschuh et al. 2010). In contrast, little attention has been given to organism flow in the opposite direction (reviewed in Blitzer et al. 2012) and even though it has been predicted by existing theories (Tscharntke et al. 2005, Rand et al. 2006), information on insect spillover from crop fields to adjacent semi-natural habitats is still rare (but see Rand & Louda 2006, Gladbach et al. 2010).

However, mass spillover of pest insects from monoculture fields may strongly increase herbivore damage at noncrop habitats, thereby directly affecting reproductive success and long-term altering species composition of native plant communities occurring on grassland habitats embedded within an agricultural landscape. Given the multiple links between agriculture and biodiversity, research on integrating both sides by applying appropriate conservation measures has become a key subject in modern ecology (Tilman 2000, Kremen 2005, Balmford et al. 2005, Matson & Vitousek 2006, Dorrough et al. 2007, Vandermeer & Perfecto 2007).

RESEARCH OBJECTIVE AND HYPOTHESIS

The general scope of our subproject integrated into the Biodiversity Exploratories research platform was directed at multiple aspects of small- and large-scale land use intensification effects on herbivore and predator insect communities in grasslands. We further assessed landscape composition and configuration effects on distribution patterns of pest insects from crop fields, spilling over on grasslands as well as its impact on fruit set of wild plants. Finally we give implications for biodiversity conservation practices on local and landscape scales. This thesis is centred around four major blocks of questions, addressed in one or several chapters:

Block A: Land use and management effects on herbivores and predators

Q A1*: Does grassland management intensity consistently and negatively affect diversity and abundance across different regions? (Chapter 2)*

Q A2*: Which local management practices affect diversity and abundance the most? (Chapter 2)*

Block B: Influence of vegetation characteristics on herbivores

Q B1*: Does plant species richness enhance diversity and abundance? (Chapter 2)*

Q B2*: Do taller plants facilitate colonization success? (Chapters 2 and 3)*

Block C: Landscape composition and configuration effects on herbivores and plant damage

Q C1*: Can crop fields in the surrounding landscape facilitate spillover of pest insects on grasslands? (Chapter 4)*

Q C2*: Does spillover of pest insect increase herbivore damage on wild plants? (Chapter 4)*

Block D: Biodiversity conservation management

***Q D1**: Does short-term and small-scale experimental succession increase diversity of herbivores and predators? (Chapter 2)*

***Q D2**: How efficient are successional islets as a conservation measure? (Chapters 2 and 3)*

***Q D3**: How can pest-induced damage to wild grassland plants be reduced in landscapes dominated by mass-flowering crops? (Chapter 4)*

OUTLINE OF CHAPTERS AND MAIN RESULTS

In **Chapter 2**, we address questions **Q** (**A1**), (**A2**), (**B1**), (**B2**), (**D1**) and (**D2**), and study the effects of local land use intensification on herbivore and predator guilds (Coleoptera and Heteroptera; Plate 1) in grassland ecosystems, using a large-scale and multi-site (N=126 study plots) experiment, located in three regions of Germany along a 600-km north-south gradient. We use two different approaches to calculate land use intensification on grasslands. First, we analyse effects of single management practices separately, by quantifying grazing intensity, cutting frequency and fertilizer input. In a second step, we combine these different managements and calculate a continuous overall land use intensity index to account for the quantitative variation of multiple land use types in heterogeneous landscapes. After setting up the land use intensity gradient, we experimentally manipulate local land use intensity on all plots by excluding grassland management in a small-scale subplot (successional islets) for one year (Plate 2a). This chapter shows that overall land use intensification with cutting as a key factor has a consistent negative effect on herbivore diversity and abundance and is closely related to decreasing plant species richness at the three study regions. Effects of vegetation height on herbivores are less consistent and differ between regions. Predators do not respond negatively to land use intensification nor any single management practices, but indirectly via herbivore availability and increase with rising herbivore diversity and abundance. Experimental successional islets enhance herbivore diversity, which in turn increases predator diversity via bottom-up effects. Efficiency of this conservation management practice, i.e. the difference in herbivore diversity of successional to land-use subplots, increases with land use intensity, in particular with mowing frequency.

Chapter 3 focuses on questions **Q** (**B2**) and (**D2**) and relates management-induced changes in host plant height to colonization success of associated specialized grass-shoot miners. In this study, changes in host plant heights are modulated via a temporal component of set-aside as another important aspect of question **Q** (**D2**). We simulate a temporal gradient of set-aside: abandoned (≥2-seasons; n=10 a priori selected subplots; Plate 2b), 1-season unmanaged (n=19 subplots experimentally excluded from management, Plate 2a) and continuously managed (n=12) areas (Plate 2a). Abundance of three common stem-borer species (Plate 3), at islets providing equal abundances of host grass shoots, is compared among the three levels of set-aside duration. Our results show that abundances are negatively affected by management–induced reduction in grass shoot length. Abandoned areas harboring longest shoots facilitate colonization success of two out of three stem-borer species, reflecting a strong effect of management reducing (host) plant height on herbivore specialists.

Chapter 4 addresses questions **Q** (**C1**), (**C2**) and (**D3**) and presents a grassland phytometer experiment (Plate 4) that quantifies scale dependent crop-noncrop spillover of rape pollen beetles (*Brassicogethes aeneus*) and fruit set of insecticide-treated and untreated wild mustard plants (*Sinapis arvensis*) as a consequence of herbivore damage. We use a set of 20 grassland plots along a gradient of increasing proportion of oilseed rape (OSR) within eight buffers (250 to 2000 m) around the centre of each plot. Exact measures of landscape parameters containing OSR fields, arable land (mainly cereals), forests, grasslands and semi-natural habitats are calculated on the basis of aerial photographs taken in the season. Pollen beetle and pollinator (bee) abundances are monitored during the experiment to distinguish between herbivore and pollination effects on phytometer fruit set. The chapter shows that pest insect spillover from crop fields is triggered by pulsing availability of mass-flowering crops (OSR) at different spatial scales. Reduction of fruit set on phytometer plants is highest on nearby grasslands (250 m). Hence alternative host plants occurring in the vicinity of cropland suffer most strongly from increased herbivore spillover.

STUDY REGIONS - THE BIODIVERSITY EXPLORATORIES

This thesis is part of a large-scale and long-term project for functional diversity research termed "Biodiversity Exploratories" (for more details see http://www.biodiversity-exploratories.de), which was initiated in 2006 to address feedback loops between land use intensification, biodiversity change and their consequences for ecosystem functioning and services in real-world ecosystems (Fischer et al. 2010).

The Biodiversity Exploratories are split into three areas located along a 600-km north-south gradient across Germany (Fig. 1). Each area ("Exploratory") consists of a balanced set of grassland and forest study plots. The three areas are: (i) the Schwäbische Alb near the city of Münsingen (Southwestern Germany), (ii) the Hainich-Dün area near Mühlhausen (Central Germany; including the Hainich National Park) and (iii) the UNESCO Biosphere Reserve Schorfheide-Chorin near Angermünde (Northeastern Germany). Study sites for our single experiments were selected from a total set of 1,500 potentially available grassland plots (500 per Exploratory, 50x50 m each).

Fig. 1. Locations of the three Exploratory regions in Germany.

Management intensity on these plots ranged from hardly managed semi-arid grasslands (Plate 5a, b) to highly fertilized and intensively used meadows (Plate 5 c, d) and pastures (Plate 5 e, f), most of the range of variation in land use that can typically be found in Germany's grasslands. Farming practice was assessed based on interviews with farmers and land owners (see Fischer et al. 2010). To integrate landscape features surrounding the study plots (Plate 6a), we calculated the proportion of habitat types within eight circles (250, 500, 750, 1000, 1250, 1500, 1750 and 2000 m) around the centre of each plot (Plate 6b) in ArcView 3.2 (ESRI Redlands, USA). Habitat types included oilseed rape (OSR) fields, arable land (mainly cereals), forest, grassland and semi-natural habitat, on the basis of digitized areal pictures taken in June 2009 (Hansa Luftbild, Münster).

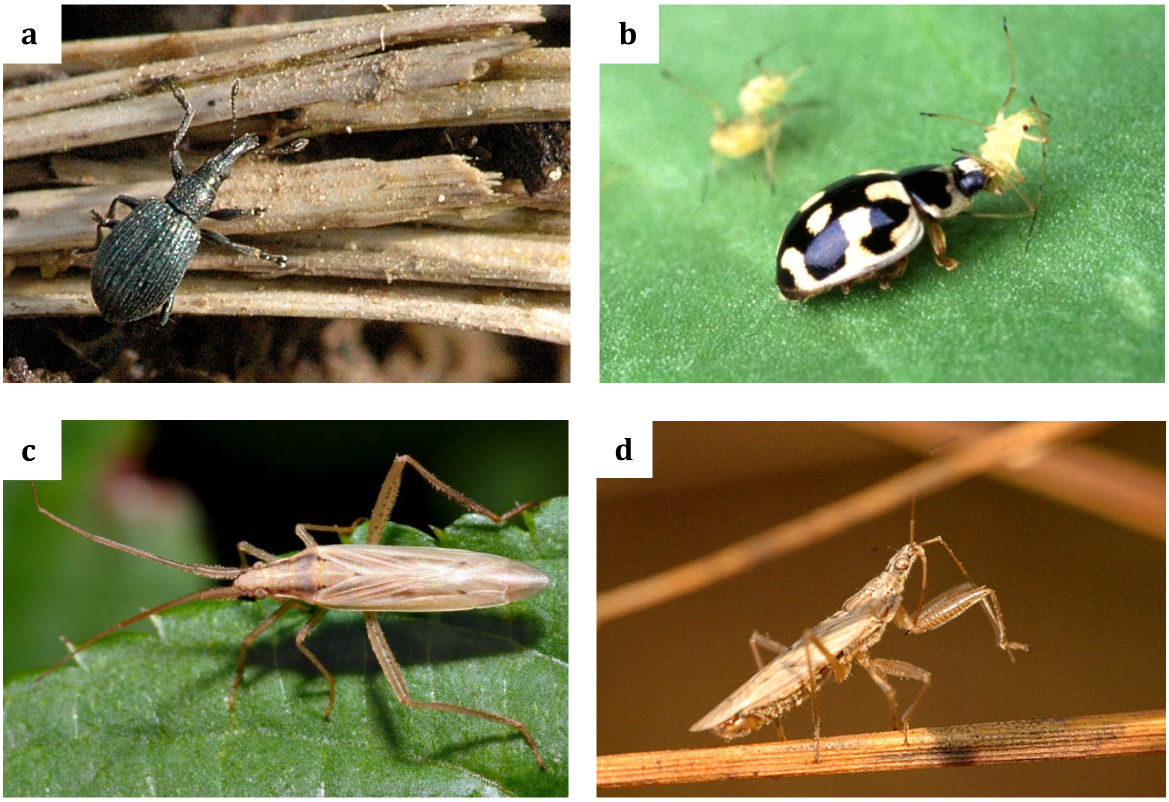

Plate 1: Common Coleopteran (a, b) and Heteropteran (c, d) herbivores (a, c) and predators (b, d) occurring on grasslands during our experiment.
(**a**) *Ischnopterapion virens* (**b**) *Propylea quatuordecimpunctata*
(**c**) *Stenodema laevigatum* (**d**) *Nabis rugosus*
Photos by James K. Lindsey (a, d), Scott Bauer (b) and André Karwath (c), licensed under Creative Commons.

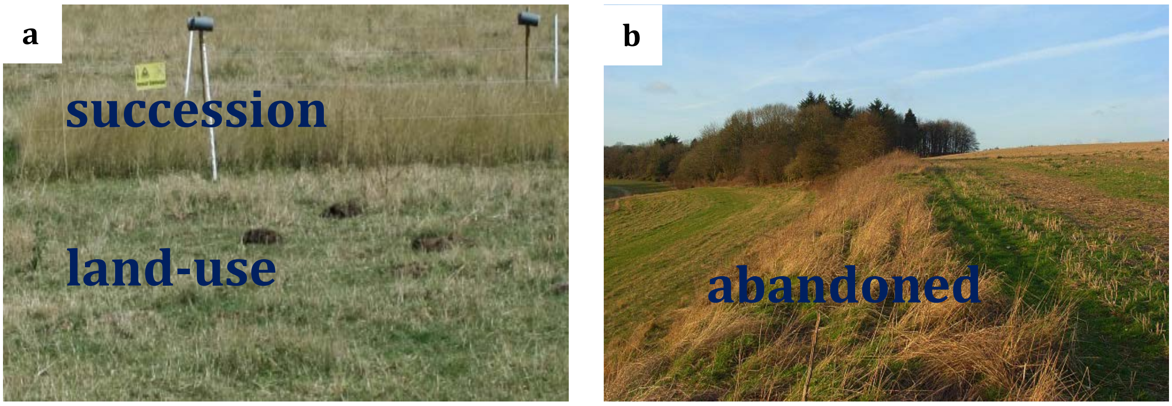

Plate 2: We established two subplot types (**a**) at grasslands in the three study regions.The 'land-use' subplot was liable to the local farmers' practice (mown zero to three times per year and/or grazed as well as heavily fertilized). At the 'succession' subplot no mowing, grazing or fertilization took place. To prevent grazing we set up electrical fences. For the stem-borer experiment we additionally sampled abandoned areas (**b**) to simulate a temporal gradient of set-aside.

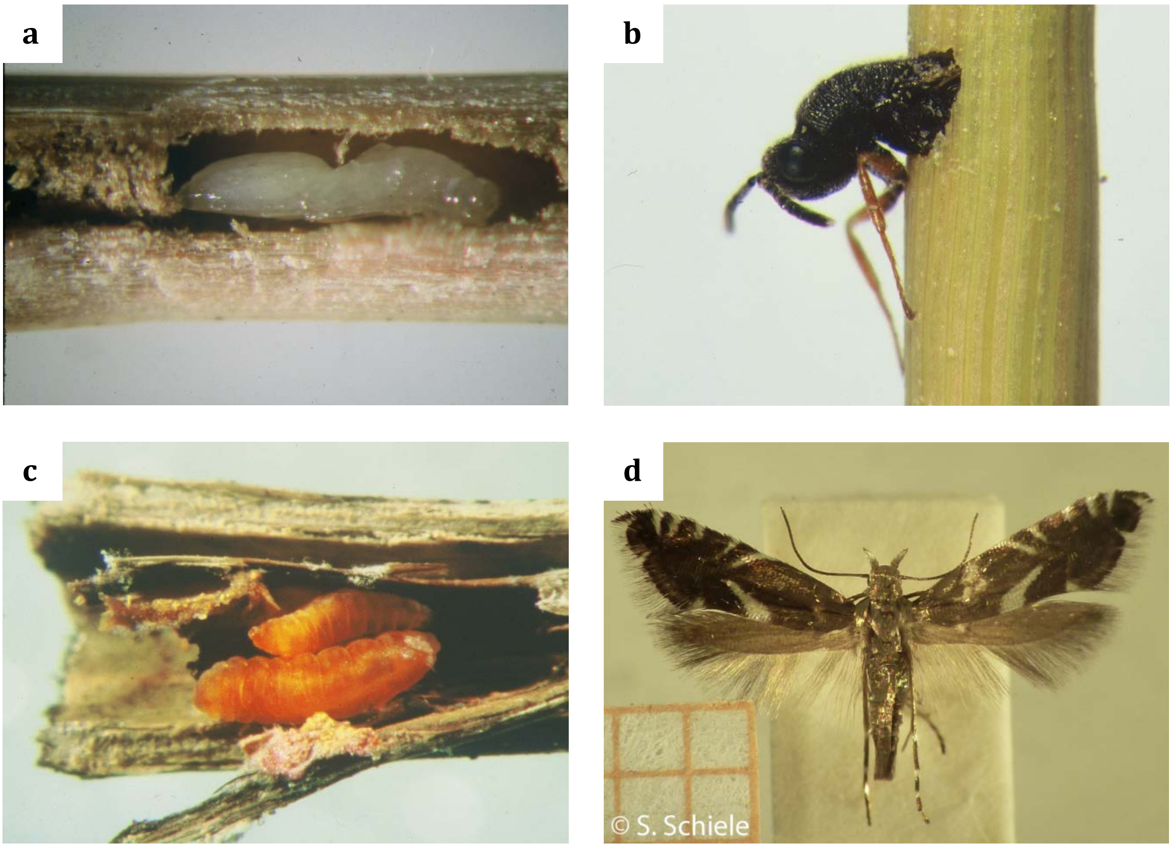

Plate 3: Three common stem-boring species in our experiment.
(**a**) Larva of *Tetramesa sp.* (Hymenoptera, Eurytomidae)
(**b**) Adult of *Tetramesa sp.* (Hymenoptera, Eurytomidae))
(**c**) Larvae of *Lasipotera sp.* (Diptera, Cecidomyiidae)
(**d**) Adult of *Gylphipterix fischeriella* (Lepidoptera, Glyphipterigiedae)
Photos by Teja Tscharntke (a, b, c) and Susanne Schiele (d).

Plate 4: Grassland Phytometer Experiment with young *Sinapis arvensis* plants. To prevent grazing we set up electrical fences.

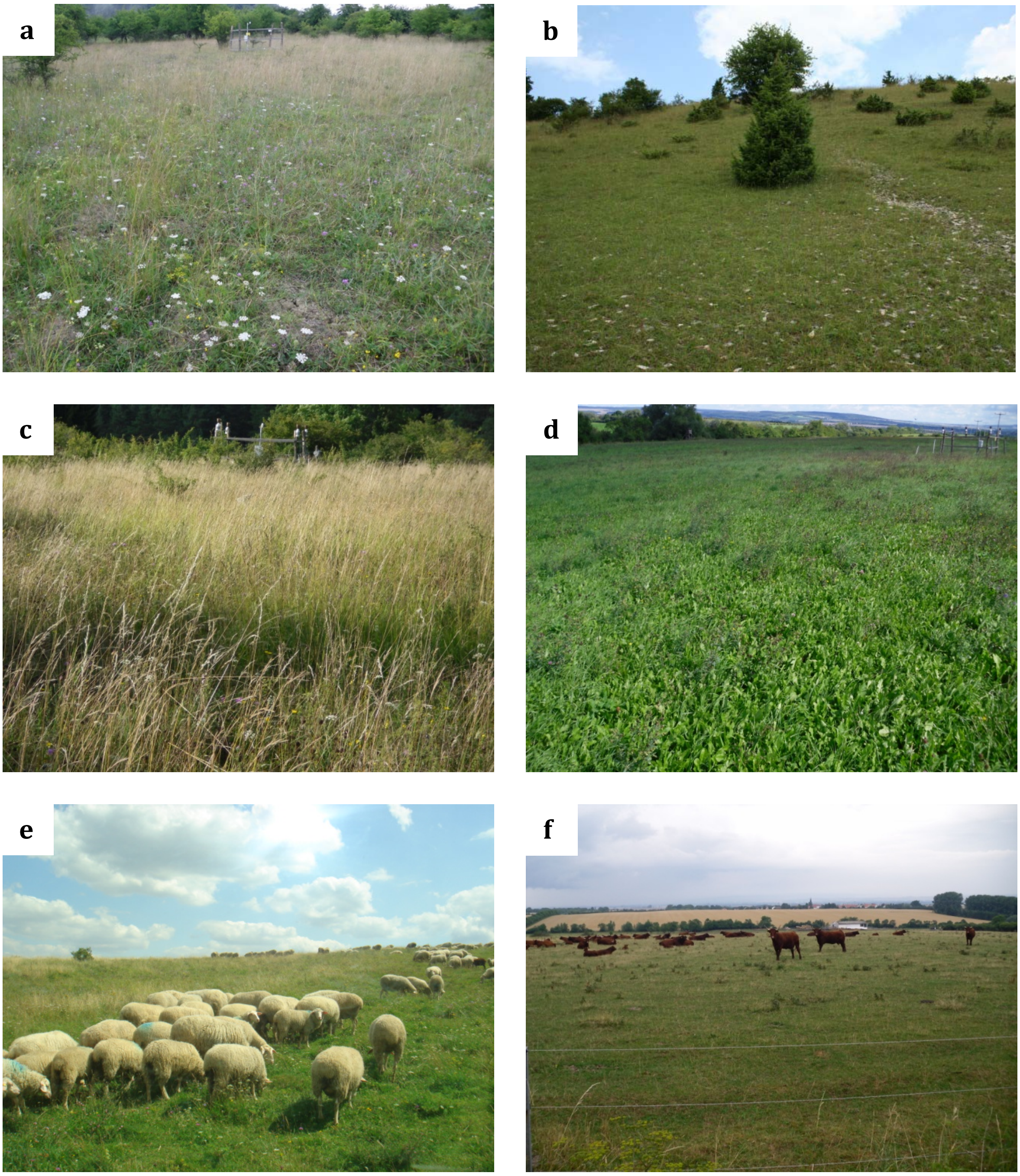

Plate 5: Management intensity on grassland plots ranged from hardly managed semi-arid grasslands (**a**, **b**) to highly fertilized and intensively used meadows (**c**, **d**) and pastures (**e**, **f**), reflecting most of the range of variation in land use that can typically be found in Germany's grasslands. Photos by Steffen Boch (a, c, d, f) and Carmen Börschig (e).

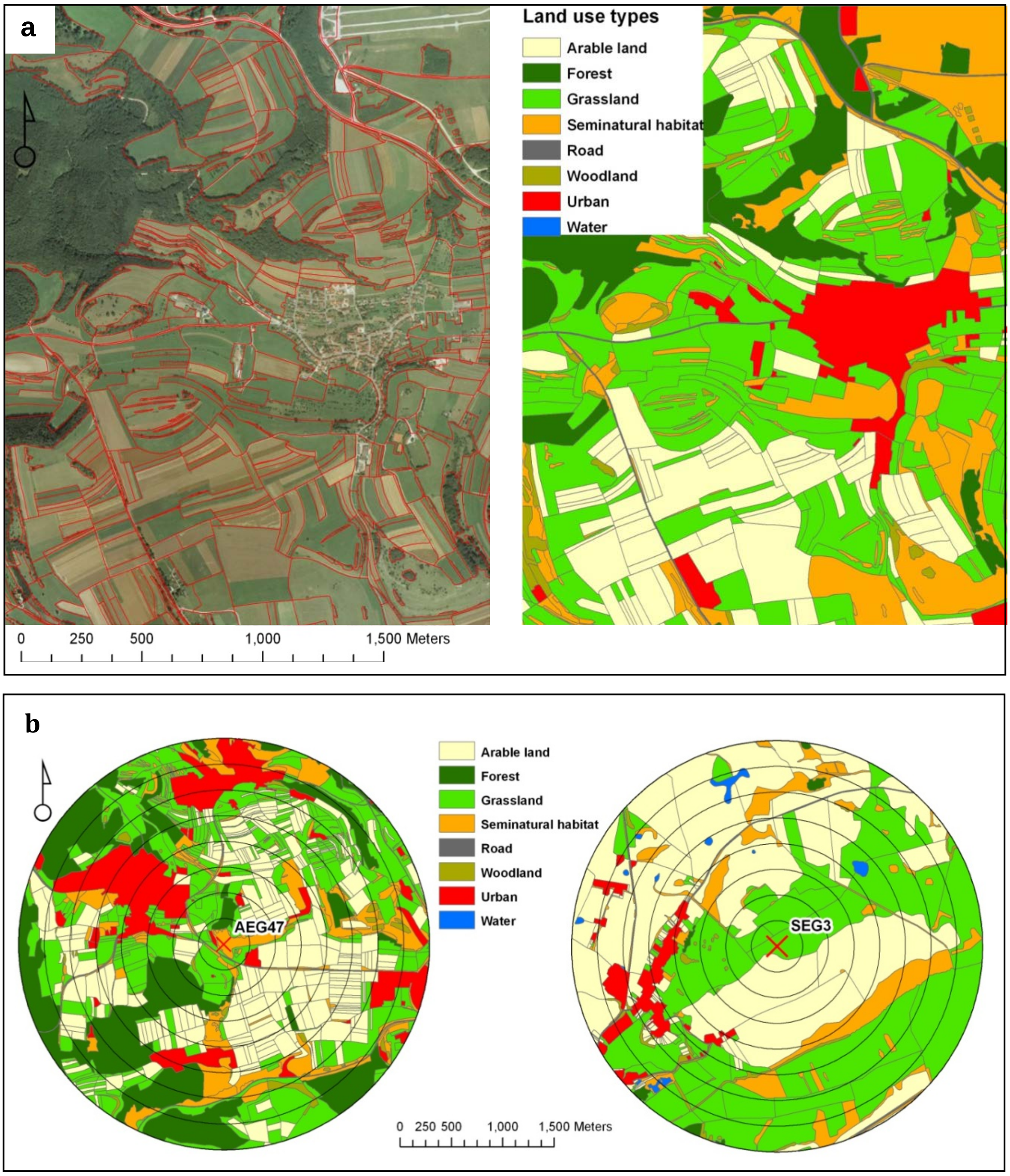

Plate 6: To integrate landscape features surrounding the study plots (**a**) we calculated the proportion of habitat types within eight circles (**b**) around the centre of each plot.

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CHAPTER 2

EFFICIENCY OF INSECT CONSERVATION MANAGEMENT ON GRASSLANDS INCREASES WITH LOCAL LAND-USE INTENSITY

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SUMMARY

Abundance and diversity of grassland insect herbivores and predators are often negatively influenced by land-use intensification. We hypothesized that efficiency of conservation management changes with land-use intensity. We used n=97 old grassland plots located in three regions of Germany to study the effects of grassland management intensity on insect herbivores and predators. In addition, we experimentally manipulated local land-use intensity on all plots in that we excluded grassland management in a small-scale subplot for one year. The resulting short-term successional islets (3.5x7 m) were hypothesized to mitigate negative effects of management and tested for their effectiveness as an insect conservational tool. Suction samples of the managed and non-managed parts of all grasslands rendered results on herbivores and predators of beetles and true bugs. We found a negative effect of land-use intensification on herbivore diversity and abundance across all three study regions. In particular mowing frequency, affecting vegetation height and local plant species richness, excelled as a key predictor of herbivore diversity decline. Predators were not directly influenced by management but bottom-up controlled via their herbivorous prey. Experimental set-aside buffered negative effects of management on herbivore diversity. Efficiency of implementing these successional areas was directly related to land-use intensity, increasing diversity on grasslands under high-intensity management. Our results indicate that even small set-aside islets, temporally excluded from management, can serve as a low cost-high benefit conservation measure introducing habitat heterogeneity and insect diversity despite of ever changing land-use practices and environmental conditions.

INTRODUCTION

About half of Europe´s farmland is managed as grassland pasture or hay meadow (Minns et al. 2001). Some grassland habitats, such as calcareous grasslands, rank among the most species-rich in Central Europe (Poschlod et al. 2002; van Swaay 2002). Management intensity is a key factor influencing biodiversity in grasslands (Plantureux et al. 2005), and extensively used grasslands are often considered as refuge habitats for insects after crop harvesting (Bianchi, Booij & Tscharntke 2006, Rand et al. 2006). Agricultural intensification on grasslands by means of grazing, fertilization and mowing alters plant species composition (Fédoroff et al. 2005, Dumont et al. 2011) and vegetation structure, thereby affecting microhabitat conditions. As many herbivorous insects exhibit feeding specialization to some degree (Bernays & Graham 1988), occupy distinct layers in the vegetation and respond sensitively to microclimate, grassland management can change resource and habitat heterogeneity, affecting biodiversity.

While it is widely acknowledged that intensive grassland management, e.g. frequent mowing and grazing activity, have negatively impacted insect diversity, experimental studies often lack the complete cross-regional range of farming practices applied in real-world management regimes. Also temporal variation in timing of these events during the season can be important for its impacts, especially in mobile organisms (Johst, Drechsler, Thomas, & Settele 2006). Vegetation recovery time after mowing events may depend on site conditions and fertilization. These management-induced fluctuations of shelter, plant resource quantity and heterogeneity of food resources (Haddad et al. 2009) should foremost affect the herbivore trophic level. The Resource Specialization (Hutchinson 1959) and Resource Concentration Hypothesis (Root 1973) predict higher diversity but lower abundances of herbivores in plant species-rich sites, even though diversity and abundance might be strongly linked (Gotelli & Graves 1996). As species of higher trophic levels directly depend on their plant-feeding prey (Haddad et al. 2009), carnivores tend to be also affected by plant species loss (Haddad et al. 2001, Cardinale et al. 2006) and management intensification (Morris & Rispin 1987), responding indirectly through bottom-up trophic cascades from plants via herbivores to predators (Scherber et al. 2010). A deeper understanding of the responses of different functional groups across a broad range of geographically varying management regimes will allow us to develop management strategies successfully enhancing insect communities in human-dominated landscapes. Efficiency of such measures should vary with land-use type and intensity, but has so far been little analyzed.

One possible way to counter insect diversity decline in agricultural landscapes is the implementation of set-aside schemes, introduced by the Common Agricultural Policy of the European Union in the late 1980s. In a set-aside project located in Germany, species richness of plants, butterflies, beetles, true bugs, parasitoids and bees was highest on 2-year-old set-aside fields compared to 1- and 3-year-old set-asides (Gathmann et al. 1994, Greiler 1994, Steffan-Dewenter & Tscharntke 1997, 2001). Unfortunately, a wide-scale uptake of this approach has economic limitations (Abensperg-Traun et al. 2004) and recent rising commodity prices for food and energy crops changed policy and led to a sudden loss of set-aside in Europe since 2006 (Tscharntke et al. 2011). One alternative is to enhance diversity by applying approaches in combination with existing profitable farming management practices (Woodcock et al. 2009). Using extensive management on field edges, resulting in semi-natural habitats such as naturally developed fallow strips, wildflower areas and grassy field margins enhances species richness of true bugs (Zürbrügg & Frank 2006), syrphid flies (Haenke et al. 2009), carabids and spiders (Kromp & Steinberger 1992) and can act as reservoirs from which arthropods can reinvade intensively used land (Sotherton 1985, Burel & Baudry 1995). Even small areas, temporarily excluded from land-use management, may contribute to regional biodiversity in various ways: as hibernation and larval development habitats (e.g. grass-shoot miners), as refuge and foraging habitats after management disturbance events (e.g. mowing), and as stepping stones for highly mobile species across the agricultural landscape.

In this study, we selected a subset of 97 plots from a total set of 1,500 grasslands across three German regions of comparable habitat complexity, to reflect the broad range of common grassland management practices typically applied by local farmers. At each grassland plot we excluded small 3.5x7 m areas from any farming practice for a period of one year, to test the cross-regional applicability of this biodiversity enhancing approach across a wide range of grassland agro-ecosystems. Beetles (Coleoptera) and true bugs (Heteroptera) were chosen, because they are highly mobile and ecologically very diverse insect orders, including herbivorous and zoophagous species as well as generalists and specialists, and they occur on a wide range of agricultural grasslands. Furthermore both groups respond sensitively to environmental changes (Schwab et al. 2002, Jonas et al 2002) and might be closely related to total insect diversity patterns (for true bugs: Duelli & Obrist 1998). We hypothesize that: (i) Land-use intensification negatively affects herbivore diversity and abundance via a bottom-up response to the simplification of the vegetation; (ii) Predator responses are due to bottom-up effects via their herbivorous prey; (iii) Short-term and small-scale experimental succession increases diversity of both trophic guilds; (iiii) being most efficient on grasslands with high-intensity management (i.e. with biggest contrast to the surrounding vegetation).

MATERIAL & METHODS

Study regions and sites

The study is part of the large-scale and long-term research platform "Biodiversity Exploratories" (Fischer et al. 2010) with study sites on the UNESCO Biosphere area 'Schwäbische Alb' near the city of Münsingen (South-western Germany), in the national park 'Hainich-Dün' near Mühlhausen (Central Germany) and in the UNESCO Biosphere Reserve 'Schorfheide-Chorin' near Angermünde (North-eastern Germany), covering a North-South gradient. For brevity, study sites will subsequently be referred to as "Exploratories". Each of these three Exploratories represents most of the range of variation in land-use that can typically be found in grasslands in Germany, covering hardly managed grasslands to highly fertilized and intensively used meadows and pastures (for more details see http://www.biodiversity-exploratories.de). Farming practice was recorded from interviews with farmers and land owners (see Fischer et al. 2010). Information on plant diversity is provided in the data base of the 'Biodiversity-Exploratories' measured on 3x3 m areas on each plot (S. Socher, unpublished data).

Local land-use intensity

Land-use intensity per grassland plot was summarized using the standardized intensity of three management types, namely ungulate grazing intensity (cattle, sheep and horses converted to livestock units ha^{-1} as presented by Fischer et al. 2010 and the number of days with grazing year^{-1}), mowing events (timing and frequency of cutting year^{-1}) and fertilizer input (kg nitrogen applied year^{-1}). These three management components were combined in a land-use intensity index (LUI), following Herzog et al. (2006) and Blüthgen et al. (2012), slightly modified to incorporate timing of cutting events (see APPENDIX S1). Preliminary analyses showed that the continuous scale of the LUI (ranging from 0 to 1) was more appropriate to characterize land-use intensity than discrete categories (such as "mown grassland" or "grazed, mown grassland"; see also Hendricks et al. 2007). Furthermore we tested the detailed impact of three single management practices separately: number of cuts year^{-1} (range: 0 – 3 times) and days grazing year^{-1} (range: 0 – 263 days) as well as fertilizer input per year^{-1} (range: 0- 125 kg Nitrogen). Vascular plant species richness and maximal vegetation height were used as additional indirect indicators of management intensity, affecting insect communities. Plant species richness ranged from 9 to 57 and vegetation height from 8 to 154 cm. The most important regional site conditions and management parameters are provided in Table 1.

Table 1. Range of management practices applied on the subplot treatments at the three regions Schwäbische Alb, Hainich and Schorfheide. Also shown are plant species richness and vegetation height as secondary consequences of land-use intensification.

					Exploratory					
			Alb			**Hainich**			**Schorfheide**	
Parameter	**Scale**	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*
Land-use intensity (LUI)	Plot	0.01	0.59	0.23	0.01	0.54	0.21	0.03	0.59	0.19
Plant species richness	Plot	18	57	33	13	43	24	9	16	23
Livestock units	Land-use subplot	0	200	34	0	83	39	0	100	38
Grazing [d*y^{-1}]	Land-use subplot	0	120	19	0	263	44	0	133	18
Cuts [y^{-1}]	Plot & land-use subplot	0	3	1	0	3	1	0	3	1
Nitrogen [kg*(ha+y)$^{-1}$]	Plot & land-use subplot	0	100	25	0	80	25	0	125	18
Vegetation height [cm]	Land-use subplot	8	111	36	4	91	44	5	49	22
Vegetation height [cm]	Succession subplot	50	130	91	53	125	93	49	153	102

Experimental design and arthropod sampling

The 97 grassland plots covered a land-use intensity gradient in the three study regions ('Schwäbische Alb', n=33; 'Hainich', n=29; 'Schorfheide-Chorin', n=35) and were selected from a total of 1,500 potentially available grassland plots (500 per Exploratory, 50x50 m each). In spring 2008 we established two subplots (3.5x7 m each) on each grassland. The 'land-use' subplot was managed by farmers, according to their local practices (mown up to three times per year and/or grazed as well as fertilized). The 'succession' subplot was a set-aside grassland islet (see Nentwig 1988 and Helden et al. 2010 for comparison) with no mowing, grazing or fertilization allowed. To prevent grazing, we set up standard electrical fences. Overall, we had a three-factor (Exploratory, plot, subplot) split-plot design with two different subplots at all Exploratories. Arthropods from each subplot were sampled using suction sampling with a D-Vac (Stihl SH 56) for 1 min (Brook et al. 2008), covering a 0.25 m^2 area of vegetation with a gauze-cage to prevent insects from escaping. We took four samples per subplot during two runs (from 15th May to 2nd July and 11th August to 1st September) per season (n=1008). In addition, maximal vegetation height inside the gauze cage was measured using a ruler. Samples were transferred into 70% Ethanol for later identification. We identified true bugs and beetles to species level and grouped them into herbivores and predators according to literature (Böhme 2001, Goecke et al. 2004, 2006, 2007, 2008) and expert opinions. Species belonging to other trophic levels or with unknown feeding habits were only included for calculation of relative abundance of predators and herbivores. We computed relative abundances of the focus groups as their percentage relative to all Heteroptera and Coleoptera individuals obtained from the same subplot.

Statistical analysis

For data analysis we used R 2.12.1 (R Development Core Team 2010). Data from both sampling periods were pooled on subplot level. We calculated Shannon diversity of herbivores and predators based on count data obtained from suction samples. We used Shannon diversity instead of pure species richness since it not only accounts for the number of species but also the evenness of the species. To determine the effects of land-use intensification on insect diversity we used linear mixed effects models (nlme package; Pinheiro & Bates 2000) that were simplified using the stepAICc function (modified from the MASS package, Venables and Ripley, 2002; see APPENDIX S2). We included, respectively, absolute herbivore or predator abundances on plot level as a covariate in all models.

Shifts in herbivore and predator abundances relative to overall insect abundance were analyzed with generalized linear mixed models fit by penalized quasi-likelihood (R: glmmPQL, MASS library). We used relative instead of absolute abundances since total insect abundances at the particular sampling dates were strongly influenced by recently applied management practices such as increased mortalities during the harvesting process (Humbert et al. 2010) or insect removal from the field when baling. For glmmPQL models, model simplification was achieved through manual deletion of terms from maximal models (Crawley 2007). For all models we used local plots as random, subplot type and Exploratory as fixed factors (see APPENDIX S2). Subplot and Exploratory as design based parameters remained in all minimal adequate models.

Effectiveness of successional islets as insect conservational tool was calculated as the difference in herbivore diversity of successional to land-use subplots (H' subplot succession-H' subplot land-use). We tested effectiveness along the land-use intensity gradient (LUI) of the three regions in a separate lme model using Exploratory as fixed and local plots as random factors (see APPENDIX S2).

We checked for spatial autocorrelation by fitting lme models to continuous response variables, where Exploratories were treated as random effects and Gauss-Krüger coordinates were used as spatial covariates, assuming a spherical spatial correlation structure (Pinheiro and Bates, 2000). In addition, we plotted model residuals against the Gauss Kruger coordinates to ensure that no spatial patterns had been overlooked (APPENDIX S3).

RESULTS

Plot residuals were not spatially autocorrelated since AICc increased when models were updated using a spherical autocorrelation function. Diversity and abundance of the herbivore community was negatively affected by land-use intensification across all three study regions, while in contrast, predators were not directly influenced by management practices. Short-term and small-scale succession enhanced herbivore diversity, which in turn had a positive effect on predator diversity. The efficiency of this conservation management practice, expressed as the difference in herbivore diversity of successional to land-use subplots, increased with land-use intensity, in particular with mowing frequency.

Insect communities

We collected a total of 10,380 insects belonging to two orders. Coleoptera richness was, with 361 species, more than three times higher than Heteroptera richness with 105 species (for a full species list and trophic level classification see APPENDIX S4.1 and S4.2). 171 beetle and 90 true bug species were obligate herbivores, and 121 beetle and 15 true bug species were predators. We excluded 69 beetle species (19.1 %) from our analysis since they belonged to other trophic guilds or their feeding habits were unknown. The total species richness of herbivores comprised 261 species, while the predatory group made up to 136 species. Altogether we found beetle abundance with 8,139 individuals more than three times as large as for true bugs with 2241 specimens. We assigned 4494 beetles and 2042 true bugs to the herbivore and 861 beetles and 199 true bugs to the predatory guild, while the remaining 2784 beetles (34.2 %) were considered only in the calculation of total insect abundances. Accordingly, total herbivorous group abundance comprised 6536 individuals, while the predatory group included 1060 individuals.

Land use intensification affects herbivores

Shannon diversity of herbivores did not differ between regions (Table 2) and consistently decreased with higher overall land-use intensity LUI (Fig. 1a-c) on the land-use subplot. This decrease was less pronounced in the succession subplot. Detailed analyses of management practices revealed that the negative LUI effects were consistently due to the mowing frequency across all regions (Table 2).

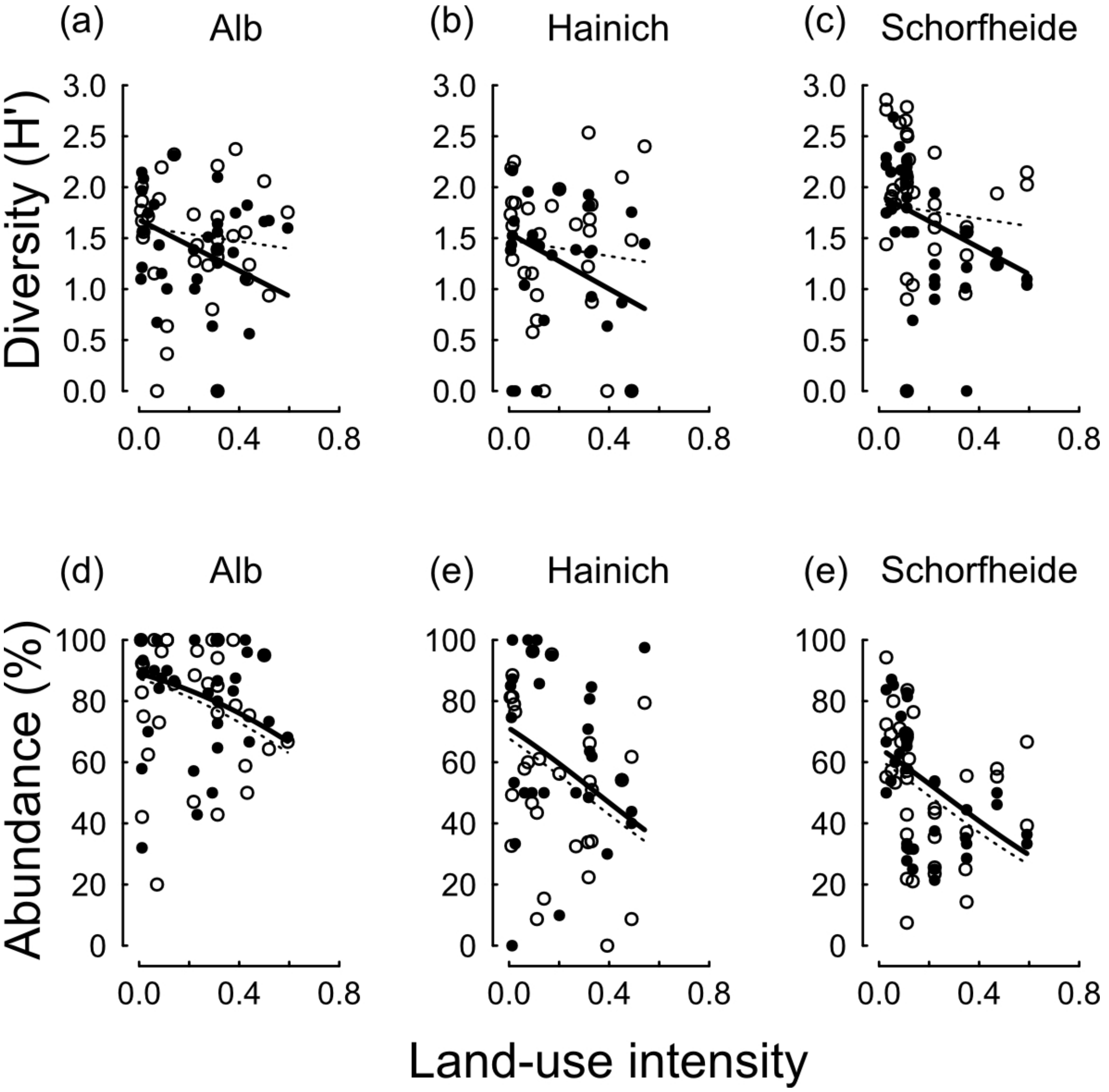

Fig. 1. Relationships between land use intensity and herbivore insect community for land-use (filled circles, solid line) and succession subplots (open circles, dashed line) at the three regions Schwäbische Alb, Hainich and Schorfheide. Shannon diversity (a-c) and relative abundance of herbivores (d-f) predicted by values from the models decreased with land use intensification at all Exploratories.

Herbivore diversity significantly decreased on grasslands cut two or three times compared to those that were cut only once a year or not at all (Fig. 2, dark bars). Neither grazing nor fertilization had a direct effect on herbivore diversity, except at Schorfheide, where higher fertilization levels were related to a decrease of herbivore species (Table 2). Since plant species richness and LUI were negatively correlated (Spearman correlation, ρ=-0.355, P<0.001), herbivore diversity declined with plant species loss (Fig. 3a). Effects of vegetation height were similar in both subplots but differed between regions. At Schorfheide, we found enhanced herbivore diversity with increasing vegetation height (significant interaction term in Table 2), while at Schwäbische Alb and Hainich more herbivore species were found at sites with lower vegetation.

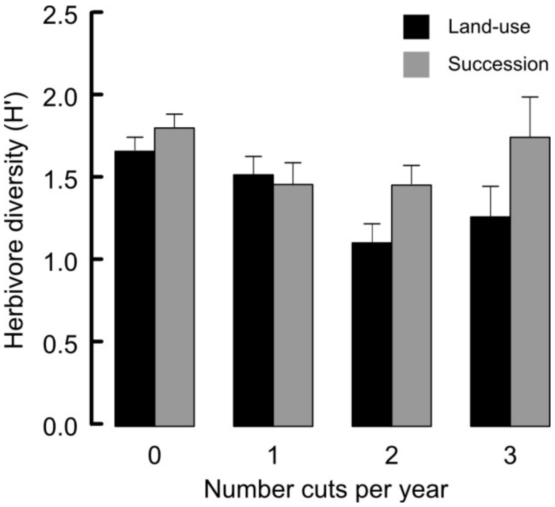

Fig. 2. Change in overall Shannon diversity of herbivores (±SE) in response to the number of cuts year^{-1} and for land-use (black bars) and succession subplots (grey bars). Mowing reduced herbivore diversity at the land-use subplot compared to the succession subplot at frequently mown grasslands.

We found highest herbivore abundances at Schwäbische Alb (Table 2). Since herbivore abundance and diversity were correlated (Spearman correlation, ρ= 0.576, P<0.001), herbivore abundance was similarly reduced with increasing LUI at all regions and for both subplots (Fig. 1d-f). Mowing effects on abundance of herbivores were less consistent, only reducing herbivores at Schorfheide, as indicated by their significant interaction in the model (Table 2). Again, grazing and fertilization did not have any direct impact on herbivore abundance. However, herbivore abundance was, equal to diversity, positively related to plant species richness (Fig. 3b). Vegetation height affected herbivore abundances on subplot level, as we found a slightly negative relationship between abundance and vegetation height only within the succession subplots (Table 2).

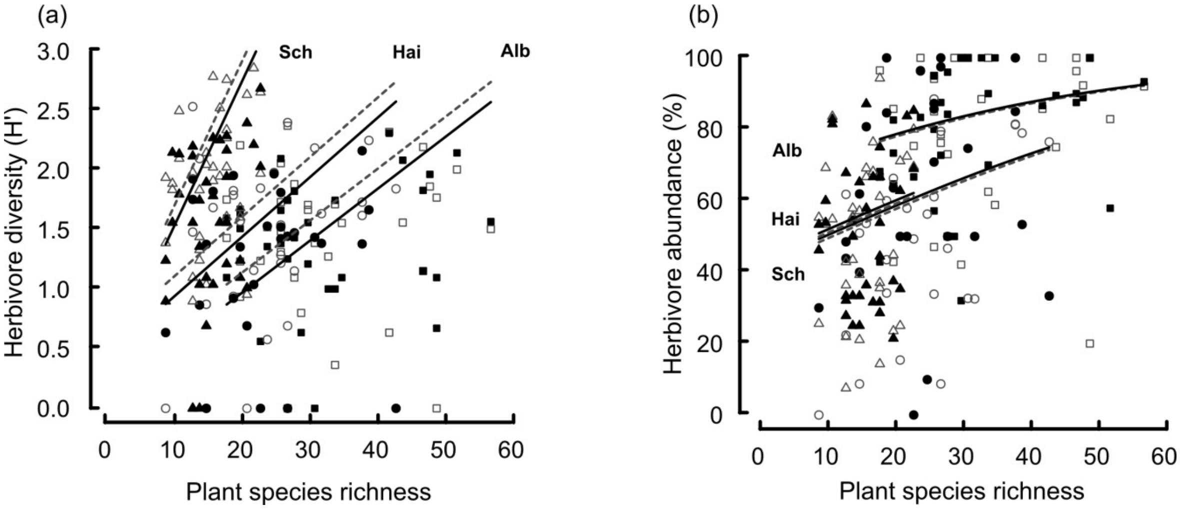

Fig. 3. Relationships between plant species richness and herbivore insect community for land-use (filled symbols, solid lines) and succession subplots (open symbols, dashed lines) at the three regions Schwäbische Alb (Alb, squares), Hainich (Hai, circles) and Schorfheide (Sch, triangles). Shannon diversity (a) and relative abundance of herbivores (b) predicted by values from the models increased with higher plant species richness at all Exploratories.

Table 2. Results for mixed effects models identifying the effects of overall land use intensification and single management practices on the herbivore insect community for land-use and succession subplots at the three regions Schwäbische Alb, Hainich and Schorfheide. Shannon diversity and relative abundance (percentage of the focus group relative to all Heteroptera and Coleoptera individuals obtained from the same subplot) are based 4x0.25 m^2 areas, suction sampled for 1min, respectively. Vascular plant species richness is based on vegetation relieves on a 3x3 m^2 area for each plot. Where ns = not significant; for all models the intercept is provided.

	Herbivores									
	Shannon diversity H' (1/m^2)					**Relative abundance (1/m^2)**				
Explanatory	*Est*	*Error*	*df*	*t*	*P*	*Est*	*Error*	*df*	*t*	*P*
(Intercept)	1.38	0.13	93	10.50	<0.001	2.08	0.27	93	7.58	<0.001
Herbivore abundance (1/m^2)	0.06	0.02	88	3.65	<0.001	-	-	-	-	-
Hainich	-0.13	0.12	93	-1.06	0.293	-1.19	0.28	93	-4.24	<0.001
Schorfheide	0.22	0.12	93	1.91	0.059	-1.54	0.27	93	-5.67	<0.001
LUI	-0.92	0.34	93	-2.67	0.009	-1.72	0.65	93	-2.63	0.010
Succession	-0.06	0.10	88	-0.63	0.528	-0.16	0.11	90	-1.44	0.152
LUI : Succession	0.66	0.35	88	1.87	0.064	-	-	-	-	ns
(Intercept)	0.96	0.39	88	2.47	0.015	0.11	0.67	89	0.16	0.870
Herbivore abundance (1/m^2)	0.06	0.02	84	3.32	0.001	-	-	-	-	-
Hainich	0.01	0.28	88	0.05	0.957	-0.54	0.38	89	-1.44	0.153
Schorfheide	0.28	0.30	88	0.93	0.353	-0.07	0.46	89	-0.14	0.886
Vegetation height (cm)	0.00	0.00	84	2.16	0.034	-	-	-	-	-
Plant species richness (1/9m^2)	0.02	0.01	88	2.16	0.034	0.00	0.00	87	0.94	0.348
Cuts (y-1)	-0.21	0.07	88	-2.99	0.004	0.03	0.01	89	2.21	0.030
Grazing (d*y-1)	-	-	-	-	ns	-	-	-	-	ns
Nitrogen (kg*(ha+y)-1)	0.01	0.00	88	1.83	0.071	-	-	-	-	ns
Succession	-0.01	0.10	84	-0.14	0.887	0.74	0.44	87	1.70	0.092
Veg_height : Hainich	0.00	0.00	84	0.31	0.758	-	-	-	-	ns
Veg_height : Schorfheide	0.01	0.00	84	2.45	0.016	-	-	-	-	ns
Grazing : Succession	-	-	-	-	ns	-	-	-	-	ns
Cuts : Succession	0.18	0.06	84	2.95	0.004	-	-	-	-	ns
Veg_height : Succession	-	-	-	-	ns	-0.01	0.01	87	-2.12	0.037
Nitrogen : Hainich	0.00	0.00	88	-0.68	0.501	-	-	-	-	ns
Nitrogen : Schorfheide	-0.01	0.00	88	-2.02	0.047	-	-	-	-	ns
Cuts : Hainich	-	-	-	-	ns	-0.40	0.25	89	-1.62	0.109
Cuts : Schorfheide	-	-	-	-	ns	-0.81	0.25	89	-3.18	0.002

Predator community drivers

In contrast to herbivore diversity, predator diversity differed significantly between regions, with Schorfheide and Hainich exhibiting more predatory species than Schwäbische Alb. Predator diversity was not significantly affected by land-use intensity of management, but indirectly via diversity (Table 3) and associated abundance of the herbivore trophic level. Predator diversity increased significantly with rising herbivore diversity levels at all sites and consistently across subplots. At Hainich sites, predator abundances were lower compared to the two other regions. Predator abundance was highly correlated with predator diversity (Spearman correlation, ρ= 0.891, P<0.001) and not influenced by LUI, nor any single management practice, except at Schorfheide, where an increase in land-use intensity through frequent cutting was found to increase relative abundances of predators. Neither predator diversity nor abundance was related to plant species richness and vegetation height and experimental succession did not directly alter the predator community.

Short-term succession affects herbivores

Experimental succession buffered negative effects of frequently applied mowing practices on herbivore diversity in the three regions as indicated by their significant interaction (Table 2). Set-aside from grazing and fertilization had no direct effect on herbivore diversity (Table 2). Thus, succession subplots established on grasslands mown more than once per year significantly increased herbivore diversity (Fig. 2). In contrast, herbivore abundance did not differ between land-use and succession subplots (Fig. 1d-f) and maximal vegetation height within the succession plots even had a significant but weak negative effect on their relative abundances. The efficiency of this conservation management practice, the difference in herbivore diversity of successional to land-use subplots (H' subplot succession-H' subplot land-use), improved with increasing land-use intensity (lme: Est = 0.72, Err = 0.34, df = 89, t = 2.15, P = 0.034) across all regions (Fig. 4 a-c).

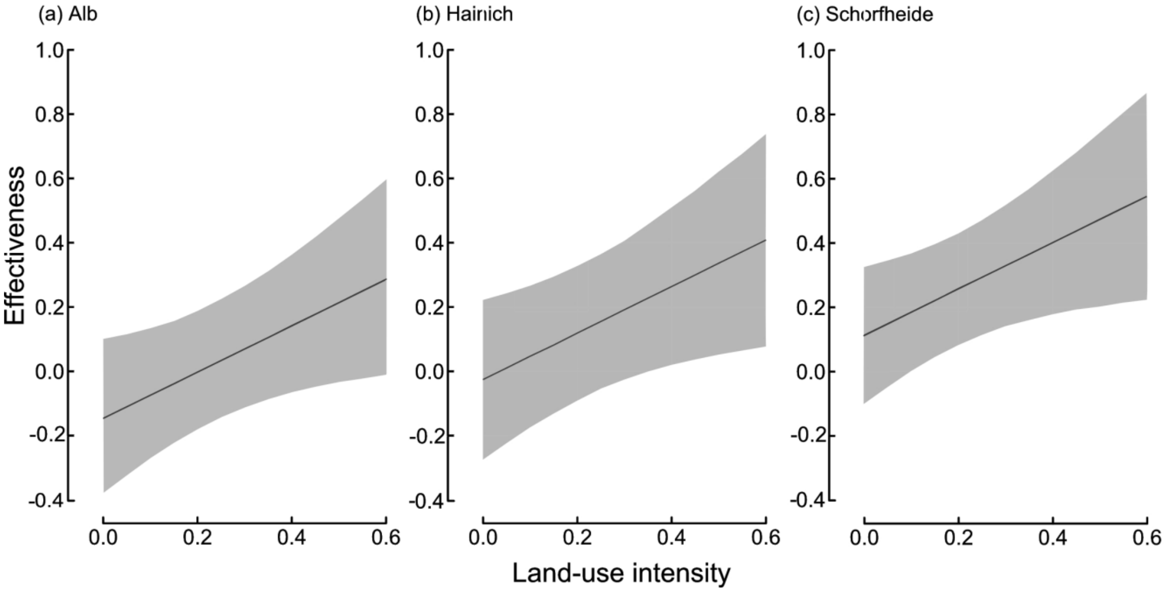

Fig. 4. Effectiveness of small-scale succession on diversity of herbivores in relation to land-use intensity at the three regions (a) Schwäbische Alb, (b) Hainich and (c) Schorfheide. Effectiveness of the successional islets, calculated as the difference in Shannon diversity between succession and land-use subplots (H' subplot succession-H' subplot land-use), increased with land-use intensity (lme: *Est* = 0.72, *Err* = 0.34, *df* = 89, *t* = 2.15, *P* = 0.034). Length of solid lines refers to data range of land-use intensity at each Exploratory. Shaded areas show the 95% confidence intervals.

Predator community drivers

In contrast to herbivore diversity, predator diversity differed significantly between regions, with Schorfheide and Hainich exhibiting more predatory species than Schwäbische Alb. Predator diversity was not significantly affected by land-use intensity of management, but indirectly via diversity (Table 3) and associated abundance of the herbivore trophic level. Predator diversity increased significantly with rising herbivore diversity levels at all sites and consistently across subplots. At Hainich sites, predator abundances were lower compared to the two other regions. Predator abundance was highly correlated with predator diversity (Spearman correlation, ρ= 0.891, P<0.001) and not influenced by LUI, nor any single management practice, except at Schorfheide, where an increase in land-use intensity through frequent cutting was found to increase relative abundances of predators. Neither predator diversity nor abundance was related to plant species richness and vegetation height and experimental succession did not directly alter the predator community.

Table 3. Results for mixed effects models identifying the effects of overall land use intensification, single management practices and herbivore diversity on the predator community for land-use and succession subplots at the three regions Schwäbische Alb, Hainich and Schorfheide. Where ns = not significant; for all models the intercept is provided.

	Predators									
	Shannon diversity H' (1/m^2)					**Relative abundance (1/m^2)**				
Explanatory	*Est*	*Error*	*df*	*t*	*P*	*Est*	*Error*	*df*	*t*	*P*
(Intercept)	-0.33	0.12	73	-2.64	0.010	-1.06	0.38	71	-2.77	0.007
Predator abundance (1/m^2)	0.56	0.05	46	11.03	<0.001	-	-	-	-	-
Hainich	0.11	0.07	73	1.47	0.146	-1.29	0.47	71	-2.75	0.008
Schorfheide	0.22	0.07	73	2.99	0.004	-0.77	0.42	71	-1.86	0.067
LUI	0.27	0.17	73	1.63	0.106	-1.10	1.28	71	-0.85	0.396
Succession	-0.01	0.05	46	-0.22	0.824	-0.23	0.20	47	-1.12	0.269
LUI : Hainich	0.66	0.35	88	1.87	0.064	0.13	1.75	71	0.07	0.943
LUI : Schorfheide	-	-	-	-	ns	3.23	1.61	71	2.01	0.048
(Intercept)	-0.91	0.21	67	-4.38	<0.001	-1.28	0.31	71	-4.09	<0.001
Predator abundance (1/m^2)	0.52	0.05	42	10.37	<0.001	-	-	-	-	-
Hainich	0.53	0.22	67	2.41	0.019	-1.26	0.29	71	-3.12	0.003
Schorfheide	0.93	0.29	67	3.27	0.002	-0.80	0.34	71	-2.31	0.024
Vegetation height (cm)	-	-	-	-	ns	-	-	-	-	ns
Plant species richness (1/9m^2)	-	-	-	-	ns	-	-	-	-	ns
Herbivore diversity H' (1/m^2)	0.42	0.11	42	3.93	<0.001	-	-	-	-	-
Cuts (y^{-1})	0.08	0.05	67	1.52	0.133	-	-	-	-	ns
Grazing (d*y^{-1})	0.00	0.00	67	0.30	0.763	-	-	-	-	ns
Nitrogen (kg*(ha+y)$^{-1}$)	-	-	-	-	ns	-	-	-	-	ns
Succession	-0.03	0.05	42	-0.53	0.600	-0.18	0.19	47	-0.95	0.345
Herbivore H' : Hainich	-0.35	0.12	42	-2.81	0.008	-	-	-	-	ns
Herbivore H' :Schorfheide	-0.35	0.14	42	-2.55	0.015	-	-	-	-	ns
Grazing : Hainich	0.00	0.00	67	0.36	0.724	-	-	-	-	ns
Grazing : Schorfheide	0.00	0.00	67	-1.59	0.116	-	-	-	-	ns
Cuts : Hainich	0.07	0.07	67	0.98	0.330	-0.06	0.30	71	-0.20	0.840
Cuts : Schorfheide	-0.12	0.08	67	-1.46	0.148	0.71	0.26	71	2.72	0.008

DISCUSSION

This study utilized a large-scale and multi-site experiment within the research platform "Biodiversity Exploratories" to identify the responses of herbivores and predators to land-use intensification and the potential of short-term set-aside to buffer biodiversity losses in real-world grassland ecosystems. In our approach we used a continuous and reproducible index to account for the quantitative variation of multiple land-use types in heterogeneous landscapes and found that it was an adequate and relatively easily accessible tool to quantify agricultural intensification.

Applying this experimental framework, we found a direct negative effect of overall land-use intensification on diversity and abundance of the herbivore community on the land-use subplots, consistently at the three study regions, which confirms our initial hypothesis. In particular, mowing frequency, directly affecting vegetation height and long-term decreasing plant species richness (Zechmeister et al. 2003), excelled as a key driver of herbivore diversity decline. Frequent mowing regimes, with more than one cut per year, reduced herbivore diversity at the land-use subplot compared to the succession subplot. Cutting leads to a sudden decrease in resource heterogeneity and quantity in addition to mechanically harming and killing individuals (Humbert et al. 2010). This confronts herbivores with bottlenecks in food resource availability frequently throughout the year and limits overall diversity and abundance. Reported negative effects of cutting are in agreement with a well-established body of literature (e.g. Morris & Rispin 1987; Gerstmeier & Lang 1996; Bell et al. 2001; Johst et al. 2006). In contrast to our findings, in some studies disturbance through grazing, without changes in vegetation, was found to directly decrease herbivore species richness (Kruess & Tscharntke 2002a, Kruess & Tscharntke 2002b, Woodcock et al. 2009) on pastures with high livestock densities. However, observed grazing practices, with on-site stocking densities of 37 units ha^{-1} and durations of 27 days year^{-1} on average, did possibly not reduce plant resource availability to a critical bottleneck situation for herbivores. Moderate grazing intensity may also stimulate grass growth (e.g. by inducing new tillers or lateral shoots; Tscharntke & Greiler 1995) which may also explain the weak negative effects of high and more aged vegetation on herbivore abundances within the succession plots. Herbivores at the Schorfheide Exploratory showed additional negative responses to management practices that were not observed at the other two regions. We found slight herbivore diversity decreases with increasing fertilizer application, indicating that fertilization levels at Schorfheide above a threshold of ca. 100 kg nitrogen ha^{-1} changed herbivore species diversity. In addition, the negative effect of cutting on herbivore abundance was most pronounced at Schorfheide, which might be a consequence of the lowest vegetation heights found. As plant species richness declined with increasing land-use intensity, which is often shown to be a long-term consequence of land-use intensification (e.g. Zechmeister et al. 2003), herbivore diversity and abundance also decreased, in line with the Resource Specialization Hypothesis. Positive effects of higher vegetation on herbivore abundance seem to gain in importance especially at the plant species-poor sites found at Schorfheide, since at Schwäbische Alb and Hainich more herbivores were found at sites with lower vegetation but higher plant species richness.

We have shown that herbivores but not predators are directly affected by grassland management, supporting the findings of Scherber et al. (2010) along an experimental grassland plant diversity gradient. In agreement with our second hypothesis, we found predator diversity significantly increasing with higher herbivore diversity and abundance levels at all regions indicating predators are bottom-up controlled via herbivore availability. We found the steepest increase in diversity of predators with herbivores at the Schwäbische Alb Exploratory, generally harboring also the highest herbivore abundances, emphasizing the prevalence of bottom-up effects. Therefore, grasslands managed extensively and not cut more than once per year may provide sufficient resources along the bottom-up trophic cascades to bear locally species-rich insect interaction webs.

Our third hypothesis that short-term and small-scale experimental set-aside increases diversities, holds only for herbivores, since predators did not respond directly to land-use intensification and management practices at all. It is often expected that set-aside does exhibit steadily increasing species richness with successional age (Brown & Southwood 1987), but biodiversity benefits of short-term set-aside has been often underestimated (Tscharntke et al. 2011). In fact, successional islets established on frequently mown grasslands significantly increased herbivore diversity, whereas set-aside on less intensively used grasslands did not alter herbivore diversities. These results demonstrate that the efficiency of set-aside islets as a conservational tool varies with land-use intensification and local management practices. Accordingly, as predicted by our fourth hypothesis, the establishment of short-term succession areas on grasslands becomes more efficient with increasing land-use intensification levels, primarily higher mowing frequencies. At this, even small areas temporarily excluded from management can mitigate negative effects of cutting, and provide suitable refuge from which insects can re-colonize sward islets on surrounding and intensively managed grasslands.

In conclusion, the data presented here show that overall land-use intensification consistently reduced herbivore diversity and abundance. Predators did not respond to land-use intensification or single management practices directly but were bottom-up controlled via herbivores. In particular, mowing frequency, reducing vegetation height and plant diversity, excels as a key driver of herbivore diversity decline, also affecting predator diversity through trophic cascades. Short-term set-aside increased herbivore communities on frequently mown plots, which may provide source populations for the re-colonization of the surrounding intensively managed grasslands and consequently promote important services such as biological control. Interestingly, the efficiency of this conservation management practice increased with land-use intensification. Therefore, to improve diversity of insect functional groups most effectively, we recommend farmers to relieve small areas from management especially on intensively used grasslands and notably when several cuts per year are applied. Temporarily allowing successional subplots on intensively used grasslands appeared to be a low cost-high benefit conservation measure introducing and sustaining habitat heterogeneity and insect diversity despite of ever changing land-use practices and environmental conditions. Further studies are needed to address the relationship between functional group diversity and associated processes to sustain desirable levels of ecosystem services on local and landscape scales.

ACKNOWLEDGEMENTS

We thank the managers of the three Exploratories, Swen Renner, Sonja Gockel, Andreas Hemp and Martin Gorke and Simone Pfeiffer for their work in maintaining the plot and project infrastructure, and Markus Fischer, Elisabeth Kalko, Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze and Wolfgang W. Weisser for their role in setting up the Biodiversity Exploratories project. Furthermore, we are indebted to Matthias Spiegler for help in the field and to Jochen Fründ for statistical support.

The work has been (partly) funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (TS 45/28-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

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APPENDIX

APPENDIX S1: Land use intensity index LUI

To analyze land use intensity on a local scale we combined data from farmers` interviews. In questionnaires, we asked (among others) for the following quantities:

(i) Livestock units per hectare
(ii) Duration of grazing period
(iii) Number and timing of mowing events
(iv) Number and amount of fertilizer applications

Details on questionnaires are available upon request. Based on these questionnaires, we derived four different components that were used in different models and applicable to different requirements of the particular target species:

1. Grazing intensity index:
Livestock units * days grazing

2. Mowing intensity index:
365 – (days (1.1. to 1st mowing) +
0.5 * days (2nd mowing – 1st mowing) +
0.5 * days (3rd mowing – 2nd mowing) +…

3. Fertilizer index:
Number applications * (amount N)

After scaling the different components to a continuous number between 0 (lowest) and 1 (highest intensity), we combined local land use data in an overall land use intensity index LUI. This was done using a ranging transformation which is commonly used to describe agricultural intensification (following Legendre & Legendre 1998, Herzog et al. 2006). LUI was calculated as:

$$LUI = \left(\frac{\sum_{i-1}^{n} (y_i - y_{\min}) / (y_{\max} - y_{\min})}{n} \right) \times 100$$

y_1= Mowing intensity index
y_2= Grazing intensity index
y_3= Fertilizer index

LUI is reproducible, was well correlated with local plant α-diversity (Spearman correlation, ρ=-0.355, P<0.001) and allows flexible weighting of components. Further, it shows linearity and uses only one degree of freedom (rather than factor levels) which improves statistical analysis options. It is the main explanatory variable in all data analyses performed.

APPENDIX S2: Models and R functions

Models herbivores:

```
lme (herbivore diversity~sqrt(herbivore abundance+0.5)+land use
     intensity*(Exploratory+subplot),
     data = mydata, random = ~1|PlotId, weights=varPower(form=~
     herbivore abundance),
     method = "ML", control = list(opt = "optim"))

glmmPQL (cbind(herbivore abundance, insect abundance- herbivore
     abundance)~land use intensity*(Exploratory+subplot),
     random=~1|PlotId, control=list(opt="optim"),
     family="quasibinomial")

lme (herbivore diversity ~sqrt(herbivore abundance+0.5)+(days
     grazing+plant species richness+vegetation height+number
     cuts+Nitrogen)*(Exploratory+subplot), data = mydata, random =
     ~1|PlotId, method="ML",
     control = list(opt = "optim"))

glmmPQL (cbind(herbivore abundance, insect abundance- herbivore
     abundance)~(number cuts+vegetation height+plant species
     richness+days grazing+Nitrogen.)*(Exploratory+subplot),
     random=~1|PlotId, control=list(opt="optim"),
     family="quasibinomial")
```

Models predators:

```
lme (predator diversity~sqrt(predator abundance+0.5)+land use
     intensity*(Exploratory+subplot),
     data = mydata, random = ~1|PlotId,
     weights=varExp(form=~predator abundance), method="ML",
     control = list(opt = "optim"))

glmmPQL (cbind(predator abundance, insect abundance-predator
     abundance)~land use intensity*(Exploratory+subplot),
     random=~1|PlotId,control=list(opt="optim"),
     family="quasibinomial")

lme (predator diversity~sqrt(predator abundance+0.5)+(herbivore
     diversity+days
     grazing+vegetation height+number
     cuts+Nitrogen)*(Exploratory+subplot),
     data = mydata, random = ~1|PlotId,
     weights=varExp(form=~predator abundance),
     method="ML", control = list(opt = "optim"))

glmmPQL (cbind(predator abundance, insect abundance-predator
     abundance)~(number cuts+vegetation height+plant species
     richness+days grazing+Nitrogen)*(Exploratory+subplot),
     random=~1|PlotId, control=list(opt="optim"),
     family="quasibinomial")
```

R functions used to perform stepwise model selection based on AICc

```
# This code consists of the following functions:
#
# (1) extractAICc
# (2) dropterm.AICc
# (3) addterm.AICc
# (4) stepAICc
#
# Code originally written by B.D. Ripley and W.N. Venables
# with changes in the extractAICc function and others written
# by C. Scherber, 4th/5th May 2009.
#
# The function stepAICc may be used to perform AICc-based
# model selection if sample sizes are too small to use AIC.
#
# AICc is a version of AIC corrected for small sample sizes
# as defined in Burnham & Anderson, 2002.

extractAICc=function (fit, scale, k = 2, ...)
{
    if (fit$method != "ML")
        stop("AIC undefined for REML fit")
    res <- logLik(fit)
    edf <- attr(res, "df")
    n=length(residuals(fit))
    c(edf,-2 * res + k * edf+2*edf*(edf+1)/(n-edf-1))
}

dropterm.AICc=
function (object, scope, scale = 0, test = c("none", "Chisq"),
    k = 2, sorted = FALSE, trace = FALSE, ...)
{
    tl <- attr(terms(object), "term.labels")
    if (missing(scope))
        scope <- drop.scope(object)
    else {
        if (!is.character(scope))
            scope <- attr(terms(update.formula(object, scope)),
                "term.labels")
        if (!all(match(scope, tl, 0L)))
            stop("scope is not a subset of term labels")
    }
    ns <- length(scope)
    ans <- matrix(nrow = ns + 1L, ncol = 2L, dimnames =
      list(c("<none>",
        scope), c("df", "AIC")))
    ans[1, ] <- extractAICc(object, scale, k = k, ...)
    env <- environment(formula(object))
    n0 <- length(object$residuals)
    for (i in seq(ns)) {
        tt <- scope[i]
        if (trace) {
            message("trying -", tt)
            utils::flush.console()
```

```
        }
        nfit <- update(object, as.formula(paste("~ . -", tt)),
            evaluate = FALSE)
        nfit <- eval(nfit, envir = env)
        ans[i + 1, ] <- extractAICc(nfit, scale, k = k, ...)
        if (length(nfit$residuals) != n0)
            stop("number of rows in use has changed: remove
     missing values?")
    }
    dfs <- ans[1L, 1L] - ans[, 1L]
    dfs[1L] <- NA
    aod <- data.frame(Df = dfs, AIC = ans[, 2])
    o <- if (sorted)
        order(aod$AIC)
    else seq_along(aod$AIC)
    test <- match.arg(test)
    if (test == "Chisq") {
        dev <- ans[, 2L] - k * ans[, 1L]
        dev <- dev - dev[1L]
        dev[1L] <- NA
        nas <- !is.na(dev)
        P <- dev
        P[nas] <- safe_pchisq(dev[nas], dfs[nas], lower.tail =
     FALSE)
        aod[, c("LRT", "Pr(Chi)")] <- list(dev, P)
    }
    aod <- aod[o, ]
    head <- c("Single term deletions", "\nModel:",
     deparse(as.vector(formula(object))))
    if (scale > 0)
        head <- c(head, paste("\nscale: ", format(scale), "\n"))
    class(aod) <- c("anova", "data.frame")
    attr(aod, "heading") <- head
    aod
}

##
addterm.AICc=function (object, scope, scale = 0, test = c("none",
     "Chisq"),
    k = 2, sorted = FALSE, trace = FALSE, ...)
{
    if (missing(scope) || is.null(scope))
        stop("no terms in scope")
    if (!is.character(scope))
        scope <- add.scope(object, update.formula(object, scope))
    if (!length(scope))
        stop("no terms in scope for adding to object")
    ns <- length(scope)
    ans <- matrix(nrow = ns + 1L, ncol = 2L, dimnames =
     list(c("<none>",
        scope), c("df", "AIC")))
    ans[1L, ] <- extractAICc(object, scale, k = k, ...)
    n0 <- length(object$residuals)
    env <- environment(formula(object))
    for (i in seq(ns)) {
        tt <- scope[i]
```

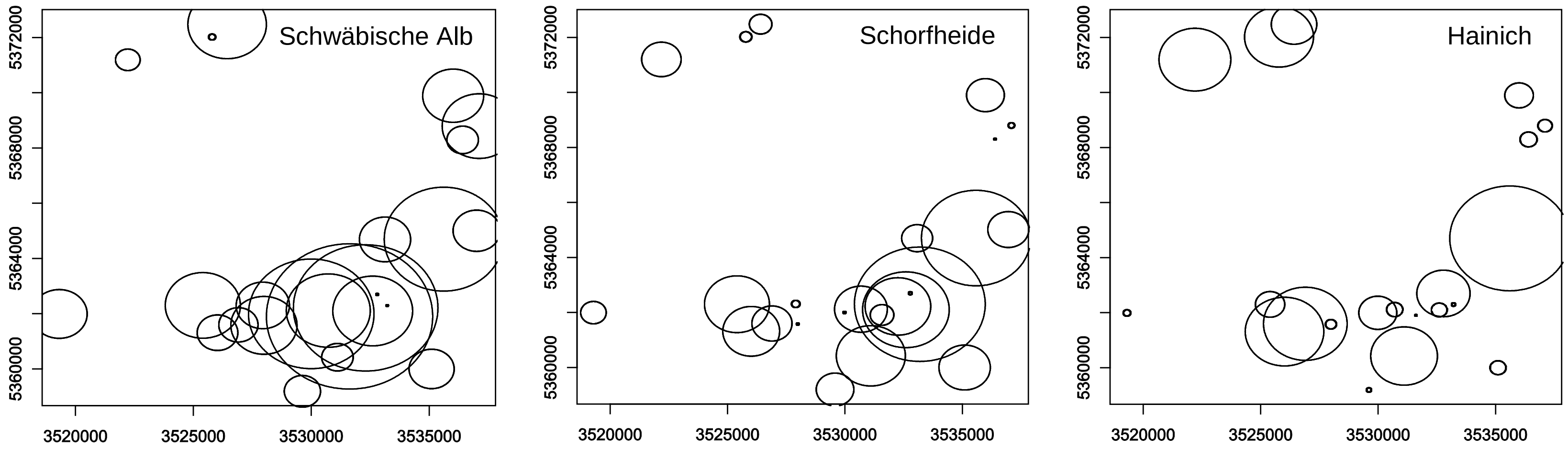
```
        if (trace) {
            message("trying +", tt)
            utils::flush.console()
        }
        nfit <- update(object, as.formula(paste("~ . +", tt)),
            evaluate = FALSE)
        nfit <- eval(nfit, envir = env)
        ans[i + 1L, ] <- extractAICc(nfit, scale, k = k, ...)
        if (length(nfit$residuals) != n0)
            stop("number of rows in use has changed: remove
     missing values?")
    }
    dfs <- ans[, 1L] - ans[1L, 1L]
    dfs[1L] <- NA
    aod <- data.frame(Df = dfs, AIC = ans[, 2L])
    o <- if (sorted)
        order(aod$AIC)
    else seq_along(aod$AIC)
    test <- match.arg(test)
    if (test == "Chisq") {
        dev <- ans[, 2L] - k * ans[, 1L]
        dev <- dev[1L] - dev
        dev[1L] <- NA
        nas <- !is.na(dev)
        P <- dev
        P[nas] <- safe_pchisq(dev[nas], dfs[nas], lower.tail =
     FALSE)
        aod[, c("LRT", "Pr(Chi)")] <- list(dev, P)
    }
    aod <- aod[o, ]
    head <- c("Single term additions", "\nModel:",
     deparse(as.vector(formula(object))))
    if (scale > 0)
        head <- c(head, paste("\nscale: ", format(scale), "\n"))
    class(aod) <- c("anova", "data.frame")
    attr(aod, "heading") <- head
    aod
}

##
stepAICc=function (object, scope, scale = 0, direction = c("both",
     "backward",
    "forward"), trace = 1, keep = NULL, steps = 1000, use.start =
     FALSE,
    k = 2, ...)
{
    mydeviance <- function(x, ...) {
        dev <- deviance(x)
        if (!is.null(dev))
            dev
        else extractAICc(x, k = 0)[2L]
    }
    cut.string <- function(string) {
        if (length(string) > 1L)
            string[-1L] <- paste("\n", string[-1L], sep = "")
        string
```

```
    }
    re.arrange <- function(keep) {
        namr <- names(k1 <- keep[[1L]])
        namc <- names(keep)
        nc <- length(keep)
        nr <- length(k1)
        array(unlist(keep, recursive = FALSE), c(nr, nc),
     list(namr,
            namc))
    }
    step.results <- function(models, fit, object, usingCp = FALSE)
     {
        change <- sapply(models, "[[", "change")
        rd <- sapply(models, "[[", "deviance")
        dd <- c(NA, abs(diff(rd)))
        rdf <- sapply(models, "[[", "df.resid")
        ddf <- c(NA, abs(diff(rdf)))
        AIC <- sapply(models, "[[", "AIC")
        heading <- c("Stepwise Model Path \nAnalysis of Deviance
     Table",
            "\nInitial Model:",
     deparse(as.vector(formula(object))),
            "\nFinal Model:", deparse(as.vector(formula(fit))),
            "\n")
        aod <- if (usingCp)
            data.frame(Step = change, Df = ddf, Deviance = dd,
                `Resid. Df` = rdf, `Resid. Dev` = rd, Cp = AIC,
                check.names = FALSE)
        else data.frame(Step = change, Df = ddf, Deviance = dd,
            `Resid. Df` = rdf, `Resid. Dev` = rd, AIC = AIC,
            check.names = FALSE)
        attr(aod, "heading") <- heading
        class(aod) <- c("Anova", "data.frame")
        fit$anova <- aod
        fit
    }
    Terms <- terms(object)
    object$formula <- Terms
    if (inherits(object, "lme"))
        object$call$fixed <- Terms
    else if (inherits(object, "gls"))
        object$call$model <- Terms
    else object$call$formula <- Terms
    if (use.start)
        warning("'use.start' cannot be used with R's version of
     glm")
    md <- missing(direction)
    direction <- match.arg(direction)
    backward <- direction == "both" | direction == "backward"
    forward <- direction == "both" | direction == "forward"
    if (missing(scope)) {
        fdrop <- numeric(0)
        fadd <- attr(Terms, "factors")
        if (md)
            forward <- FALSE
    }
```

```
else {
    if (is.list(scope)) {
        fdrop <- if (!is.null(fdrop <- scope$lower))
            attr(terms(update.formula(object, fdrop)),
 "factors")
        else numeric(0)
        fadd <- if (!is.null(fadd <- scope$upper))
            attr(terms(update.formula(object, fadd)),
 "factors")
    }
    else {
        fadd <- if (!is.null(fadd <- scope))
            attr(terms(update.formula(object, scope)),
 "factors")
        fdrop <- numeric(0)
    }
}
models <- vector("list", steps)
if (!is.null(keep))
    keep.list <- vector("list", steps)
if (is.list(object) && (nmm <- match("nobs", names(object),
    0)) > 0)
    n <- object[[nmm]]
else n <- length(residuals(object))
fit <- object
bAIC <- extractAICc(fit, scale, k = k, ...)
edf <- bAIC[1L]
bAIC <- bAIC[2L]
if (is.na(bAIC))
    stop("AIC is not defined for this model, so stepAIC cannot
 proceed")
nm <- 1
Terms <- terms(fit)
if (trace) {
    cat("Start:  AICc=", format(round(bAIC, 2)), "\n",
 cut.string(deparse(as.vector(formula(fit)))),
        "\n\n", sep = "")
    utils::flush.console()
}
models[[nm]] <- list(deviance = mydeviance(fit), df.resid = n
 -
    edf, change = "", AIC = bAIC)
if (!is.null(keep))
    keep.list[[nm]] <- keep(fit, bAIC)
usingCp <- FALSE
while (steps > 0) {
    steps <- steps - 1
    AIC <- bAIC
    ffac <- attr(Terms, "factors")
    if (!is.null(sp <- attr(Terms, "specials")) && !is.null(st
 <- sp$strata))
        ffac <- ffac[-st, ]
    scope <- factor.scope(ffac, list(add = fadd, drop =
 fdrop))
    aod <- NULL
    change <- NULL
```

```
    if (backward && length(scope$drop)) {
        aod <- dropterm.AICc(fit, scope$drop, scale = scale,
trace = max(0,
            trace - 1), k = k, ...)
        rn <- row.names(aod)
        row.names(aod) <- c(rn[1L], paste("-", rn[-1L], sep =
" "))
        if (any(aod$Df == 0, na.rm = TRUE)) {
            zdf <- aod$Df == 0 & !is.na(aod$Df)
            nc <- match(c("Cp", "AIC"), names(aod))
            nc <- nc[!is.na(nc)][1L]
            ch <- abs(aod[zdf, nc] - aod[1, nc]) > 0.01
            if (any(ch)) {
              warning("0 df terms are changing AIC")
              zdf <- zdf[!ch]
            }
            if (length(zdf) > 0L)
              change <- rev(rownames(aod)[zdf])[1L]
        }
    }
    if (is.null(change)) {
        if (forward && length(scope$add)) {
            aodf <- addterm.AICc(fit, scope$add, scale =
scale,
              trace = max(0, trace - 1), k = k, ...)
            rn <- row.names(aodf)
            row.names(aodf) <- c(rn[1L], paste("+", rn[-1L],
              sep = " "))
            aod <- if (is.null(aod))
              aodf
            else rbind(aod, aodf[-1, , drop = FALSE])
        }
        attr(aod, "heading") <- NULL
        if (is.null(aod) || ncol(aod) == 0)
            break
        nzdf <- if (!is.null(aod$Df))
            aod$Df != 0 | is.na(aod$Df)
        aod <- aod[nzdf, ]
        if (is.null(aod) || ncol(aod) == 0)
            break
        nc <- match(c("Cp", "AIC"), names(aod))
        nc <- nc[!is.na(nc)][1L]
        o <- order(aod[, nc])
        if (trace) {
            print(aod[o, ])
            utils::flush.console()
        }
        if (o[1L] == 1)
            break
        change <- rownames(aod)[o[1L]]
    }
    usingCp <- match("Cp", names(aod), 0) > 0
    fit <- update(fit, paste("~ .", change), evaluate = FALSE)
    fit <- eval.parent(fit)
    if (is.list(fit) && (nmm <- match("nobs", names(fit),
        0)) > 0)
```

```
            nnew <- fit[[nmm]]
        else nnew <- length(residuals(fit))
        if (nnew != n)
            stop("number of rows in use has changed: remove
     missing values?")
        Terms <- terms(fit)
        bAIC <- extractAICc(fit, scale, k = k, ...)
        edf <- bAIC[1L]
        bAIC <- bAIC[2L]
        if (trace) {
            cat("\nStep:  AICc=", format(round(bAIC, 2)), "\n",
                cut.string(deparse(as.vector(formula(fit)))),
                "\n\n", sep = "")
            utils::flush.console()
        }
        if (bAIC >= AIC + 1e-07)
            break
        nm <- nm + 1
        models[[nm]] <- list(deviance = mydeviance(fit), df.resid
     = n -
            edf, change = change, AIC = bAIC)
        if (!is.null(keep))
            keep.list[[nm]] <- keep(fit, bAIC)
    }
    if (!is.null(keep))
        fit$keep <- re.arrange(keep.list[seq(nm)])
    step.results(models = models[seq(nm)], fit, object, usingCp)
}
```



Appendix S3. Plots of model residuals to assess spatial autocorrelation, separately for each Exploratory region. Plots were produced by fitting gls models with exponential variance function, where Gauss-Krüger coordinates were used as spatial covariates, assuming a spherical spatial correlation structure. Residuals were not spatially autocorrelated, i.e. likelihood of models decreased when spatial autocorrelation was included in the models.

Appendix S4.1. Coleoptera species and abundance list:

Family	Genus	Species	Trophic level	Alb	Hai	Sch
Carabidae	*Acupalpus*	*parvulus* (STURM) 1825	predator	0	0	1
Elateridae	*Agriotes*	*gallicus* BOISD. & LACOR. 1835	herbivore	0	1	0
Elateridae	*Agriotes*	*lineatus* (LINNÉ) 1767	herbivore	0	1	0
Elateridae	*Agriotes*	*obscurus* (LINNÉ) 1758	herbivore	1	3	0
Elateridae	*Agriotes*	*sputator* (LINNÉ) 1758	herbivore	4	0	0
Staphylinidae	*Aleochara*	*bipustulata* (LINNÉ) 1761	predator	1	0	0
Staphylinidae	*Aleochara*	*lanuginosa* GRAVENHORST 1802	predator	0	0	1
Staphylinidae	*Aloconota*	*gregaria* (ERICHSON) 1839	predator	0	0	1
Curculionidae	*Alophus*	*triguttatus* (FABRICIUS) 1775	herbivore	1	0	0
Chrysomelidae	*Altica*	*pusilla* DUFTSCHMID 1825	herbivore	2	0	0
Chrysomelidae	*Altica*	*spec.*	herbivore	4	0	4
Staphylinidae	*Amischa*	*analis* (GRAVENHORST) 1802	predator	2	5	6
Staphylinidae	*Amischa*	*bifoveolata* (MANNERHEIM) 1830	predator	0	1	0
Staphylinidae	*Amischa*	*decipiens* SHARP 1869	predator	0	0	1
Staphylinidae	*Amischa*	*nigrofusca* (STEPHENS) 1832	predator	1	1	0
Chrysomelidae	*Aphthona*	*cyanella* (REDTENBACHER) 1849	herbivore	1	0	0
Apionidae	*Apion*	*cruentatum* WALTON 1844	herbivore	2	0	0
Apionidae	*Apion*	*frumentarium* (LINNÉ) 1758	herbivore	0	0	2
Chrysomelidae	*Asiorestia*	*ferruginea* (SCOPOLI) 1763	herbivore	74	10	92
Staphylinidae	*Atheta*	*elongatula* (GRAVENH.) 1802	predator	1	0	0
Carabidae	*Badister*	*bullatus* (SCHRANK) 1798	predator	0	2	0
Curculionidae	*Bagous*	*tempestivus* (HERBST) 1795	herbivore	0	0	1
Carabidae	*Bembidion*	*gilvipes* STURM 1825	predator	1	0	9
Carabidae	*Bembidion*	*guttula* (FABRICIUS) 1792	predator	0	4	2
Carabidae	*Bembidion*	*lampros* (HERBST) 1784	predator	1	2	5
Carabidae	*Bembidion*	*mannerheimii* SAHLBERG 1827	predator	0	0	1
Carabidae	*Bembidion*	*obtusum* SERVILLE 1821	predator	0	24	0
Carabidae	*Bembidion*	*properans* STEPHENS 1828	predator	0	0	2
Carabidae	*Brachinus*	*crepitans* (LINNÉ) 1758	predator	0	1	0
Pselaphidae	*Brachygluta*	*sinuate* (AUBÉ) 1833	predator	0	0	1
Kateretidae	*Brachypterus*	*urticae* (FABRICIUS) 1792	herbivore	0	0	1
Bruchidae	*Bruchus*	*loti* PAYKULL 1800	herbivore	1	0	0
Carabidae	*Calathus*	*fuscipes* (GOEZE) 1777	predator	0	0	1
Carabidae	*Calathus*	*melanocephalus* (LINNÉ) 1758	predator	1	0	8
Cantharidae	*Cantharis*	*fulvicollis* FABRICIUS 1792	predator	4	0	0
Cantharidae	*Cantharis*	*fusca* LINNÉ 1758	predator	0	0	2
Cantharidae	*Cantharis*	*rufa* LINNÉ 1758	predator	0	1	1
Chrysomelidae	*Cassida*	*denticollis* SUFFRIAN 1844	herbivore	1	0	1
Apionidae	*Catapion*	*pubescens* (KIRBY) 1811	herbivore	0	1	3
Apionidae	*Catapion*	*seniculus* (KIRBY) 1808	herbivore	2	10	0
Chrysomelidae	*Chaetocnema*	*aridula* (GYLLENHAL) 1827	herbivore	0	8	20
Chrysomelidae	*Chaetocnema*	*concinna* (MARSHAM) 1802	herbivore	0	0	1
Chrysomelidae	*Chaetocnema*	*hortensis* (GEOFFROY) 1785	herbivore	7	7	27

Family	**Genus**	**Species**	**Trophic level**	**Alb**	**Hai**	**Sch**
Malachiidae	*Charopus*	*flavipes* (PAYKULL) 1798	predator	0	4	0
Oedemeridae	*Chrysanthia*	*viridissima* (LINNÉ) 1758	herbivore	1	0	0
Chrysomelidae	*Chrysolina*	*oricalcia* (MÜLLER,O.F) 1776	herbivore	0	0	1
Malachiidae	*Clanoptilus*	*marginellus* (OLIVIER) 1790	predator	0	0	1
Chrysomelidae	*Clytra*	*quadripunctata* (LINNÉ) 1758	herbivore	0	1	0
Coccinellidae	*Coccidula*	*rufa* (HERBST) 1783	predator	0	0	11
Coccinellidae	*Coccinella*	*septempunctata* LINNÉ 1758	predator	4	2	14
Coccinellidae	*Coccinula*	*quatuordecimpustulata* (L.) 1758	predator	0	0	1
Malachiidae	*Cordylepherus*	*viridis* (FABRICIUS) 1787	predator	0	0	3
Staphylinidae	*Cryptobium*	*collare* REITTER 1884	predator	1	0	0
Apionidae	*Cyanapion*	*columbinum* (GERMAR) 1817	herbivore	0	1	0
Apionidae	*Cyanapion*	*spencii* (KIRBY) 1808	herbivore	0	1	0
Staphylinidae	*Cypha*	*longicornis* (PAYKULL) 1800	predator	0	2	0
Scirtidae	*Cyphon*	*palustris* THOMSON 1855	predator	0	0	1
Elateridae	*Dalopius*	*marginatus* (LINNÉ) 1758	herbivore	0	0	1
Chrysomelidae	*Dibolia*	*cryptocephala* (KOCH) 1803	herbivore	8	0	0
Apionidae	*Diplapion*	*stolidum* (GERMAR) 1817	herbivore	0	1	0
Carabidae	*Dromius*	*linearis* (OLIVIER) 1795	predator	0	2	3
Staphylinidae	*Drusilla*	*canaliculata* (FABRICIUS) 1787	predator	0	10	4
Carabidae	*Dyschirius*	*globosus* (HERBST) 1784	predator	0	0	10
Carabidae	*Epaphius*	*secalis* (PAYKULL) 1790	predator	0	2	1
Nitidulidae	*Epuraea*	*aestival* (LINNÉ) 1758	herbivore	1	0	0
Staphylinidae	*Euaestethus*	*laeviusculus* (MANNERHEIM) 1844	predator	0	0	1
Curculionidae	*Eusomus*	*ovulum* GERMAR 1824	herbivore	0	0	3
Staphylinidae	*Eusphalerum*	*sorbi* (GYLLENHAL) 1810	herbivore	1	0	0
Staphylinidae	*Gabrius*	*spec.*	predator	1	0	2
Staphylinidae	*Gabrius*	*subnigritulus* (REITTER) 1909	predator	1	0	0
Chrysomelidae	*Galeruca*	*tanaceti* (LINNÉ) 1758	herbivore	0	1	0
Curculionidae	*Glocianus*	*punctiger* (GYLLENHAL) 1837	herbivore	8	7	62
Curculionidae	*Gymnetron*	*pascuorum* (GYLLENHAL) 1813	herbivore	0	0	9
Curculionidae	*Gymnetron*	*rostellum* (HERBST) 1795	herbivore	0	0	3
Curculionidae	*Gymnetron*	*veronicae* (GERMAR) 1821	herbivore	1	0	0
Hydrophilidae	*Helophorus*	*brevipalpis* BEDEL 1881	herbivore	0	0	1
Hydrophilidae	*Helophorus*	*grandis* ILLIGER 1798	herbivore	0	0	1
Hydrophilidae	*Helophorus*	*nubilus* (FABRICIUS) 1777	herbivore	0	0	1
Elateridae	*Hemicrepidius*	*niger* (LINNÉ) 1758	herbivore	9	0	4
Apionidae	*Hemitrichapion*	*pavidum* (GERMAR) 1817	herbivore	1	0	0
Staphylinidae	*Heterothops*	*dissimilis* (GRAVENHORST) 1802	predator	0	0	2
Coccinellidae	*Hippodamia*	*notata* (LAICHARTING) 1781	predator	2	0	0
Coccinellidae	*Hippodamia*	*tredecimpunctata* (LINNÉ) 1758	predator	1	0	4
Chrysomelidae	*Hippodamia*	*variegata* (GOEZE) 1777	herbivore	0	1	3
Apionidae	*Hispella*	*atra* (LINNÉ) 1767	herbivore	0	0	1
Apionidae	*Holotrichapion*	*aethiops* (HERBST) 1797	herbivore	0	0	1
Curculionidae	*Hylastinus*	*obscurus* (MARSHAM) 1802	herbivore	0	1	0
Curculionidae	*Hypera*	*diversipunctata* (SCHRANK) 1798	herbivore	0	0	1

Family	**Genus**	**Species**	**Trophic level**	**Alb**	**Hai**	**Sch**
Curculionidae	*Hypera*	*meles* (FABRICIUS) 1792	herbivore	0	1	2
Curculionidae	*Hypera*	*nigrirostris* (FABRICIUS) 1775	herbivore	5	15	2
Curculionidae	*Hypera*	*postica* (GYLLENHAL) 1813	herbivore	0	1	0
Curculionidae	*Hypera*	*venusta* (FABRICIUS) 1781	herbivore	0	0	1
Curculionidae	*Hypera*	*zoilus* (SCOPOLI) 1763	herbivore	0	0	1
Apionidae	*Ischnopterapion*	*loti* (KIRBY) 1808	herbivore	2	5	0
Apionidae	*Ischnopterapion*	*virens* (HERBST) 1797	herbivore	78	596	181
Kateretidae	*Kateretes*	*pedicularius* (LINNÉ) 1758	herbivore	0	0	8
Carabidae	*Lebia*	*chlorocephala* (HOFFMANN) 1803	predator	0	0	1
Carabidae	*Leistus*	*ferrugineus* (LINNÉ) 1758	predator	0	0	1
Chrysomelidae	*Lema*	*cyanella* (LINNÉ) 1758	herbivore	0	0	1
Curculionidae	*Limobius*	*borealis* (GYLLENHAL) 1792	herbivore	0	0	3
Chrysomelidae	*Longitarsus*	*atricillus* (LINNÉ) 1761	herbivore	0	0	1
Chrysomelidae	*Longitarsus*	*luridus* (SCOPOLI) 1763	herbivore	24	197	4
Chrysomelidae	*Longitarsus*	*melanocephalus* (DEGEER) 1775	herbivore	6	39	31
Chrysomelidae	*Longitarsus*	*noricus* LEONARDI 1976	herbivore	18	3	21
Chrysomelidae	*Longitarsus*	*obliterates* (ROSENHAUER) 1847	herbivore	2	0	0
Chrysomelidae	*Longitarsus*	*pellucidus* (FOUDRAS) 1860	herbivore	0	0	2
Chrysomelidae	*Longitarsus*	*pratensis* (PANZER) 1794	herbivore	26	166	18
Chrysomelidae	*Longitarsus*	*symphyti* HEIKERTINGER 1912	herbivore	0	0	2
Malachiidae	*Malachius*	*bipustulatus* (LINNÉ) 1758	predator	0	1	0
Curculionidae	*Mecinus*	*pyraster* (HERBST) 1795	herbivore	2	1	0
Nitidulidae	*Meligethes*	*aeneus* (FABRICIUS) 1775	herbivore	18	0	57
Nitidulidae	*Meligethes*	*kunzei* ERICHSON 1845	herbivore	1	0	0
Nitidulidae	*Meligethes*	*nigrescens* STEPHENS 1830	herbivore	0	0	1
Carabidae	*Microlestes*	*maurus* (STURM) 1827	predator	0	5	0
Carabidae	*Microlestes*	*minutulus* (GOEZE) 1777	predator	0	0	1
Mordellidae	*Mordellistena*	*micantoides* ERMISCH 1954	herbivore	0	1	0
Coccinellidae	*Nephus*	*redtenbacheri* (MULSANT) 1846	predator	7	6	0
Carabidae	*Notiophilus*	*palustris* (DUFTSCHMID) 1812	predator	0	0	1
Oedemeridae	*Oedemera*	*lurida* (MARSHAM) 1802	herbivore	1	0	0
Elateridae	*Oedostethus*	*quadripustulatus* (FABR.) 1792	herbivore	0	0	5
Phalacridae	*Olibrus*	*aeneus* (FABRICIUS) 1792	herbivore	0	0	1
Phalacridae	*Olibrus*	*affinis* (STURM) 1807	herbivore	0	0	22
Phalacridae	*Olibrus*	*bicolor* (FABRICIUS) 1792	herbivore	2	87	44
Phalacridae	*Olibrus*	*bimaculatus* KÜSTER 1848	herbivore	0	1	1
Phalacridae	*Olibrus*	*norvegicus* MÜNSTER 1901	herbivore	0	0	1
Curculionidae	*Omiamima*	*mollina* (BOHEMAN) 1834	herbivore	0	3	0
Curculionidae	*Orthochaetes*	*setiger* (BECK) 1817	herbivore	0	9	0
Curculionidae	*Otiorhynchus*	*morio* (FABRICIUS) 1781	herbivore	1	0	0
Chrysomelidae	*Oulema*	*gallaeciana* (HEYDEN) 1870	herbivore	0	1	0
Chrysomelidae	*Oulema*	*melanopus* (LINNÉ) 1758	herbivore	0	0	11
Staphylinidae	*Oxypoda*	*brachyptera* (STEPHENS) 1832	predator	0	1	0
Staphylinidae	*Oxypoda*	*haemorrhoa* (MANNERHEIM) 1830	predator	0	0	1
Apionidae	*Oxystoma*	*craccae* (LINNÉ) 1767	herbivore	0	0	1

Family	**Genus**	**Species**	**Trophic level**	**Alb**	**Hai**	**Sch**
Staphylinidae	*Paederus*	*littoralis* GRAVENHORST 1802	predator	0	1	4
Staphylinidae	*Paederus*	*riparius* (LINNÉ) 1758	predator	0	0	1
Apionidae	*Perapion*	*curtirostre* (GERMAR) 1817	herbivore	3	0	1
Apionidae	*Perapion*	*violaceum* (KIRBY) 1808	herbivore	1	2	1
Staphylinidae	*Philonthus*	*carbonarius* GRAVENHORST 1810	predator	1	0	1
Staphylinidae	*Philonthus*	*nitidulus* (GRAVENHORST) 1802	predator	0	0	2
Curculionidae	*Phyllobius*	*viridaeris* (LAICHARTING 1781)	herbivore	0	0	2
Scarabaeidae	*Phyllopertha*	*horticola* (LINNÉ) 1758	herbivore	1	0	0
Chrysomelidae	*Phyllotreta*	*exclamationis* (THUNBERG) 1784	herbivore	0	0	2
Chrysomelidae	*Phyllotreta*	*vittula* REDTENBACHER 1849	herbivore	0	7	4
Coccinellidae	*Platynaspis*	*luteorubra* (GOEZE) 1777	predator	0	1	0
Carabidae	*Poecilus*	*versicolor* (STURM) 1824	predator	1	0	2
Coccinellidae	*Propylea*	*quatuordecimpunctata* (L.) 1758	predator	6	1	4
Apionidae	*Protapion*	*apricans* (HERBST) 1797	herbivore	6	45	1
Apionidae	*Protapion*	*assimile* (KIRBY) 1808	herbivore	7	20	1
Apionidae	*Protapion*	*fulvipes* (FOURCROY) 1785	herbivore	10	21	25
Apionidae	*Protapion*	*nigritarse* (KIRBY) 1808	herbivore	0	3	3
Apionidae	*Protapion*	*trifolii* (LINNÉ) 1768	herbivore	0	1	0
Carabidae	*Pterostichus*	*diligens* (STURM) 1824	predator	0	0	1
Carabidae	*Pterostichus*	*strenuus* (PANZER) 1797	predator	1	1	1
Staphylinidae	*Quedius*	*boops* (GRAVENHORST) 1802	predator	1	1	3
Staphylinidae	*Quedius*	*nitipennis* STEPHENS 1833	predator	0	1	0
Staphylinidae	*Quedius*	*vexans* EPPELSHEIM 1881	predator	1	0	0
Cantharidae	*Rhagonycha*	*limbata* THOMSON 1864	predator	1	0	0
Curculionidae	*Rhinoncus*	*pericarpius* (LINNÉ) 1758	herbivore	2	0	2
Curculionidae	*Rhynchaenus*	*fagi* (LINNÉ) 1758	herbivore	2	0	0
Coccinellidae	*Rhyzobius*	*chrysomeloides* (HERBST) 1792	predator	0	0	1
Staphylinidae	*Rugilus*	*erichsoni* FAUVEL 1867	predator	0	0	2
Staphylinidae	*Rugilus*	*rufipes* (GERMAR) 1836	predator	1	0	0
Pselaphidae	*Rybaxis*	*longicornis* (LEACH) 1817	predator	0	0	1
Staphylinidae	*Scopaeus*	*minutus* ERICHSON 1840	predator	1	0	0
Coccinellidae	*Scymnus*	*femoralis* GYLLENHAL 1827	predator	2	2	0
Coccinellidae	*Scymnus*	*frontalis* (FABRICIUS) 1787	predator	0	1	0
Coccinellidae	*Scymnus*	*haemorrhoidalis* HERBST 1797	predator	1	5	9
Coccinellidae	*Scymnus*	*mimulus* CAPRA & FÜRSCH 1967	predator	2	3	3
Curculionidae	*Sitona*	*gressorius* (FABRICIUS) 1792	herbivore	0	0	1
Curculionidae	*Sitona*	*hispidulus* (FABRICIUS) 1777	herbivore	4	9	29
Curculionidae	*Sitona*	*humeralis* STEPHENS 1831	herbivore	0	3	0
Curculionidae	*Sitona*	*lepidus* GYLLENHAL 1834	herbivore	2	13	38
Curculionidae	*Sitona*	*lineatus* (LINNÉ) 1758	herbivore	9	127	34
Curculionidae	*Sitona*	*macularius* (MARSHAM) 1802	herbivore	0	1	2
Curculionidae	*Sitona*	*ononidis* SHARP 1866	herbivore	0	1	0
Curculionidae	*Sitona*	*sulcifrons* (THUNBERG) 1798	herbivore	0	6	0
Chrysomelidae	*Smaragdina*	*salicina* (SCOPOLI) 1763	herbivore	0	1	0
Curculionidae	*Smicronyx*	*jungermanniae* (REICH) 1797	herbivore	1	0	0

Family	**Genus**	**Species**	**Trophic level**	**Alb**	**Hai**	**Sch**
Apionidae	*Squamapion*	*cineraceum* (WENCKER) 1864	herbivore	1	1	0
Curculionidae	*Stenocarus*	*ruficornis* (STEPHENS) 1831	herbivore	0	0	1
Staphylinidae	*Stenus*	*brunnipes* STEPHENS 1833	predator	0	0	5
Staphylinidae	*Stenus*	*cicindeloides* SCHALLER 1783	predator	0	0	1
Staphylinidae	*Stenus*	*circularis* GRAVENHORST 1802	predator	0	0	1
Staphylinidae	*Stenus*	*clavicornis* (SCOPOLI) 1763	predator	8	9	13
Staphylinidae	*Stenus*	*flavipes* STEPHENS 1833	predator	11	0	0
Staphylinidae	*Stenus*	*fulvicornis* STEPHENS 1833	predator	8	0	10
Staphylinidae	*Stenus*	*geniculatus* GRAVENHORST 1806	predator	0	0	1
Staphylinidae	*Stenus*	*humilis* ERICHSON 1839	predator	5	0	0
Staphylinidae	*Stenus*	*impressus* GERMAR 1824	predator	1	0	0
Staphylinidae	*Stenus*	*ludyi* FAUVEL 1885	predator	3	0	0
Staphylinidae	*Stenus*	*ochropus* KIESENWETTER 1858	predator	0	1	7
Staphylinidae	*Stenus*	*providus* ERICHSON 1839	predator	0	0	1
Staphylinidae	*Stenus*	*pusillus* STEPHENS 1833	predator	0	0	2
Staphylinidae	*Stenus*	*similis* (HERBST) 1784	predator	0	1	0
Staphylinidae	*Stenus*	*spec.*	predator	1	0	0
Staphylinidae	*Sunius*	*melanocephalus* (FABRICIUS) 1792	predator	2	2	2
Carabidae	*Syntomus*	*truncatellus* (LINNÉ) 1761	predator	0	3	5
Curculionidae	*Tanymecus*	*palliatus* (FABRICIUS) 1787	herbivore	0	0	1
Curculionidae	*Trachyphloeus*	*alternans* GYLLENHAL 1834	herbivore	1	2	0
Curculionidae	*Trachyphloeus*	*aristatus* GYLLENHAL 1827	herbivore	0	0	1
Curculionidae	*Trachyphloeus*	*bifoveolatus* (BECK) 1817	herbivore	0	0	3
Curculionidae	*Trachyphloeus*	*scabriculus* (LINNÉ) 1771	herbivore	0	0	1
Buprestidae	*Trachys*	*fragariae* BRISOUT 1874	herbivore	0	1	0
Carabidae	*Trechus*	*quadristriatus* (SCHRANK) 1781	predator	0	5	4
Curculionidae	*Trichosirocalus*	*troglodytes* FABRICIUS 1787	herbivore	9	31	39
Curculionidae	*Tychius*	*lineatulus* STEPHENS 1831	herbivore	1	0	0
Curculionidae	*Tychius*	*micaceus* DESBROCHERS 1873	herbivore	0	1	0
Curculionidae	*Tychius*	*picirostris* (FABRICIUS) 1787	herbivore	3	15	48
Curculionidae	*Tychius*	*tomentosus* (HERBST) 1795	herbivore	3	6	0
Staphylinidae	*Xantholinus*	*linearis* (OLIVIER) 1795	predator	1	0	0
Staphylinidae	*Xantholinus*	*longiventris* HEER 1839	predator	0	0	5
Curculionidae	*Zacladus*	*geranii* (PAYKULL) 1800	herbivore	1	0	0

Appendix S4.2. Heteroptera species and abundance list:

Family	**Genus**	**Species**	**Trophic level**	**Alb**	**Hai**	**Sch**
Tingidae	*Acalypta*	*marginata* (WOLFF) 1804	herbivore	4	25	1
Tingidae	*Acalypta*	*parvula* (FALLÉN) 1807	herbivore	1	2	0
Miridae	*Acetropis*	*carinata* (HERR.-SCHAEFFER) 1841	herbivore	0	2	0
Miridae	*Adelphocoris*	*lineolatus* (GOEZE) 1778	herbivore	1	0	0
Miridae	*Adelphocoris*	*seticornis* (FABRICIUS) 1775	herbivore	2	0	0
Pentatomidae	*Aelia*	*acuminata* (LINNÉ) 1758	herbivore	0	12	40
Miridae	*Amblytylus*	*brevicollis* FIEBER 1858	herbivore	0	0	3
Miridae	*Amblytylus*	*nasutus* (KIRSCHBAUM) 1856	herbivore	4	3	100
Miridae	*Atomoscelis*	*onusta* (FIEBER) 1861	herbivore	1	0	0
Berytidae	*Berytinus*	*clavipes* (FABRICIUS) 1775	herbivore	5	24	0
Berytidae	*Berytinus*	*crassipes* (HERR.-SCHAEFFER) 1835	herbivore	1	23	0
Berytidae	*Berytinus*	*hirticornis* (BRULLÉ) 1836	herbivore	0	1	0
Berytidae	*Berytinus*	*minor* (HERR.-SCHAEFFER) 1835	herbivore	1	1	1
Miridae	*Calocoris*	*roseomaculatus* (DE GEER) 1773	herbivore	4	0	0
Miridae	*Capsus*	*ater* (LINNÉ) 1758	herbivore	13	14	24
Miridae	*Capsus*	*pilifer* (REMANE) 1950	herbivore	0	0	1
Miridae	*Capsus*	*wagneri* (REMANE) 1950	herbivore	0	0	1
Pentatomidae	*Carpocoris*	*purpureipennis* (DE GEER) 1773	herbivore	1	1	3
Miridae	*Charagochilus*	*gyllenhalii* (FALLÉN) 1807	herbivore	1	0	0
Miridae	*Chlamydatus*	*pulicarius* (FALLÉN) 1807	herbivore	0	0	3
Miridae	*Chlamydatus*	*pullus* (REUTER) 1870	herbivore	0	0	1
Miridae	*Chlamydatus*	*saltitans* (FALLÉN) 1807	predator	0	0	6
Coreidae	*Coreus*	*marginatus* (LINNÉ) 1758	herbivore	0	0	1
Lygaeidae	*Cymus*	*claviculus* (FALLÉN) 1807	herbivore	0	0	1
Tingidae	*Dictyonota*	*strichnocera* FIEBER 1844	herbivore	0	1	2
Pentatomidae	*Dolycoris*	*baccarum* (LINNÉ) 1758	herbivore	2	3	3
Lygaeidae	*Drymus*	*sylvaticus* (FABRICIUS) 1775	herbivore	0	34	29
Scutelleridae	*Eurygaster*	*maura* (LINNÉ) 1758	herbivore	0	1	1
Lygaeidae	*Geocoris*	*grylloides* (LINNÉ) 1761	predator	1	0	0
Pentatomidae	*Graphosoma*	*lineatum* (LINNÉ) 1758	herbivore	1	2	0
Pentatomidae	*Holcostethus*	*strictus vernalis* (WOLFF) 1804	herbivore	0	1	0
Miridae	*Horistus*	*orientalis* (GMELIN) 1790	herbivore	16	0	0
Lygaeidae	*Ischnocoris*	*hemipterus* (SCHILLING) 1829	herbivore	1	0	0
Tingidae	*Kalama*	*tricornis* (SCHRANK) 1801	herbivore	0	0	19
Lygaeidae	*Kleidocerys*	*resedae* (PANZER) 1797	herbivore	0	0	1
Miridae	*Lepidargyrus*	*ancorifer* (FIEBER) 1858	herbivore	1	0	0
Miridae	*Leptopterna*	*dolabrata* (LINNÉ) 1758	herbivore	232	3	135
Miridae	*Lygus*	*pratensis* (LINNÉ) 1758	herbivore	0	0	2
Miridae	*Lygus*	*punctatus* (ZETTERSTEDT) 1838	herbivore	1	0	0
Miridae	*Lygus*	*rugulipennis* POPPIUS 1911	herbivore	0	1	20
Miridae	*Megaloceroea*	*recticornis* (GEOFFROY) 1785	herbivore	9	0	16
Miridae	*Megalocoleus*	*molliculus* (FALLÉN) 1807	herbivore	1	0	0
Lygaeidae	*Megalonotus*	*chiragra* (FABRICIUS) 1794	herbivore	0	1	11

Family	**Genus**	**Species**	**Trophic level**	**Alb**	**Hai**	**Sch**
Miridae	*Myrmecoris*	*gracilis* (R. F. SAHLBERG) 1848	predator	0	3	0
Rhopalidae	*Myrmus*	*miriformis* (FALLÉN) 1807	herbivore	2	0	0
Nabidae	*Nabis*	*brevis* SCHOLTZ 1847	predator	0	0	3
Nabidae	*Nabis*	*ericetorum* SCHOLTZ 1847	predator	7	22	1
Nabidae	*Nabis*	*ferus* (LINNÉ) 1758	predator	0	6	24
Nabidae	*Nabis*	*flavomarginatus* SCHOLTZ 1847	predator	1	0	0
Nabidae	*Nabis*	*pseudoferus* REMANE 1949	predator	0	0	1
Nabidae	*Nabis*	*rugosus* (LINNÉ) 1758	predator	4	3	8
Berytidae	*Neides*	*tipularius* (LINNÉ) 1758	herbivore	0	0	1
Miridae	*Notostira*	*elongata* (GEOFFROY) 1785	herbivore	33	37	32
Miridae	*Notostira*	*erratica* (LINNÉ) 1758	herbivore	5	0	12
Lygaeidae	*Nysius*	*ericae* (SCHILLING) 1829	herbivore	0	0	1
Pentatomidae	*Palomena*	*prasina* (LINNÉ) 1761	herbivore	0	1	0
Lygaeidae	*Peritrechus*	*geniculatus* (HAHN) 1832	herbivore	0	3	3
Lygaeidae	*Peritrechus*	*nubilus* (FALLÉN) 1807	herbivore	0	3	0
Reduviidae	*Phymata*	*crassipes* (FABRICIUS) 1775	predator	2	0	0
Miridae	*Pithanus*	*maerkelli* (HERR.-SCHAEFFER) 1838	herbivore	1	2	9
Miridae	*Plagiognathgus*	*chrysanthemi* (WOLFF) 1804	herbivore	1	0	0
Scutelleridae	*Podops*	*inunctus* (FABRICIUS) 1775	herbivore	0	6	1
Miridae	*Polymerus*	*holosericeus* HAHN 1831	herbivore	0	0	1
Miridae	*Polymerus*	*nigrita* (FALLÉN) 1807	herbivore	1	0	0
Miridae	*Polymerus*	*unifasciatus* (FABRICIUS) 1794	herbivore	18	0	0
Rhopalidae	*Rhopalus*	*conspersus* (FIEBER) 1837	herbivore	2	0	0
Rhopalidae	*Rhopalus*	*maculatus* (FIEBER) 1837	herbivore	1	0	1
Rhopalidae	*Rhopalus*	*parumpunctatus* SCHILLING 1829	herbivore	0	0	7
Lygaeidae	*Rhyparochromus*	*pini* (LINNÉ) 1758	herbivore	0	2	8
Lygaeidae	*Rhyparochromus*	*vulgaris* (SCHILLING) 1829	herbivore	0	0	3
Saldidae	*Saldula*	*saltatoria* (J. SAHLBERG) 1870	predator	0	0	3
Saldidae	*Saldula*	*orthochila* (FIEBER) 1859	predator	0	2	1
Pentatomidae	*Sciocoris*	*cursitans* (FABRICIUS) 1794	herbivore	6	3	0
Miridae	*Stenodema*	*calcarata* (FALLÉN) 1807	herbivore	4	3	111
Miridae	*Stenodema*	*laevigata* (LINNÉ) 1758	herbivore	0	3	2
Miridae	*Stenotus*	*binotatus* (FABRICIUS) 1794	herbivore	49	0	24
Miridae	*Strongylocoris*	*leucocephalus* (LINNÉ) 1758	herbivore	2	0	0
Lygaeidae	*Stygnocoris*	*fuligineus* (GEOFFROY) 1785	herbivore	0	0	1
Lygaeidae	*Stygnocoris*	*rusticus* (FALLÉN) 1807	herbivore	3	6	0
Lygaeidae	*Stygnocoris*	*sabulosus* (SCHILLING) 1829	herbivore	0	1	3
Coreidae	*Syromastus*	*rhombeus* (LINNÉ) 1767	herbivore	0	0	1
Lygaeidae	*Taphropeltus*	*contractus* (HERR.-SCHAEFFER) 1835	herbivore	0	3	0
Miridae	*Teratocoris*	*saundersi* (DOUGLAS & SCOTT) 1869	predator	0	0	1
Tingidae	*Tingis*	*auriculata* (A. COSTA) 1847	herbivore	0	1	0
Tingidae	*Tingis*	*maculata* (HERR.-SCHAEFFER) 1838	herbivore	1	1	0
Lygaeidae	*Trapezonotus*	*desertus* SEIDENSTÜCKER 1951	herbivore	1	0	0
Miridae	*Trigonotylus*	*caelestialium* (KIRKALDY) 1902	herbivore	3	0	21
Miridae	*Trigonotylus*	*ruficornis* (GEOFFROY) 1785	herbivore	2	0	0

Family	**Genus**	**Species**	**Trophic level**	**Alb**	**Hai**	**Sch**
Lygaeidae	*Tropistethus*	*holosericeus* (SCHOLTZ) 1864	herbivore	5	1	0
Miridae	*Tytthus*	*pubescens* (KNIGHT) 1931	herbivore	0	0	1
Miridae	*Tytthus*	*pygmaeus* (ZETTERSTEDT) 1838	herbivore	1	1	50

CHAPTER 3

GRASSLAND MANAGEMENT FOR STEM-BORING INSECTS: ABANDONING SMALL PATCHES IS BETTER THAN REDUCING OVERALL INTENSITY

Christoph Rothenwöhrer, Christoph Scherber and Teja Tscharntke

ABSTRACT

Grasses are a dominant component of meadows and pastures, harboring an often overlooked diversity of non-pest stem-boring insects that feed and develop exclusively enclosed by plant tissue inside grass shoots. Surprisingly, the effects of land-use management on these highly specialized communities have rarely been studied. Here, the applicability of short-term management reduction as a conservational tool, increasing stem-borer colonization success, was examined. On 41 grasslands in Germany a temporal gradient of set-aside treatments was established by experimentally excluding subplots from management, or by a priori selection of already abandoned grassland patches. Stem-borer abundances and attack heights on resulting managed, 1-season unmanaged and ≥2-seasons abandoned treatments were compared.

Grassland management had a negative effect on stem-borer colonization success and spatial niche differentiation. Reducing management over an 1-season period did not enhance abundances. Two out of three species responded positively only to an abandoning treatment lasting ≥2-seasons, which was also reflected by the decreasing spatial overlap in this treatment. Even though grass shoots at the unmanaged areas were on average 14.9 cm taller than in managed areas, stem-borer abundances did not differ between the latter treatments. Hence, preserving essential larval development and hibernation habitats in future rotational set-aside schemes requires a management exclusion period of at least two growing seasons. From these grassy strips, e.g. located at meadow edges, highly specialized stem-borers can re-colonize sward islets on surrounding intensively managed grasslands, despite of ever changing land-use practices and environmental conditions.

INTRODUCTION

About half of Europe´s farmland is managed as grassland pasture or hay meadow (Minns et al. 2001). Management intensification by means of ungulate grazing and cutting is a key factor influencing biodiversity in grasslands (Plantureux et al. 2005) and may impact on native flora (Blackstock et al. 1999, Zechmeister at al. 2003) and fauna (Van Swaay 2002, WallisDeVries et al. 2002).

Effects of grassland management on phytophagous insect communities can be divided into long- and short-term effects. In the long term, grassland management may simplify plant community composition and vegetation structure (Day and Detling 1990), leading to decreases in herbivore species richness and abundance (Scherber et al. 2010, Siemann 1998). Such simplification effects may also be present on a shorter time scale. However, short-term intensification effects on herbivores can be more complex to predict since they may have (1) negative effects caused by the simplification of plant architecture (Danell and Huss-Danell 1985, Price et al. 1987, Strong et al. 1984), e.g. through the destruction of specific feeding niches on smaller host plants (Hutchinson and King 1980) and thinner grass shoots (Tscharntke 1997) as well as (2) positive effects due to the increasing availability of soft and nutrient-rich plant tissue, re-growing after grazing and cutting events (Tscharntke and Greiler 1995) later in the season.

Even though grasses are a dominant component of meadows and pastures, the effects of land-use intensification on specialized herbivorous insects, associated with different grass species, have rarely been studied (but see Dubbert 1998) or focused on the control of single agricultural pests species such as the stem-boring frit fly (*Oscinella frit*) (e.g. East and Pottinger 1983). From a conservation perspective, especially endophagous insects that feed and develop exclusively enclosed by plant tissue inside grass shoots, should be considered as specific grassland inhabitants, providing an often overlooked diversity (see Greiler 1994, Tscharntke and Greiler 1995). For example, some Poaceae, e.g. *Calamagrostis epigeios* (L.) or *Phragmites australis* (Cav.) Trin ex Steud., are attacked by various species of stem-borers (Dubbert et al. 1998, Tscharntke 1999). Information about how highly specialized stem-borer communities, probably widely colonizing as ‘aerial plankton’ and overriding effects of spatial scale, area or isolation (Dubbert et al. 1998) are affected by grassland management like grazing and mowing is scarce.

While grasses have a comparatively simple plant architecture, Tscharntke (1997) found that the species richness of stem-borers associated with different grass species may increase with shoot length. In laboratory experiments, Stiling and Strong (1983) observed severe interspecific competition among stem-borers associated with the salt marsh cordgrass (*Spartina alterniflora* Loisel.), since larval encounters resulted in aggression and murder of larvae within stems. Subsequently, Dubbert et al. (1998) showed that co-occurring stem-borer species separate spatially, attacking grass shoots at specific diameters. Since intensive grazing and cutting generally reduce shoot length and promote grasses that are able to produce short leaves and flowering shoots (Brock et al. 1996), it can be assumed that grassland management scales down stem-borer communities when restricting colonization space availability on shorter shoots.

The aim of this study was to examine the applicability of short-term management reduction as a conservation tool to preserve suitable habitats that promote the establishment of non-pest stem-borer colonization on grasslands. Stem-borer abundances on naturally occurring Cocksfoot (*Dactylis glomerata* L.) patches at three different types of grassland habitats, representing a temporal gradient of increasing short-term set-aside, were compared: continuously managed, 1-season unmanaged and ≥2-seasons abandoned plots. It was hypothesized that management-induced reduction in grass shoot length (i) limits overall colonization success and (ii) increases interspecific overlap in attack heights for associated stem-boring insect communities. Finally, (iii) both effects are expected to become less pronounced when increasing unmanaged periods.

MATERIAL & METHODS

The perennial grass, *Dactylis glomerata* L. (Poaceae), provides shoots between 50 to 120 cm length (Rothmaler 2007) that can serve as hibernation and larval development habitats for up to six stem-boring insect species that feed and pupate inside the shoots (Dubbert 1998). Cocksfoot (*D. glomerata*) was chosen as host grass species for its ability to persist even under intensive grazing and cutting regimes by producing shorter leaves and flowering shoots (Brock et al. 1996) in comparison to stands found on less intensively managed grasslands. Furthermore, this grass species represents a highly abundant food resource for specialist herbivores, as it is part of commercial seed mixtures and widely occurs on pastures and meadows across Europe (Klapp and Opitz von Boberfeld 2006).

In spring 2008, 41 grasslands, all providing high densities of *D. glomerata*, were selected within the "Biodiversity Exploratories" region 'Hainich-Dün' (Fischer et al. 2010) near Mühlhausen (Central Germany). Local site management during the years 2006-2008 was quantified using a land-use intensification index, which summarizes the standardized intensity of three components of land-use, namely fertilization, mowing, and livestock grazing at each site (for more details see Blüthgen et al. 2012). On these 41 plots, a temporal gradient of set-aside was established by experimentally excluding a small area (subplot) from management, or by a priori selection of subplots along a short-term set-aside gradient. Set-aside treatment was a factor with three levels: managed (continuously grazed and/or cut; n=12), 1-season unmanaged (n=19) and ≥2-seasons abandoned (n=10) subplots.

On N=19 plots, a 3.5x7 m subplot was marked with wooden poles and excluded from management for one year. To prevent grazing, we set up standard electrical fences. On another N=10 plots, an already existing abandoned subplot (e.g. close to farm tracks or fences) was selected that had been unmanaged for at least two years. Finally, subplots at the remaining twelve plots were managed by farmers, according to their local practices (mown up to three times per year and/or grazed as well as fertilized).

In September 2008, 50 cocksfoot shoots (2050 shoots in total) on each of the resulting managed, 1-season unmanaged and ≥2-seasons abandoned treatments were sampled. Fully grown grass shoots with inflorescences were cut directly above the ground and dissected in the laboratory. Larvae or pupae were identified using the insect collection of H.-J. Greiler and S. Vidal, based on the determination of reared adults. To characterize grass shoot architecture at the sampling areas, shoot and inflorescence length (cm), basal shoot diameter (mm) and the number of nodes per shoot was measured.

Statistical analysis

For data analysis we used the software package R 2.12.1 (R Development Core Team 2010). For practical reasons, our treatments were either applied to subplots within a 50x50 m plot (N=19) or to subplots located at different plots (N=22). This was to ensure equally high availability of *D. glomerata* stems (range: 61-78 stems) within each treatment area. Therefore, we needed to ensure that (i) plots did not differ in land-use intensity and (ii) no spatial autocorrelation was present both between and within plots.

To test whether location of set-aside treatments were unaffected by land-use intensity, recorded from 2006 to 2008 with reference to the respective or adjacent grassland plot, as well as for differences in shoot length, pairwise Welch Two Sample t-tests were applied, working at a Type I error rate of $P<0.017$. Spatial autocorrelation was checked by fitting gls models with exponential variance function, where Gauss-Krüger coordinates were used as spatial covariates, assuming a spherical spatial correlation structure (Pinheiro and Bates 2000). In addition, model residuals were plotted against the Gauss Krüger coordinates to ensure that no spatial patterns had been overlooked.

To determine set-aside treatment effects on herbivores, species abundances at managed, unmanaged and abandoned areas were compared, using negative binomial generalized linear models (R: glm.nb, MASS library version 7.3-22; Venables and Ripley 2002; model formula: abundance~treatment) since data indicated overdispersion. Changes in interspecific spatial niche overlap were examined by analyzing attack heights of all species at the three treatments with a linear mixed effects model (nlme package version 3.1-106; Pinheiro and Bates 2000; fixed-effects formula: attack height~treatment). In these models, we included local plots as a random factor and applied variance functions to account for heteroscedasticity. Note that for these attack height models, all individual grass shoots were included, resulting in 646 residual degrees of freedom.

RESULTS

Sample locations

Location of set-aside treatments did not differ in land-use intensity index with reference to the respective or adjacent grassland plot (range: 0.55-2.74, mean= 1.52; Welch two sample t-tests, abandoned – unmanaged area: t= 1.14, *df*= 18.8, $P_{adjusted}$=

0.81; abandoned – managed area: t= 1.86, *df*= 20.9, $P_{adjusted}$= 0.23; unmanaged – managed area: t= 1.10, *df*= 18.5, $P_{adjusted}$= 0.86; see Fig.A.1). Residuals of the gls models showed no spatial autocorrelation since AICc increased when models were updated using a spherical autocorrelation function for the treatment locations (Fig. A.2; for single species see Fig. A.3). Since length of inflorescences (Spearman's rank correlation: r_S= 0.81, P< 0.001), basal shoot diameter (Spearman's rank correlation: r_S= 0.91, P< 0.001) and the number of nodes per shoot (Spearman's rank correlation: r_S= 0.73, P< 0.001) were all positively correlated with shoot length, this parameter was chosen to describe grass shoot architecture. Grass shoot height significantly differed between all three treatments (Welch two sample t-tests, abandoned – unmanaged area: t= 3.33, *df*= 25.4, $P_{adjusted}$= 0.008; abandoned – managed area: t= 5.24, *df*= 17.8, $P_{adjusted}$< 0.001; unmanaged – managed area: t= 2.85, *df*= 18.6, $P_{adjusted}$= 0.031). Grass shoots found at the abandoned areas (mean= 103.1 ±2.0 cm) were on average 12.6 cm higher compared to those at unmanaged areas (mean= 90 ±4.7 cm) and 27.5 cm higher compared to the managed areas (mean= 75 ±4.5 cm).

Endoherbivore abundances

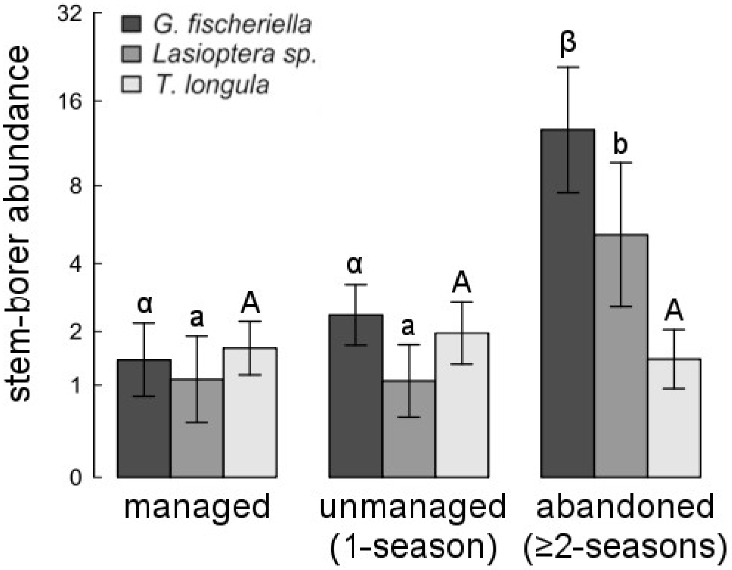
A total of 984 stem-borers belonging to three insect orders were collected. *Gylphipterix fischeriella* (Lepidoptera, Glyphipterigiedae) was the most frequently found species, representing 50.9 % (n=501) of all stem-borers. The two other species, *Lasioptera sp.* (Diptera, Cecidomyiidae) and the exclusively on *D. glomerata* feeding *Tetramesa longula* (Hymenoptera, Eurytomidae), accounted for 36.1 % (n=355) and 13.0 % (n=128), respectively.

Species abundances were strongly affected by set-aside treatment (Table 1). Abundances of *G. fischeriella* were significantly higher at abandoned compared to unmanaged and to the managed areas. The same pattern was found for *Lasioptera sp.*, even though the difference between the abandoned and the managed areas were only marginally significant. In contrast, abundances of the monophagous *T. longula* did not differ between treatments (Fig. 1).

Table 1. Results for negative binomial generalized linear model, showing the effects of continuously managed, 1-season unmanaged and ≥2-seasons abandoned grasslands patches on the abundance of three species of stem-boring insect species.

Abundance	*Est*	*Error*	*z-value*	*P*
G. fischeriella				
(Intercept)	2.07	0.23	9.05	< 0.001
abandoned – managed	2.33	0.60	3.88	< 0.001
unmanaged – abandoned	-2.12	0.54	-3.94	< 0.001
Lasioptera sp.				
(Intercept)	1.86	0.40	4.61	< 0.001
abandoned – managed	2.06	1.06	1.94	0.052
unmanaged – abandoned	-1.91	0.96	-1.99	0.046
T. longula				
(Intercept)	1.00	0.21	4.76	< 0.001
abandoned – managed	-0.03	0.56	-0.06	0.956
unmanaged – abandoned	0.62	0.50	1.25	0.212

Fig. 1. Abundance (±SE) of three stem-borer species, sampled on continuously managed, 1-season unmanaged and ≥2-seasons abandoned grassland patches. Note log scale for y-axis. Data were log+1 transformed before calculation of mean and standard error.



Interspecific spatial niche overlap

Lasioptera sp. generally attacked higher grass shoot sections in comparison to *G. fischeriella* and *T. longula* at all treatments (Fig. 2), but spatial differentiation in interspecific attack heights changed between treatments (Tab. 2). Inside the grass shoots the spatial overlap of *Lasioptera sp.* and *T. longula* increased for the unmanaged as well as for the managed areas compared to the abandoned ones. Equally, the attack heights of *Lasioptera sp.* and *G. fischeriella* were more similar at the managed, compared to the abandoned areas, while in contrast, attack heights of both species at the unmanaged areas did not differ from those at the abandoned areas.

Fig. 2. Range of attack heights of three stem-borer species, sampled on continuously managed, 1-season unmanaged and ≥2-seasons abandoned grassland patches differing in mean grass shoot length.

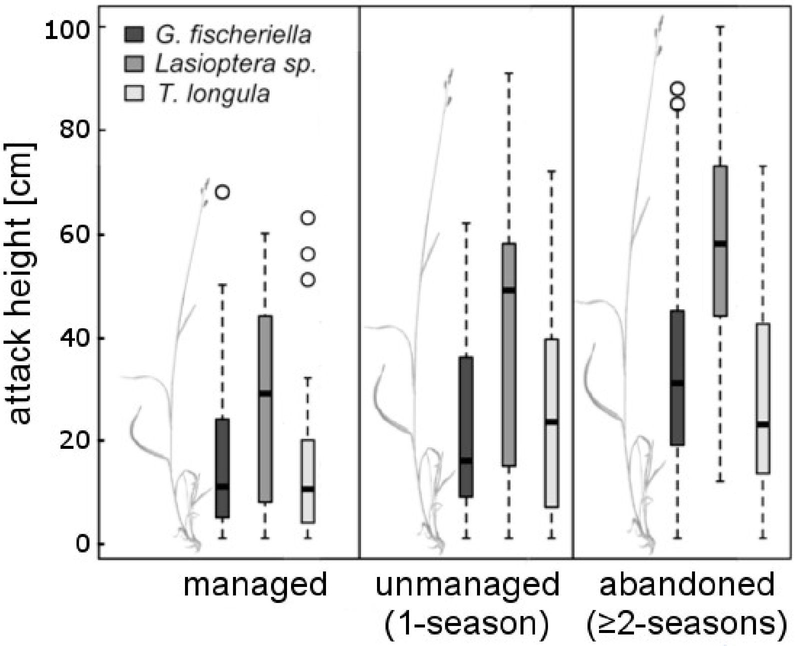


Table 2. Results of the linear mixed effects model, showing alterations in spatial overlap of interspecific attack heights of three stem-boring insect species between continuously managed, 1-season unmanaged and ≥2-seasons abandoned grassland patches. The model was fitted using REML and the varPower variance function.

Interspecific attack heights	***Est***	***Error***	***df***	***t-value***	***P***
(Intercept)	28.33	1.40	646	20.28	< 0.001
abandoned – managed	18.55	3.30	33	5.61	< 0.001
unmanaged – abandoned	-9.25	3.42	33	-2.71	0.011
Lasioptera sp. – G. fischeriella	17.48	2.80	646	6.25	< 0.001
abandoned – managed	12.20	5.60	646	2.18	0.030
unmanaged – abandoned	-7.57	7.00	646	-1.08	0.280
T. longula – Lasioptera sp.	-18.58	3.16	646	-5.88	< 0.001
abandoned – managed	-21.92	6.84	646	-3.20	0.001
unmanaged – abandoned	17.94	8.10	646	2.22	0.023

DISCUSSION

This study utilized a multi-site experiment to examine the applicability of short-term management reduction as a conservation tool to preserve suitable habitats that promote the establishment of non-pest stem-borer insects on grasslands. In our approach we sampled *D. glomerata* shoots, naturally occurring in high densities on managed grasslands to explore how management-induced changes in host plant height affect colonization success and spatial niche differentiation of common stem-borer species. Sampling locations were spatially independent replicates and independent of land-use intensity but differed in their set-aside periods (managed, 1-season unmanaged and ≥2-seasons abandoned areas). As expected from a previous experimental study on various grass species (Brock et al. 1996), grassland management clearly affected grass shoot architecture, enhancing grass shoot length according to set-aside period.

Abundances for the two generalist species *G. fischeriella* and *Lasioptera sp.* were increased only at the abandoned areas compared to the managed and unmanaged the treatments, partly confirming our first hypothesis that grassland management limits overall colonization success. Since the longest shoots were available in the abandoned treatments, these stands provided the widest colonization space for these two stem-borer species, which is in agreement with previous studies correlating shoot length with endoherbivore abundance (Dubbert et al. 1998) and species richness (Tscharntke 1997). Despite evident negative effects of management, also reducing diversities and abundances of insect pollinators and ectoherbivores on grasslands with high livestock densities (Kruess and Tscharntke 2002a, Kruess and Tscharntke 2002b, Woodcock et al. 2009) and mowing frequencies (Bell et al. 2001, Gerstmeier and Lang 1996, Johst et al. 2006, Morris and Rispin 1987), grazing may also stimulate grass growth and production of new tillers or lateral shoots (Tscharntke and Greiler 1995). For species that depend on meristematically active, soft and nutrient-rich tissue, the suitability of grass as a food resource should decline with the age of the shoot. Therefore, moderate grazing can also enhance the abundances of mono- or oligophagous stem-borers like *Lasioptera arundininis* (Diptera, Cecidomyiidae) occurring on Common reed (Tscharntke 1997) and *Oscinella frit* (Diptera, Chloropidae) on ryegrass *Lolium perenne* L. (Moore and Clements 1984), which could explain the release of grass shoot length as a limiting factor for the colonization success in the monophagous *T. longula*.

Accordingly, as also predicted by our second hypothesis, grassland management expanded interspecific overlap for stem-borers since spatial niche overlap in attack heights of *Lasioptera sp.* with *G. fischeriella* increased on the managed as well as on unmanaged areas and with *T. longula* on the managed compared to the abandoned areas, respectively. This result shows that management-induced reduction in grass shoot length can limit spatial niche differentiation for stem-borers. Consequently, on at least yearly managed grasslands, the predictability of associated endoherbivore species may depend to a greater extend on shoot abundance (Dubbert et al. 1998) than it is the case for abandoned areas.

Our third hypothesis, predicting that management effects on colonization success and spatial niche differentiation of stem-bores would dampen with increasing set-aside period was only partly confirmed, since this effect was almost not evident at the unmanaged areas. Even though the unmanaged treatment offered on average 14.9 cm taller shoots than the managed areas, abundances of *G. fischeriella* and *Lasioptera sp.* did not differ between these treatments. This effect could be caused by increased interspecific competition between both species, as indicated by the still increased overlap in attack heights at the unmanaged areas. Therefore, mean grass shoot length above 1 m at the abandoned treatment could be a threshold, boosting colonization success by increasing spatial differentiation possibilities for species. However, so far only few field studies revealed slight evidence for patterns consistent with competitive effects among co-occuring endophagous feeders such as, e.g., bark beetles (Beaver 1974) or stem-borers (Rathke 1976, Stiling and Strong 1983). Further experiments are necessary to determine to which extent this pattern limits population sizes additional to the generally reduced colonization space availability on shorter shoots, and how common this pattern becomes for other stem-borer assemblages and associated higher trophic levels, such as parsitoids.

In conclusion, our study shows that colonization success of two stem-boring species (*Lasioptera sp.* and *G. fischeriella*), associated with *D. glomerata*, a grass species commonly occurring on meadows and pastures, is clearly limited by management reducing grass shoot length below 1 m. Thus, we conclude that enhancing the abundance of stem-boring insects requires that grasslands contain areas that are excluded from cutting for at least two years.

In particular on intensively managed grasslands, the overlap in attack heights between all three species increased, narrowing spatial niche width for co-occurring species and possibly additionally affecting *Lasioptera sp.* and *G. fischeriella* abundances through enhanced interspecific spatial competition. Interestingly, one species (*T. longula*) was not affected by grass shoot length, indicating that taxonomic groups may differ in their response.

Overall, excluding small grassy stripsfrom grazing and mowing for several years, e.g. located at meadow edges, preserves essential larval development and hibernation habitats, and provides refuges from which highly specialized stem-borers can re-colonize sward islets (Helden et al. 2010) on surrounding intensively managed grasslands, despite of ever changing land-use practices and environmental conditions.

ACKNOWLEDGEMENTS

We thank the managers of the three Exploratories, Swen Renner, Sonja Gockel, Andreas Hemp and Martin Gorke and Simone Pfeiffer for their work in maintaining the plot and project infrastructure, and Markus Fischer, Elisabeth Kalko, Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze and Wolfgang W. Weisser for their role in setting up the Biodiversity Exploratories project.

The work has been (partly) funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (Ts45/28-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

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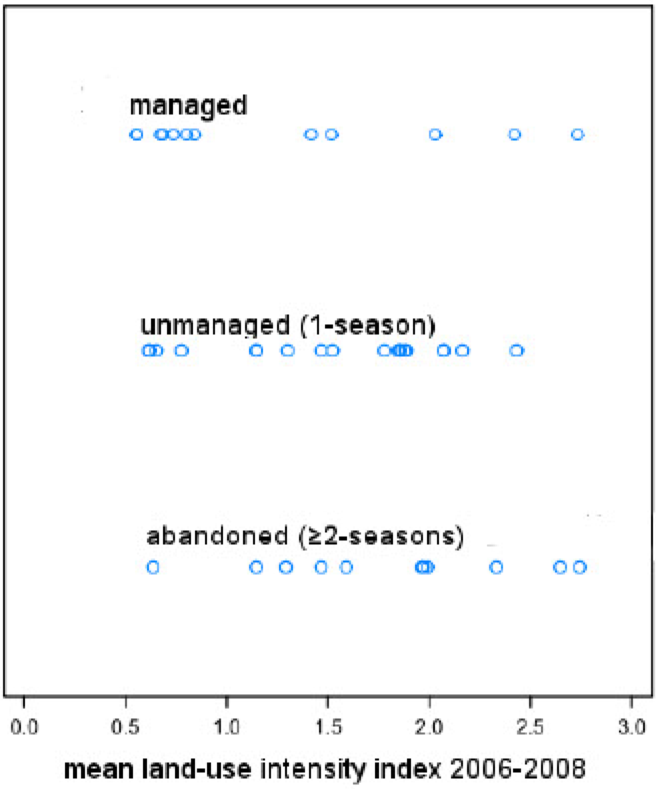
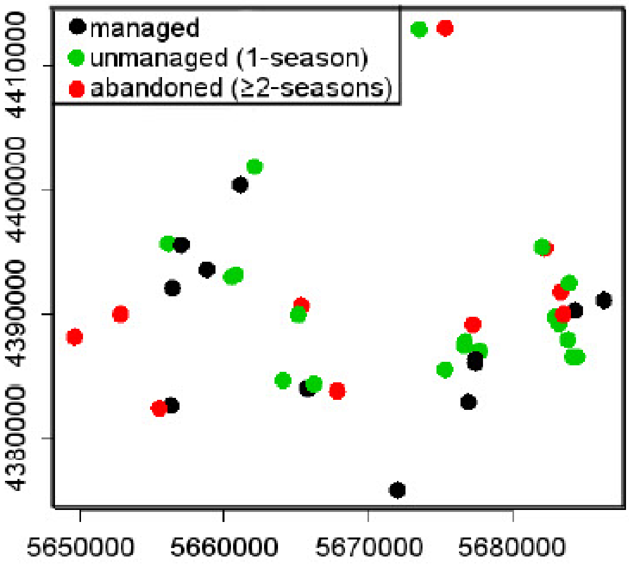
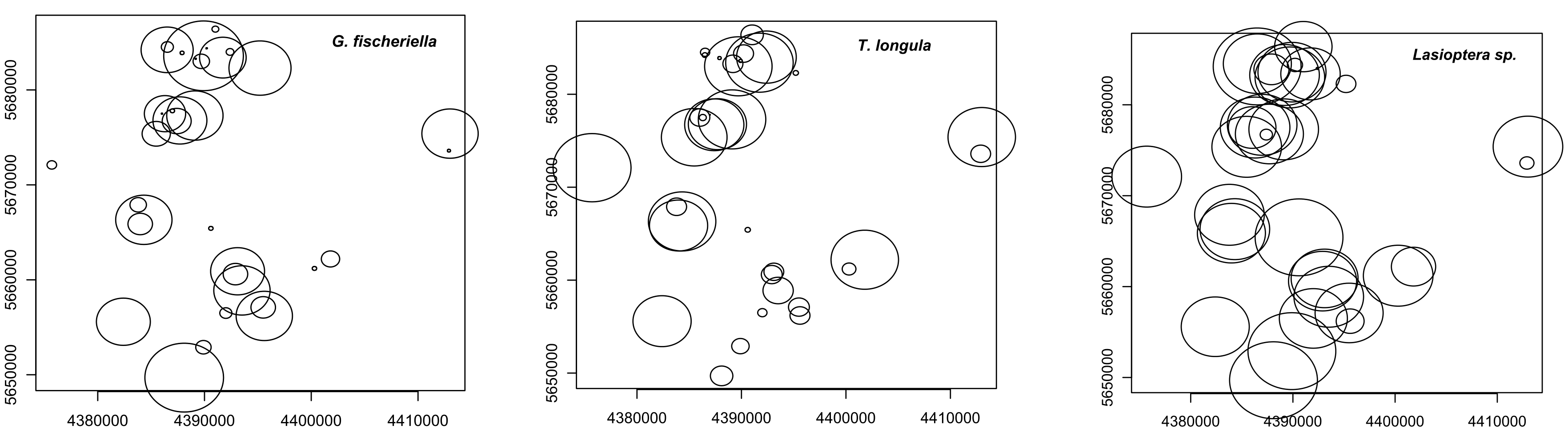
APPENDIX

Appendix A1. Mean land-use intensity indices averaged from the years 2006-2008 on sampled managed, 1-season unmanaged and ≥2-seasons abandoned locations. Location categories did not differ in land-use intensity (range: 0.55-2.74, mean= 1.52; Welch two sample t-tests, abandoned – unmanaged: t = 1.14, *df* = 18.8, $P_{adjusted}$ = 0.81; abandoned – managed area: t = 1.86, *df* = 20.9, $P_{adjusted}$ = 0.23; unmanaged – managed area: t = 1.10, *df* = 18.5, $P_{adjusted}$ = 0.86).



Appendix A2. Plot of model residuals for spatial autocorrelation by fitting gls models with exponential variance function, where Gauss-Kruger coordinates were used as spatial covariates, assuming a spherical spatial correlation structure. Plots represented spatially independent replicates since residuals were not spatially autocorrelated.





Appendix A3. Plots of model residuals to assess spatial autocorrelation, separately for each stem-boring species. Plots were produced by fitting gls models with exponential variance function, where Gauss-Kruger coordinates were used as spatial covariates, assuming a spherical spatial correlation structure. Residuals were not spatially autocorrelated, i.e. likelihood of models decreased when spatial autocorrelation was included in the models.

CHAPTER 4

HERBIVORES OF MASS-FLOWERING CROPS SPILLOVER AND DAMAGE WILD PLANTS

Christoph Rothenwöhrer, Christoph Scherber, Michaela Bellach and Teja Tscharntke

ABSTRACT

In agricultural mosaic landscapes, mobile organisms can use resources across the crop-noncrop interface, thereby influencing patterns of plant-insect interactions. We conducted a field study on 20 grassland plots to assess how small- and large-scale landscape composition (circles with a radius of 250-2000 m) affects the spillover of pollen beetle (*Brassicogethes aeneus*) from mass-flowering oilseed rape (OSR, *Brassica napus*, Brassicaceae) fields to noncrop habitats. We transplanted 12 wild mustard (*Sinapis arvensis*, Brassicaceae) phytometer plants (6 treated with insecticide) to each plot and quantified beetle and pollinator abundances before and after OSR flowering peak as well as total bud damage and fruit set of these phytometers. When OSR flowering was fading, pollen beetle density on nearby grasslands (250 m) increased, presumably due to spillover from OSR fields. These increases in local pollen beetle abundances increased and were related to the amount of OSR at the 250 m scale, but not at larger spatial scales (2000 m). Hence alternative host plants occurring in the vicinity of cropland suffer most strongly from increased herbivore spillover. We conclude that herbivore spillover from crops to adjacent wild plants and associated wild plant damage decreased (i) with increasing distance from crop fields and (ii) when flowering during the crops' mass-flowering. However, reduced herbivore damage of wild mustard may come at the cost of reduced pollination, which is probably affected in a similar way. Hence, spillover of crop-related organisms can interact with wild plant reproductive success in a complex way.

INTRODUCTION

Land use intensification and habitat loss have often been reported to be major drivers for biodiversity loss and associated declines in ecosystem services (Kleijn et al. 2009, Vitousek et al. 1997). Local land use intensity and spatial composition of ecosystems can influence important plant-insect interactions such as pollination and herbivory (e.g. Diekötter et al. 2010, Wrbka et al. 2004). In agricultural mosaic landscapes, where mobile organisms can use resources on both managed and natural habitats, plant-insect interactions in natural habitats can be strongly shaped by landscape configuration (Kareiva & Wennergren 1995, Hooper et al. 2005), e.g. by the neighbourhood to mass-flowering crops (Holzschuh et al. 2011). Current studies mainly focus on how mobile organisms occurring in managed areas benefit from neighbouring natural habitats (e.g. Holzschuh et al. 2010, Rand et al. 2006). However, information on organism spillover from managed crop fields to adjacent semi-natural habitats is rare and well-documented examples of crop-noncrop spillover almost absent (Rand et al. 2006). However, mass spillover of herbivorous pest insects from monoculture fields to noncrop habitat within an agricultural landscape can be hypothesized to strongly affect reproductive success in wild plants.

Here, we study the effects of rape pollen beetles (*Brassicogethes aeneus* Fabricius 1775), on fruit set of wild mustard plants (*Sinapis arvensis*) in grasslands. *Brassicogethes aeneus* is one of the economically most important pest species in oilseed rape (OSR, *Brassica napus* L.; Büchi 2002, Alford et al. 2005). Since most studies focus on pollen beetles and their parasitoids in OSR crop fields (e.g. Bianchi et al. 2006, Ricketts et al. 2008, Thies et al 2008), wild Brassicaceae have been considered only in their potential role as alternative host plants. Although spillover of insects from crop to noncrop habitats has been predicted to be common (Tscharntke et al. 2005, Rand et al. 2006, Rand & Louda 2006, Gladbach et al. 2011), studies measuring the effect of crop-related herbivore pest populations on reproductive success of wild plants in the agricultural landscape are scarce.

We conducted a field study on 20 grasslands to assess how small- and large-scale landscape composition affects the dynamics of pollen beetle spillover from mass-flowering OSR fields to wild Brassicaceae on semi-natural grasslands. Grasslands were selected a priori from a set of 50 established research plots (Fischer et al. 2010) along a gradient of increasing OSR crops within eight landscape circles (with a radius of 250 to 2000 m). Landscape composition parameters, such as the amounts of OSR fields, arable land (cereals and corn), forests and semi-natural habitats, were measured on the basis of digitalized areal pictures. We transplanted 12 wild mustard plants (6 treated with insecticide) to each plot and quantified pollen beetle and pollinator abundances before and after OSR flowering peak as well as total bud damage on phytometers. We test the following hypotheses:

(i) Pollen beetle abundance on grasslands decreases when the surrounding landscape contains high amounts of oilseed rape, caused by the dilution of pollen beetle populations on a landscape scale.

(ii) Pollen beetle abundance will increase on Brassicaceae on grasslands after the flowering peak of OSR in the surrounding landscape, due to concentration on the few remaining resources, and

(iii) Wild Brassicaceae (the phytometers with mustard) will produce fewer pods when local pollen beetle abundances are high.

MATERIAL & METHODS

Study area and spatial scales

The study was conducted from 1st May to 1st August 2009, on 20 grasslands (called plots in the following) selected a priori from a set of 50 grassland research plots (mean distance 16 km) within the "Biodiversity Exploratories" region 'Hainich-Dün' (Fischer et al. 2010) near Mühlhausen (Central Germany). The study area is dominated by annual crop fields, intensively managed grasslands and patchily distributed fragments of forests and semi-natural habitats such as calcareous grasslands. Grasslands were chosen according to a gradient of increasing amount of OSR within eight circles (with a radius of 250, 500, 750, 1000, 1250, 1500, 1750 and 2000 m) around the centre of each plot. Landscape-wide OSR proportion ranged from 0 to 57 % (Table A1). Exact measures of landscape parameters containing the amounts of OSR fields, arable land (mainly cereals), forests and semi-natural habitats (see APPENDIX A1) were calculated in ArcView 3.2 (ESRI Redlands, USA) on the basis of digitized areal pictures taken in June 2009 (Hansa Luftbild, Münster).

Study species

One of the economically most important pest species on OSR is *Brassicogethes aeneus* F. (Coleoptera: Nitidulidae), which can cause serious yield losses of over 80 % (Hansen 2004). Adult beetles overwinter in the litter layer under herbaceous vegetation or moist woodland debris (Nilsson 1988, Williams 2004) and emerge in spring (first generation) with temperatures over 10°C. The beetles are very mobile and able to cross distances of 1-3 km per day when they start moving into budding OSR fields in April for maturity feeding and later mating and oviposition. While searching for pollen or laying eggs in still closed buds and on open flowers, the beetles can damage the gynoecium, leading to flower drought and preventing seed set. A typical sign of herbivory caused by pollen beetles are podless stalks (Thies & Tscharntke 1999). After copulation, females deposit eggs in buds and all adults of the first generation die. Larvae of pollen beetles develop in flowers, drop to the ground, pupate and emerge after one to five weeks. The development from egg to new adult takes 30–50 days (Nilsson 1988; Alford et al. 2005). The second generation emerges and feeds on remaining oilseed-rape flowers and when OSR crops have faded on a variety of blooming wild plants (Hockkanen 2000, Gurr et al. 2003, Lehrman et al. 2008), mainly belonging to the Brassicaceae family, before moving back to their hibernation sites. Even though all developmental stages of *B. aeneus* feed on pollen, only the bud damage by adult beetles causes yield losses of economic importance.

Pollen beetle and pollinator monitoring

Pollen beetle and pollinator (bumble bees, solitary bees and honey bees) abundances on grasslands were monitored four times during the beetles' activity period. We exposed three yellow pan traps per grassland plot at local vegetation height during constantly dry weather conditions for three days over four time intervals. We did the first two surveys (05/01-05/04 and 05/23-05/26) before peak flowering of local OSR crops while the last two surveys were done afterwards (06/22-06/25 and 07/29-08/01) to sample the first and second generation of adult pollen beetles separately. We pooled beetle abundances from these four pan trap surveys based on generation levels, because first individuals of the second generation emerged within two weeks after peak flowering of OSR. Since pollinator abundance can affect fruit set, but is not the topic of this study, we used pollinator data to correct for potential pollination-mediated differences in fruit set of our phytometer plants.

Phytometer plants

We used as phytometer plants wild mustard (Brassicaceae: *Sinapis arvensis*), which is a native rural plant found ubiquitously in agricultural and semi-natural habitats. Wild mustard is self-incompatible (Ford & Kay 1985), typically flowering from April to October and commonly attacked by pollen beetles (Ekbom & Borg 1996, Cock et al. 2006). Phytometers were grown from seed in pots with standardized soil (Fruhstorfer Erde Typ T25) in an unheated greenhouse. Half of the *S. arvensis* plants were randomly treated with a systemic insecticide (Biscaya®, Bayer Crop Science) three days before exposing them on the grasslands and repeatedly treated every ten days during the two-month experiment. Only phytometer plants that already exhibited closed buds but no open flowers were transplanted to the experimental grassland plots to provide flower resources for pollen beetles before, during and after mass-flowering OSR crops.

Experimental setup

We established a patch of 12 wild mustard plants (N=240) on each grassland (15th May to 15th July) to quantify bud damage by pollen beetles. Six plants per plot were continuously treated with insecticide every tenth day throughout the experiment. To prevent phytometers from being grazed, we set up standard electrical fences. The blooming period of the phytometer plants in the field lasted approximately from two weeks before local OSR flowering in mid-May, until 2 weeks after all OSR fields faded in mid-July. During this time period, phytometers were fully accessible to pollinators and pollen beetles. We also checked plants for aphid presence each 10 days. Phytometers were removed from the grasslands as soon as they stopped flowering and before completing pod ripening, and intact pods and pod-less flower stalks were counted. Pod-less stalks occurring at dried and sagging tops of inflorescences were excluded from analysis, since those flower stalks were caused by early droughts and not indicating missing pollination or herbivore damage.

Statistical analysis

Data were analyzed using R 2.12.1 (R Development Core Team 2010). We used mixed effects models (nlme package; Pinheiro & Bates 2000) and generalized mixed effects models fit by penalized quasi-likelihood (glmmPQL; MASS library; Venables and Ripley 2002) for data analysis (see Appendix A3 for full R code). The response variables beetle abundance and plant damage were analyzed as follows.

Beetle abundance was summed over plots and time intervals, so that the final abundance dataset contained 40 data points (20 plots times 2 generations); generation was included as a fixed effect, and plots were treated as random effects.

To detect relevant spatial scales and landscape parameters, we first constructed models with all 1- and 2-fold combinations of explanatory landscape variables of all circle scales (including two-way interactions). This resulted in a total of around 1000 candidate models that were compared using Akaike´s information criterion, corrected for small sample sizes (AICc; Burnham & Anderson 2002). The best models contained only OSR abundance and generation as explanatory variables. To test for generation-dependent scale effects we used the two landscape scales best predicting beetle abundances in separate linear mixed effects models. We calculated effect size as the partial slope of %OSR in separate models for each generation and scale.

Data on plant pod damage were analyzed using glmmPQL models with random intercepts for plots. The plant damage dataset had a sample size of 20 plots x 12 plants = 240 datapoints. Plant damage was analyzed both (i) as a numerical response variable (destroyed pods, quasipoisson error distribution) with plant height as additional explanatory variable and (ii) as a binomial response variable (destroyed pods vs. intact pods). In addition, we tested for direct effects of (iii) the proportion of OSR (scales selected as described above) on pod damage (binomial response) and for a potential pollinator effect on (iv) total fruit set (intact pods, quasipoisson error distribution) with including plant height as additional explanatory variable. All models contained insecticide treatment and models i, ii and iv additionally beetle abundance as explanatory variable. Model simplification was achieved through manual deletion of terms from maximal models (Crawley 2007). Insecticide treatment as design-based parameter remained in the minimum adequate model.

Continuous explanatory variables were log-transformed if necessary to improve spread along the x axis.

For all models, we tested for spatial autocorrelation by introducing spherical spatial correlation structures based on Gauss-Krüger coordinates for each plot (Pinheiro and Bates, 2000). In addition, we plotted model residuals against the Gauss Krüger coordinates to ensure that no spatial patterns had been overlooked (APPENDIX A2).

RESULTS

Residuals of the lme models showed no spatial autocorrelation since AICc increased when models were updated using a spherical autocorrelation function for the locations. Multi model landscape parameter analysis revealed a major effect of OSR, since the best 18 models only included OSR as a predictor for pollen beetle abundance. Additionally, the best model contained the amount of OSR on the small 250m scale as well as on the large 2000m scale, indicating strongest effects of OSR on these maximal scale differences.

Pollen beetle generations showed contrasting responses to OSR on spatial scales (Tab. 1). Increasing amount of OSR before and during flowering peak at the small 250 m scale significantly decreased first generation beetle abundances (Fig. 1a, open circles – dashed line) on grasslands, while beetles abundances of the second generation increased with the amount of OSR when flowering peak passed (Fig. 1a, closed circles – solid line). At the 2000 m scale increasing percentage of OSR only reduced first generation abundance on grasslands (Fig. 1b, open circles – dashed line), while after OSR flowering peak abundances of second generation beetles were equally high on all grasslands (Fig. 1b, closed circles – solid line). Accordingly, the effect size across all eight spatial scales (i.e. taken from slopes of fitted regression models relating beetle abundance to % of OSR on each spatial scale separately for generations; see APPENDIX3) on pollen beetle abundances at grasslands showed a different pattern for generations (Fig. 2). First generation beetles found on grasslands were negatively related to the amount of OSR on large scales (1750 and 2000m), indicating a dilution of the landscape-wide pollen beetle population till flowering peak. Positive effect size on small scales (250 and 500m) of OSR found for the second generation of beetles demonstrates a strong spillover effect of beetles from OSR crop fields on grasslands with fading flowering of OSR crops.

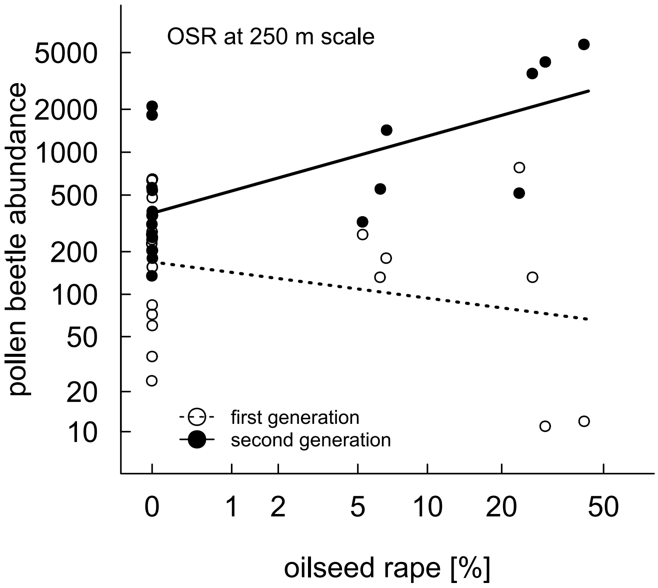


Fig. 1a. Relationships between pollen beetles abundances and amount of OSR [%] within a 250 m radius around grassland plots separately for generations. Note log scale for x- and y-axis. Abundance of second generation significantly increased with increasing amounts of OSR, indicating small scale spillover effects of pollen beetles on grasslands after OSR flowering peak.

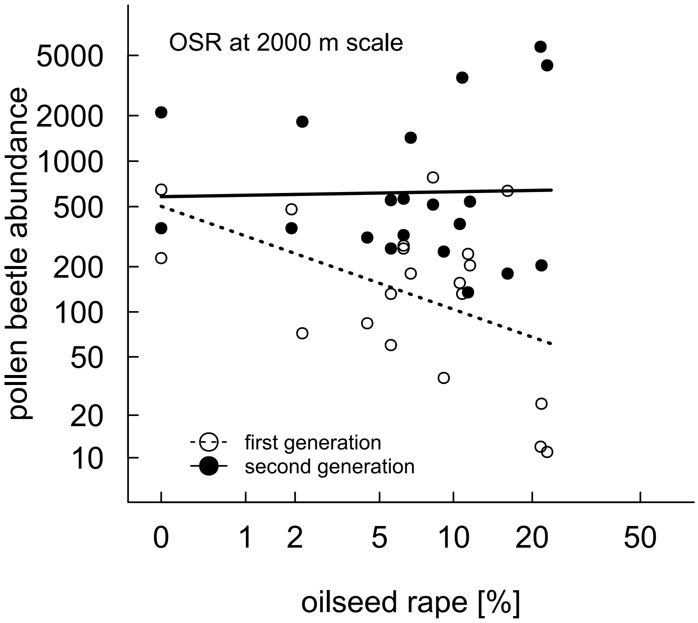


Fig. 1b. Relationships between pollen beetles abundances and amount of OSR [%] within a 2000 m radius around grassland plots separately for generations. Note log scale for x- and y-axis. Abundance of first generation significantly decreased with increasing amounts of OSR, indicating a landscape-wide dilution effect of pollen beetles on grasslands before OSR flowering peak.

Table 1. Results for linear mixed effects models, showing the small (250m) and large (2000m) scale effects of OSR on the abundance of pollen beetles on grasslands for the first and second generation separately.

Abundance pollen beetles	*Value*	*Std. Error*	*DF*	*t-value*	*P*
250m scale					
(Intercept)	4.35	0.63	18	6.86	< 0.001
log(OSR+1)	-1.02	0.37	18	-2.71	< 0.05
generation	0.79	0.40	18	1.96	0.07
log(OSR+1): generation	0.76	0.23	18	3.25	< 0.01
2000m scale					
(Intercept)	4.00	0.71	19	5.61	< 0.001
log(OSR+1)	-0.31	0.21	18	-1.50	0.151
generation	1.53	0.36	19	4.21	< 0.001
log(OSR+1): generation	-	-	-	-	n.s.

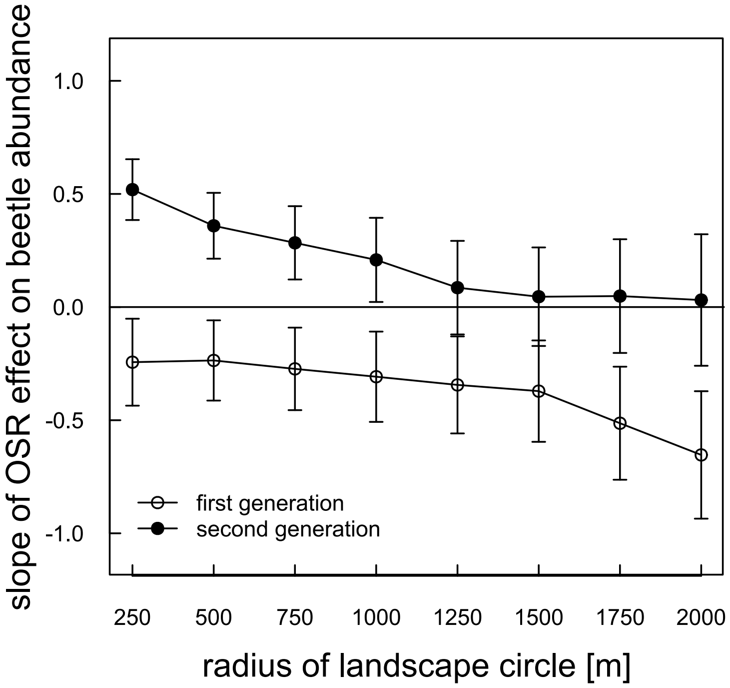


Fig. 2. Cross-scale effects of oilseed rape (OSR) on pollen beetle abundance at grassland plots separately for generations. The y-axis reflects the slope of the regression model relating beetle abundance to % of OSR on each spatial scale. The x-axis shows the scale on which % of OSR was measured. Error bars indicate the standard error of the slope. For the first generation of pollen beetles, the strongest negative effect of OSR occurred at large spatial scales (1750 and 2000m), indicating a landscape-wide dilution before OSR flowering peak. Positive effect on small scales (250 and 500m) of OSR found for the second generation of beetles demonstrates a strong spillover of beetles from OSR crop fields on grasslands with fading flowering of OSR crops.

Phytometer pod damage

Because four phytometer plants were killed by vertebrate herbivores, our pod damage dataset consisted of 236 plants. Mean number of pods per plant was 265 (range: 95 to 1011), while on average 7.8 % (mean: 18; range 0 to 157) were damaged by pollen beetles. The total amount as well as the proportion of destroyed pods significantly increased with local pollen beetle abundances, independently of plant height and pollinator abundance (Tab. 2). Insecticide treatment did not reduce pod damage by pollen beetles (Tab. 2, Fig. 3). The proportion of destroyed pods on plants significantly increased with higher amounts of OSR at the 250m scale. Total fruit set (intact pods) was not affected by pollen beetle nor pollinator abundances but positively related to plant height and insecticide treatment (Tab. 2). A paired t-test revealed that insecticide application reduced the proportion of aphid presence on phytometers (t = 2.96, *df* = 19, *p* = 0.008, mean differences = 0.222) with 26 % of insecticide treated and 48 % of untreated plants attacked by aphids, respectively.

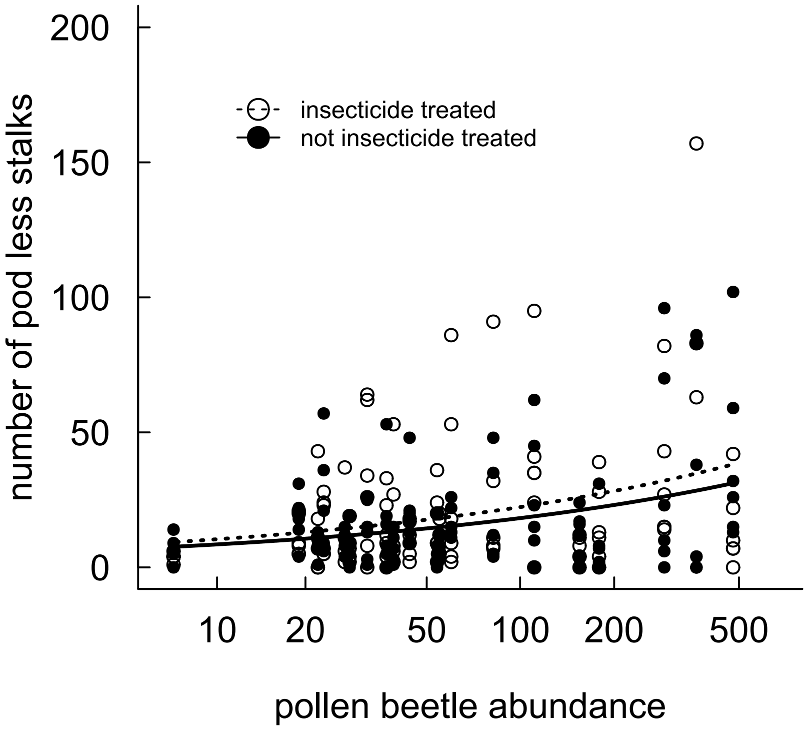


Fig. 3. Relationships between pollen beetles abundances and the number of destroyed flowers for plants with and without insecticide treatment. Note log scale for x-axis. Amount of pod less stalks for treated and untreated phytometers significantly increased with local abundance of pollen beetles, indicating that insecticide did not reduce flower damage.

Table 2. Results for generalized linear mixed models, showing the effects of pollen beetles, pollinators and OSR on the reproductive success of wild mustard plants. Amount and proportion of destroyed pods significantly increased with beetle abundance, independently of insecticide treatment and pollinators. Pod damage was highest for phytometers in the vicinity (250 m) of OSR fields. Total number of intact pods increased with plant height and insecticide treatment.

Response variable	*Value*	*Std. Error*	*DF*	*t-value*	*P*
Destroyed pods					
(Intercept)	1.32	0.31	215	4.29	< 0.001
log(beetle.abundance +1)	0.34	0.06	18	5.37	< 0.001
insecticide	0.20	0.14	215	1.46	0.145
log(pollinator.abundance +1)	-	-	-	-	n.s.
plant height [cm]	-	-	-	-	n.s.
Proportion destroyed pods					
(Intercept)	-4.12	0.35	215	-11.79	< 0.001
log(beetle.abundance +1)	0.35	0.07	18	4.67	< 0.001
insecticide	0.04	0.15	215	0.24	0.811
log(pollinator.abundance +1)	-	-	-	-	n.s.
Proportion destroyed pods					
(Intercept)	-3.00	0.14	215	-21.04	< 0.001
log(OSR.250m+1)	0.24	0.05	18	4.50	< 0.001
insecticide	0.06	0.16	215	0.37	< 0.709
log(OSR.2000m+1)	-	-	-	-	n.s.
Total fruit set (intact pods)					
(Intercept)	5.17	0.14	214	37.75	< 0.001
plant height [cm]	0.00	0.00	214	2.43	< 0.016
insecticide	0.13	0.04	214	3.31	< 0.001
log(pollinator.abundance +1)	-	-	-	-	n.s.
log(beetle.abundance +1)	-	-	-	-	n.s.

DISCUSSION

Our study showed that landscape composition influences pollen beetle abundance, but effects differed with the spatial scale considered. We found evidence for scale-dependency of crop-noncrop spillover of pest insects, negatively affecting reproductive success of wild plants.

Our results indicate that mass-flowering crops affected beetle generations on wild mustard differently, depending on spatial scale: First-generation beetles were less abundant when % OSR in the landscape was high, presumably due to a landscape-wide dilution of the pollen beetle population or due to the higher attraction by large, distant OSR fields than small mustard patches. After OSR flowering, second-generation beetles showed a higher abundance on grasslands, presumably because they dispersed out of large OSR fields, which did not longer provide flower resources, to Brassicaceae on adjacent grasslands. These findings can be interpreted as a spillover of herbivores in two directions: First, beetles are leaving the local grassland and fly far away (landscape scale resource concentration, hypothesis 1); later on, they return from OSR fields (hypothesis 2).

In contrast to the periodically high density of flowers at OSR crop areas, grasslands may provide resources constantly, but at much lower levels and therefore becoming more attractive for pollen beetles when mass-flowering crops are less available. These results indicate that the importance of alternative flower resources for pollen beetles increases as the availability of mass-flowering OSR crops at larger spatial scales decreases, a connection which has lately been shown also for pollinating bees (Holzschuh et al. 2011). Only few studies explicitly examined crop-noncrop spillover of herbivorous pest insects from agricultural fields into natural habitats. For example, McKone et al. (2001) found similar effects for western corn rootworm (*Diabrotica* spp.) after suitable crop resources (here maize reproductive tissues) began to desiccate. In contrast, Gladbach et al. (2011) could not relate OSR cropping area to infestation rates of the rape pollen beetle larvae on wild mustard phytometers. This is probably due to only using a single scale of 750 m, where small-scale spillover and large-scale dilution effects overlap. Since many agricultural pests are polyphagous and share both habitat types (Symondson et al. 2002), cross-habitat movement of herbivores from crop areas to less intensively used habitats, like grasslands, may be a common phenomenon, strongly driven by the temporal dynamics of resource availability (Blitzer et al. 2012).

As predicted by our third hypothesis, the total number and the proportion of destroyed pods in *S. arvensis* increased with local pollen beetle abundance, so pollen beetle spillover reduced fruit set in wild mustard plants occurring on surrounding grassland habitats. As pollen beetles showed a strong numerical response to temporal pulses of OSR resource availability, this result is also in line with theoretical models suggesting a strong top-down effect of consumers on alternative prey, in this case plants which are still available when crop resources decline (Sears et al. 2004). The proportion of destroyed pods on plants increased with higher amounts of OSR only at the 250m scale, indicating that wild plants occurring at close vicinity to OSR fields suffered most from pollen beetle spillover.

Pod damage and total fruit set were not related to pollinator abundance, showing that pollinators appeared to have no or only a very limited influence in our experiment. In contrast to our expectation that insecticide application would reduce pollen beetle herbivory, we found no differences in pod damage between treated and untreated plants. The observed inefficacy of the used insecticide is likely due to increasing incidence of insecticide-resistant populations across mainland Europe as reported by other studies (Ekbom & Kuusk 2001, Hansen 2003, Wegorek 2006). However, the insecticide might impinge on other insect herbivores, since application reduced aphid presence on wild mustard plants by almost 50 %. This release from aphids and possibly also other herbivores may have led to increasing plant heights and higher amounts of intact pods of insecticide treated phytometers. As the amount of intact pods was not related to pollen beetle abundances, we suggest that the high ability of compensatory plant growth, known from *S. arvensis* plants, reduced visibility of pollen beetle damage on flowers.

Hence fruit set of *S. arvensis* depends on both antagonistic and mutualistic interactions. Both pollen beetles and pollinators can be affected by the spatial and temporal dynamics of mass-flowering crops. Since pollinator abundances on grasslands may be reduced during the mass-flowering period of OSR fields as well (Holzschuh et al. 2011), consequences of nearby OSR fields for reproductive success of wild plants might be difficult to predict.

Our results show that herbivore damage of wild plants in noncrop habitats of agricultural landscapes can be increased by pest insect spillover from crop fields. Spillover of specialist herbivores is triggered by pulsing availability of mass-flowering crops at different spatial scales. During the period of high crop availability, herbivore density appears to be diluted on a landscape scale and herbivores mainly concentrate on crop fields, not patchily distributed wild plants in neighboring grasslands. When crop habitats are fading, herbivores spillover to alternative resources in nearby habitats. Wild host plants in the direct neighborhood of cropland suffer first from increased herbivore spillover, but not when cropland changes occur far away, i.e. on larger spatial scales. Therefore, herbivore spillover and damage on wild plants decreases (i) with increasing distance from crop fields and (ii) during mass-flowering peak of crops. This means benefits for wild Brassicacae budding at about the same time as mass-flowering crops appeared to be highest when occurring in the proximity of OSR fields. On the other hand when flowering beyond that period alternative host plants in the direct neighbourhood of cropland suffer first and most strongly from increased herbivore spillover. In consequence of these spatial-temporal patterns shaping pest-induced damage to wild grassland plants we recommend not to fall below a minimum distance of 250 m between large crop monocultures and particularly plant species rich habitats like calcareous grasslands while following the seasonal crop rotation scheme. Since reproductive success of self-incompatible plants generally depends on both, antagonists and mutualists, positive effects of blooming synchrony of crop and wild plant on fruit set of the wild plant might be in other situations restricted by pollinator abundance, often probably affected in a similar way through pulsing availability of mass-flowering crops.

ACKNOWLEDGEMENTS

We thank the managers of the three Exploratories, Swen Renner, Sonja Gockel, Andreas Hemp and Martin Gorke and Simone Pfeiffer for their work in maintaining the plot and project infrastructure, and Markus Fischer, Elisabeth Kalko, Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze and Wolfgang W. Weisser for their role in setting up the Biodiversity Exploratories project.

The work has been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (TS 45/28-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

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APPENDIX

Appendix A1: Amount of landscape composition parameters in eight circles around each plot

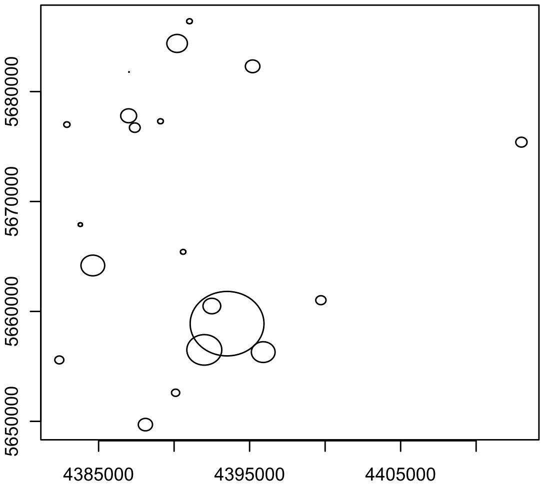
Amount of OSR [%]								
PlotId	**250m radius**	**500m radius**	**750m radius**	**1000m radius**	**1250m radius**	**1500m radius**	**1750m radius**	**2000m radius**
HEG01	0	4.5708	13.1183	14.8924	15.3982	13.2987	11.5238	11.3987
HEG03	5.2444	13.6009	14.3774	10.6546	8.7933	8.1001	7.5740	6.3063
HEG04	6.7000	23.1437	22.6286	17.1416	11.1812	7.7647	6.3100	6.7496
HEG05	0	3.8663	5.1042	10.3842	10.7090	9.2605	8.0473	6.3113
HEG09	0	0	0	0	0	0	0.2155	1.9121
HEG13	23.4708	21.3569	14.8691	15.2851	17.3056	13.6489	10.2024	8.3018
HEG16	0	0	0	0.4208	6.2861	9.1962	9.5028	9.1586
HEG18	41.9228	57.1112	45.9947	38.1066	30.7402	26.0593	22.5101	21.4860
HEG23	0	0	0	0	0	0	0	0
HEG24	0	0	0	0	0	0.2725	1.3949	2.1839
HEG25	26.4636	22.1986	18.8405	14.6447	10.8335	9.3363	9.2729	10.8223
HEG28	0	0.0453	7.8588	11.3336	12.0064	10.1990	10.0604	10.5832
HEG32	0	0	0	1.98148	9.8633	15.9771	15.5291	16.1555
HEG34	0	0	0	0	0	0	0	0
HEG35	0	0	0	0	0	0	1.0113	4.4219
HEG37	0	13.4015	14.2575	14.7041	16.0157	14.9397	13.4308	11.6035
HEG42	6.2938	20.3017	22.4422	16.6086	11.7950	9.4397	7.2955	5.5856
HEG43	29.6703	46.4288	47.4815	41.0684	35.9512	30.5263	25.3957	22.7363
HEG44	0	0	0.7971	5.8345	6.5859	6.3513	6.3402	5.5856
HEG46	0	7.1889	16.0041	23.0797	26.7893	25.5381	22.9825	21.6471

Amount of forest [%]								
PlotId	**250m radius**	**500m radius**	**750m radius**	**1000m radius**	**1250m radius**	**1500m radius**	**1750m radius**	**2000m radius**
HEG01	17.5866	32.3066	32.3066	32.3066	32.3066	32.3066	32.3066	32.3066
HEG03	21.0529	13.7881	9.3143	6.6416	4.6585	3.2493	3.1880	4.5649
HEG04	16.8875	11.3452	17.7485	22.3640	25.6210	29.3022	33.8454	38.5909
HEG05	4.7230	19.6725	24.8672	27.0236	27.3939	28.7002	32.3690	37.2673
HEG09	11.1427	26.4741	32.0726	35.5142	33.0489	26.8826	23.6446	22.5073
HEG13	20.3045	16.5784	11.4149	7.7065	4.9323	4.7959	7.4265	9.7343
HEG16	15.7368	42.3266	46.5030	50.8427	51.9712	52.6738	52.8570	52.5629
HEG18	0.0000	1.7011	15.2170	23.8569	23.2082	22.0490	21.5819	20.6497
HEG23	53.0677	56.7142	64.4559	67.3865	67.0795	62.9690	61.1726	61.7135
HEG24	51.2288	62.2782	63.4536	66.1000	68.7750	71.1953	71.8811	70.6908
HEG25	26.8118	19.8001	11.5619	7.2280	5.2968	4.5354	4.3978	4.5058
HEG28	0.0000	3.2474	5.3621	7.5408	7.9436	9.5356	10.9029	12.5228
HEG32	9.0205	7.4861	10.4185	16.0470	16.9839	17.3898	18.9453	21.1534
HEG34	36.8131	24.9097	27.2584	34.1886	37.6720	40.6644	40.6096	38.9804
HEG35	0.0000	0.0000	0.1737	1.3478	1.6346	1.2588	1.8449	4.0013
HEG37	13.5053	8.3357	10.3284	13.9960	17.8939	19.1180	20.3024	20.4290
HEG42	25.1249	27.3765	33.6431	40.0474	44.2607	49.8719	55.1022	59.8374
HEG43	0.0000	7.1569	17.5660	19.0809	16.8011	18.9815	21.1077	19.7464
HEG44	7.4415	33.6646	43.1636	48.8223	49.7576	49.8695	51.4115	52.7283
HEG46	44.3421	28.8180	25.2171	24.9279	22.1293	24.0336	26.0417	25.1604

Amount of grassland [%]								
PlotId	**250m radius**	**500m radius**	**750m radius**	**1000m radius**	**1250m radius**	**1500m radius**	**1750m radius**	**2000m radius**
HEG01	80.3961	52.3247	52.3247	52.3247	52.3247	52.3247	52.3247	52.3247
HEG03	52.5978	38.3523	23.9838	16.5425	13.3429	13.2320	13.3350	13.2735
HEG04	35.1736	13.8213	11.8811	11.9278	10.7525	10.3272	10.7255	9.7200
HEG05	93.6812	55.0224	35.5917	26.7946	21.8228	17.8866	15.7589	14.2477
HEG09	0.0000	4.5277	7.1210	6.5065	8.9461	9.4716	9.4874	9.9501
HEG13	42.6541	23.4823	11.8698	6.9833	6.9243	7.0693	7.7265	8.7011
HEG16	63.4795	32.9371	26.2058	22.2820	16.9661	12.4783	9.5525	7.3135
HEG18	0.0000	0.7577	3.0538	4.2547	5.7460	9.5560	13.9358	16.0049
HEG23	41.3335	22.4596	18.5983	15.7333	14.5607	14.7146	14.4423	13.5304
HEG24	41.8982	32.7009	29.6457	29.6703	26.5702	23.9964	20.9043	20.1651
HEG25	21.3935	18.6870	14.8855	13.3505	11.4366	10.7601	10.0109	9.2038
HEG28	60.2604	36.6151	26.0245	25.6045	26.0846	25.7267	24.5029	22.0393
HEG32	86.4349	58.3675	38.4517	25.6166	17.9844	13.7836	11.5410	9.9057
HEG34	36.5700	21.5754	19.5634	14.7922	14.4698	11.4794	10.8804	10.3683
HEG35	25.0092	9.5128	11.8980	14.3625	16.2287	15.9987	15.5625	14.1483
HEG37	50.2085	25.1321	16.1769	15.8171	12.0448	10.5263	8.7482	8.7131
HEG42	50.7817	38.8928	36.7698	37.3519	36.2987	33.2819	30.8264	27.4294
HEG43	33.3929	13.7797	8.1363	12.1975	15.6616	16.1534	14.7247	13.6419
HEG44	61.4901	50.7828	42.4632	31.4755	29.7000	29.5598	28.7331	27.7077
HEG46	36.4316	18.7707	9.8544	7.5437	5.3792	3.9818	3.4003	3.4314

Amount of semi-natural habitat [%]								
PlotId	**250m radius**	**500m radius**	**750m radius**	**1000m radius**	**1250m radius**	**1500m radius**	**1750m radius**	**2000m radius**
HEG01	2.0172	1.0718	1.0718	1.0718	1.0718	1.0718	1.0718	1.0718
HEG03	7.7681	18.1698	26.2017	30.3000	32.9787	37.1959	38.6397	38.2085
HEG04	21.7341	33.7330	27.9086	24.4039	22.9620	19.9249	16.7432	14.3225
HEG05	0.0000	0.0894	0.6739	1.2283	1.3652	1.4657	1.4784	1.4439
HEG09	83.2126	62.6490	44.9330	33.0669	25.6800	20.4064	16.7284	13.7244
HEG13	12.7339	6.1749	5.3710	5.8613	5.6155	5.8241	5.5250	4.9735
HEG16	1.6379	4.1886	7.8828	7.3155	10.6894	14.7710	18.4018	20.5434
HEG18	48.4291	23.9841	17.4950	14.3035	10.9319	9.2827	8.3077	7.4764
HEG23	0.0000	0.7244	0.4539	0.8974	1.2695	2.3643	2.5343	2.7165
HEG24	4.5025	1.6943	4.5936	2.7816	2.4073	2.4525	2.0959	2.0268
HEG25	1.7236	4.3021	4.6110	3.7742	3.6605	4.5503	4.3166	4.1752
HEG28	39.7396	48.5591	39.0357	29.2023	23.5044	19.7337	17.2030	15.7579
HEG32	2.2425	3.4742	4.1770	6.0950	12.0667	15.6942	18.9616	18.8302
HEG34	0.9082	5.6371	9.3582	12.6888	13.8456	13.9156	12.9269	12.0414
HEG35	2.3853	2.8290	3.2978	4.4880	4.6378	5.1088	5.4186	5.3934
HEG37	26.4974	16.8514	10.8364	10.4778	8.4330	7.1836	6.1728	5.0904
HEG42	18.1376	13.5599	7.1179	4.8371	5.1583	5.5294	4.8322	4.5802
HEG43	14.6171	7.7530	7.8806	6.6241	4.8254	4.1778	4.4888	4.3042
HEG44	30.4356	13.8585	11.7215	8.8730	6.3476	5.3527	4.7861	4.6336
HEG46	3.5474	18.9358	14.8411	11.1186	11.1460	10.3755	9.8374	8.9967

Amount of arable land [%]								
PlotId	**250m radius**	**500m radius**	**750m radius**	**1000m radius**	**1250m radius**	**1500m radius**	**1750m radius**	**2000m radius**
HEG01	0.0000	14.2968	14.2968	14.2968	14.2968	14.2968	14.2968	14.2968
HEG03	14.3027	20.4679	28.1007	27.4995	27.5713	26.2924	25.3281	24.7407
HEG04	24.5954	39.2434	41.0149	38.3412	34.5918	32.5115	31.9612	32.0206
HEG05	0.0000	14.1384	24.6884	27.2594	32.8448	36.2429	35.4191	34.0537
HEG09	0.0000	1.1612	12.6617	22.7795	30.3085	39.2482	43.4542	44.6666
HEG13	23.5006	44.3971	59.9091	67.3429	69.0157	69.5080	68.9663	67.2474
HEG16	12.0022	15.3102	14.7295	15.7419	16.6032	16.9917	16.6173	17.3090
HEG18	51.5709	71.0811	59.5926	51.8624	50.7127	46.5217	42.9930	43.7867
HEG23	5.4017	12.8781	8.0055	9.3647	11.7903	15.1024	17.4024	17.8386
HEG24	0.0000	0.0000	0.0000	0.0000	0.0000	0.2814	1.9453	3.4210
HEG25	46.7752	55.5911	66.7796	67.8806	66.6564	68.8021	72.2103	73.5062
HEG28	0.0000	10.5032	26.3662	34.0252	35.7896	37.0086	40.4353	43.1763
HEG32	0.4586	28.6949	44.6428	50.1592	47.0673	46.9067	44.7082	44.5218
HEG34	25.7087	47.4514	41.3784	29.6443	23.0363	23.2197	25.3290	28.4372
HEG35	50.4541	73.9179	67.5788	61.3430	56.7869	55.1851	51.5719	48.4360
HEG37	8.1160	42.5269	53.4039	47.9340	44.4827	45.3608	47.4330	50.0873
HEG42	5.9557	20.1708	22.4693	17.7636	13.9608	10.9616	8.5050	6.5553
HEG43	49.9679	70.7304	64.9679	60.5652	59.8006	55.8135	54.0997	56.0659
HEG44	0.0000	0.0000	1.2780	8.8755	10.3076	10.9611	11.3680	12.0052
HEG46	0.0000	12.8397	33.3889	45.1876	54.0337	56.0788	55.3098	57.3897



Appendix A2. Plot of model residuals for spatial autocorrelation by fitting gls model with exponential variance function, where Gauss-Kruger coordinates were used as spatial covariates, assuming a spherical spatial correlation structure. Plots represented spatially independent replicates since residuals were not spatially autocorrelated.

Appendix A3: Models and R code

Spatial scale models sorted according to Akaike´s information criterion

```
18.       (Intercept), rape.1250, rape.750,  AICc: 154.6077
17.       (Intercept), rape.1250, rape.1750, AICc: 154.5266
16.       (Intercept), rape.1750, rape.2000, AICc: 154.4521
15.       (Intercept), rape.2000, rape.750,  AICc: 154.4415
14.       (Intercept), rape.1750, rape.750,  AICc: 154.1810
13.       (Intercept), rape.100, rape.1500,  AICc: 153.8502
12.       (Intercept), rape.1000, rape.500,  AICc: 153.8097
11.       (Intercept), rape.1250, rape.250,  AICc: 152.3818
10.       (Intercept), rape.1250, rape.500,  AICc: 152.0622
 9.       (Intercept), rape.100, rape.1750,  AICc: 152.0175
 8.       (Intercept), rape.2000, rape.500,  AICc: 151.7349
 7.       (Intercept), rape.1500, rape.500,  AICc: 151.7273
 6.       (Intercept), rape.1750, rape.500,  AICc: 151.3711
 5.       (Intercept), rape.1500, rape.250,  AICc: 151.0117
 4.       (Intercept), rape.1500, rape.1750, AICc: 150.9023
 3.       (Intercept), rape.100, rape.2000,  AICc: 150.0307
 2.       (Intercept), rape.1750, rape.250,  AICc: 150.0063
 1.       (Intercept), rape.2000, rape.250,  AICc: 149.1645
```

Models OSR scales

```
model.fit1=lme(lBrass~lrape.250+GEN+ lrape.250:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))

model.fit2=lme(lBrass~lrape.500+GEN+ lrape.500:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))

model.fit3=lme(lBrass~lrape.750+GEN+ lrape.750:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))

model.fit4=lme(lBrass~lrape.1000+GEN+ lrape.1000:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))

model.fit5=lme(lBrass~lrape.1250+GEN+ lrape.1250:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))

model.fit6=lme(lBrass~lrape.1500+GEN+ lrape.1500:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))
```

```
model.fit7=lme(lBrass~lrape.1750+GEN+ lrape.1750:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))

model.fit8=lme(lBrass~lrape.2000+GEN+ lrape.2000:GEN,
     random = ~ 1|plotid,data =
     r10,control=list(opt="optim"))
```

Model phytometer pod damage

```
model.fit1=glmmPQL(destroyed.pods ~
log(beetles.sum.experiment +1) +
log(pollinators.sum.experiment +1) +
insecticide + plant.height,
random=~1|plotid,control=list(opt="optim"),
na.action=na.exclude, family="quasipoisson")

model.fit2=glmmPQL(cbind(destroyed.pods,
intact.pods - destroyed.pods) ~
log(beetles.sum.experiment +1) +
log(pollinators.sum.experiment +1) + insecticide,
random=~1|plotid,control=list(opt="optim"),
na.action=na.exclude, family="quasibinomial")

model.fit3=glmmPQL(intact.pods ~
log(pollinators.sum.experiment +1) +
log(beetles.sum.experiment +1) +
insecticide,
random=~1|plotid,control=list(opt="optim"),
na.action=na.exclude, family="quasipoisson")
```

R functions used to perform pairwise landscape parameter combination and model selection based on AICc

```
pp=paste(
combn(names(dataset)[c(4:47)],2)[1,],
combn(names(dataset)[c(4:47)],2)[2,],sep="+")

ll=lapply(pp,function(x)
     as.formula(
     paste(
          "log(brassicogethes.sum.gen+1)~",x)))
```

```
a1=aggregate(cbind(melingethes.sum.gen1,melingethes.sum.gen2,
     rape.250, rape.500, rape.750, rape.1000, rape.1250,
     rape.1500, rape.1750, rape.2000, arable.250, arable.500,
     arable.750, arable.1000, arable.1250, arable.1500,
     arable.1750, arable.2000, forest.250, forest.500,
     forest.750, forest.1000, forest.1250, forest.1500,
     forest.1750, forest.2000, grassland.250, grassland.500,
     grassland.750, grassland.1000, grassland.1250,
     grassland.1500, grassland.1750, grassland.2000,
     seminatural.250, seminatural.500, seminatural.750,
     seminatural.1000, seminatural.1250, seminatural.1500,
     seminatural.1750, seminatural.2000,)
     ~ plotid, mean, data=r9)


sx=lapply(1:990,function(x)model[[x]]=lme(fixed=ll[[x]],
random = ~ generation|plotid,
data = r10,control=list(opt="optim")))


myAICcs=lapply(sx,function(x)
list(
vars=toString(names(summary(x)$tTable[,1])),
AICc=AICc(x)[1]
)
)

mydf <- data.frame(vars=sapply(myAICcs,function(x)x$vars),
     AICc=sapply(myAICcs,function(x)x$AICc))
mydf[order(mydf$AICc,decreasing=F),]
```

CHAPTER 5

SYNOPSIS

GENERAL DISCUSSION

The results presented in this thesis show that land use intensification reduces diversity and abundance of insect communities in grasslands via direct and indirect effects. In particular, mowing frequency, directly affecting vegetation height and long-term decreasing plant species richness, excels as a key driver of herbivore diversity decline in all three regions. We show that even small and easily set up succession islets on meadows and pastures can serve as important refuges for the diversity of herbivores and associated predators and that the efficiency of this conservation practice increases with land use intensity and duration of set-aside. Finally we prove that pest insect spillover across the crop-noncrop interface in agricultural mosaic landscapes can reduce fruit set of wild plants.

In this thesis, we used different approaches to study land use intensification effects on herbivores and predators in grasslands, influencing plant-herbivore-antagonist interactions within agricultural landscapes. We combined an observational approach with experimental treatments to minimize the influence of confounding factors, which are a pervasive problem in many ecological studies. The advantage of this combination is that we are able to infer strong causality of land use intensification on herbivores and predators under the complexity of environmental conditions and processes occurring in real-world grassland ecosystems. In our approach we used a continuous and reproducible land use index to account for the quantitative variation of multiple land use types in heterogeneous landscapes and found that it was an adequate and relatively easily accessible tool to quantify agricultural intensification.

In the following, I discuss the main results (research objectives) addressed in this thesis within the four major blocks (A, B, C and D):

Block A: Land use and management effects on herbivores and predators

***Q A1**: Does grassland management intensity consistently and negatively affect diversity and abundance across different regions? (Chapter 2)*

For herbivores we found a direct negative effect of overall land use intensification on diversity and abundance, consistently at the three study regions. Predators did not respond directly to land use intensification, but we found predator diversity significantly increasing with higher herbivore diversity and abundance levels at all regions, indicating predators are bottom-up controlled via herbivore availability. This prevalence of bottom-up effects is in line with the findings of Scherber et al. (2010) along an experimental grassland plant diversity experiment. These results emphasize that in particular extensively managed grasslands, e.g. calcareous grasslands of which many also rank among the most species-rich in Central Europe (Poschlod et al. 2002; Van Swaay 2002), may provide sufficient resources along the bottom-up trophic cascades to sustain locally species-rich insect communities.

***Q A2**: Which local management practices affect diversity and abundance the most? (Chapter 2)*

In particular, mowing frequency excelled as a key driver of herbivore diversity decline in all three regions, while predators did not directly respond to management practices at all. Reported negative effects of cutting are in agreement with a well-established body of literature (e.g. Morris & Rispin 1987; Gerstmeier & Lang 1996; Bell et al. 2001; Johst et al. 2006). Cutting leads to a sudden decrease in resource heterogeneity and quantity, directly regulating herbivore resources and subsequently predator diversity. Neither grazing nor fertilization did have any direct impact on herbivore diversity and abundance across Exploratory regions. In contrast to our findings, in some studies disturbance through grazing was found to directly decrease herbivore species richness (Kruess & Tscharntke 2002a, Kruess & Tscharntke 2002b, Woodcock et al. 2009) on pastures with high livestock densities. However, moderate grazing practices in our study possibly did not reduce plant resource availability to a critical bottleneck situation for herbivores.

Block B: Influence of vegetation characteristics on herbivores

***Q B1**: Does plant species richness enhance diversity and abundance? (Chapter 2)*

As plant species richness declined with increasing land use intensity, which is often shown to be a long-term consequence of land use intensification (e.g. Zechmeister et al. 2003), herbivore diversity and abundance also decreased. The Resource Specialization (Hutchinson 1959) and Resource Concentration Hypothesis (Root 1973) predict higher diversity but lower abundances of herbivores in plant species-rich sites, even though diversity and abundance might be strongly linked (Gotelli & Graves 1996). Our results are in line with the Resource Specialization Hypothesis but may also reflect a generally low presence of specialized herbivores at the sampled sites, indicating that mechanisms of the Resource Concentration Hypothesis gain importance only in more simplified plant communities than found on intensively managed grasslands.

***Q B2**: Do taller plants facilitate colonization success? (Chapters 2 and 3)*

The effects of vegetation height on herbivore abundance are less pronounced and overcome by plant diversity effects across the three study regions. Vegetation height positively affects herbivores at Schorfheide Exploratory bearing clearly the species-poorest plant communities, while at Schwäbische Alb and Hainich Exploratory more herbivore species were found at sites with lower vegetation but generally higher plant species richness.

However, when looking at a single but commonly on meadows and pastures occurring grass species (*D. glomerata*), beneficial effects of increasing host plant height on colonization success of associated specialists become obvious. Taller shoots provide the widest colonization space and increase abundance of stem-borers, probably broadly colonizing as 'aerial plankton' and overriding effects of spatial scale, area or isolation (Dubbert et al. 1998). Even though the 1-season unmanaged areas offered, on average, 14.9 cm taller shoots than the managed areas, herbivore abundances did not differ between these locations. This identifies mean grass shoot length above 1 m at the ≥2-seasons abandoned areas as a threshold, boosting colonization success for both species. This result is in agreement with previous studies correlating shoot length with endoherbivore abundance (Dubbert et al. 1998) and species richness (Tscharntke 1997).

Block C: Landscape composition and configuration effects on herbivores and plant damage

***Q C1**: Can crop fields in the surrounding landscape facilitate spillover of pest insects on grasslands? (Chapter 4)*

Our results indicate that mass-flowering crops affect pest insect abundance, depending on spatial scale. During the period of high crop availability, herbivore density appears to be diluted on a landscape scale and herbivores mainly concentrate on crop fields and not on patchily distributed wild plants in neighboring grasslands. When crop habitats are fading, herbivores spill over to alternative resources like Brassicaceae on adjacent grasslands. These findings can be interpreted as a spillover of herbivores in two directions: First, beetles are leaving the local grassland and fly far away and later on they return from OSR fields. Increases of local pollen beetle abundances on grassland were positively related to the amount of OSR at the 250 m scale, but not at larger spatial scales (2000 m). Since many agricultural pests are polyphagous and share both habitat types (Symondson et al. 2002), cross-habitat movement of herbivores from crop areas to less intensively used habitats, like grasslands, may be a common phenomenon, strongly driven by the temporal dynamics of resource availability (Blitzer et al. 2012).

***Q C2**: Does spillover of pest insect increase herbivore damage on wild plants? (Chapter 4)*

When oilseed rape flowering is fading, pollen beetles spillover and damage phytometer plants, leading to reduced fruit set. In contrast to our expectation that insecticide application would reduce pollen beetle herbivory, we found no differences in pod damage between treated and untreated plants. The observed inefficacy of the used insecticide is likely due to increasing incidence of insecticide-resistant populations across mainland Europe as reported by other studies (Ekbom & Kuusk 2001, Hansen 2003, Wegorek 2006). Wild host plants in the direct neighborhood of cropland (250 m) suffered first from increased herbivore spillover, but not when cropland changes occur far away, i.e. on larger spatial scales. Therefore, herbivore spillover and damage on wild plants increases with decreasing distance from crop fields after mass-flowering peak of crops. Hence alternative host plants occurring in the vicinity of cropland suffer most strongly from increased herbivore spillover.

Block D: Biodiversity conservation management

***Q D1**: Does short-term and small-scale experimental succession increase diversity of herbivores and predators? (Chapter 2)*

Experimental successional islets established on frequently mown grasslands increased herbivore diversity across all regions up to levels found on extensively managed grasslands in the surroundings. However, this conservation measure does not directly increase predator abundance and diversity since they do not respond to land use intensification and management practices at all but are bottom-up controlled via herbivore availability. Nevertheless, these results emphasize that even small areas, temporally excluded from management, can serve as stepping stones for insects in agricultural landscapes. We therefore recommend set-aside of even small areas on intensively managed grasslands to locally support insect diversities and promote associated ecosystem processes. Since several studies, dealing with set-aside fields of different age, found higher plant and insect diversities on two than one or three year old succession areas (Gathmann et al. 1994, Greiler 1994, Steffan-Dewenter & Tscharntke 1997, 2001), we assume the highest benefit of grassland set-asides within the first two years of succession.

***Q D2**: How efficient are successional islets as a conservation measure? (Chapters 2 and 3)*

The establishment of short-term succession areas on grasslands becomes increasingly more efficient for enhancing diversity with rising land use intensification levels, especially induced through higher mowing frequencies. In our study, allowing succession for one year already enhanced herbivore diversity across all study regions, which in turn increased predator diversity via bottom-up effects. This low-cost and high-benefit conservation measure may provide suitable refuges from which insects can re-colonize sward islets (Helden et al. 2010) on surrounding and intensively managed grasslands, despite of ever changing land use practices and environmental conditions.

As it is often expected that set-aside does exhibit steadily increasing species richness with successional age (Brown & Southwood 1987), abandoned areas (≥2-seasons) provided higher stem-borer abundances compared to 1-season unmanaged and continuously managed areas. This mechanism is driven by a management–induced reduction in host shoot length over time, potentially narrowing spatial niche width for co-occurring species as indicated by increasing overlaps in attack heights particularly on intensively managed grasslands. Therefore, implementation of small grassy strips e.g. located at grassland edges and excluded from grazing and mowing for at least two years should be highly effective in supporting a diverse and abundant insect community.

***Q D3**: How can pest-induced damage to wild grassland plants be reduced in landscapes dominated by mass-flowering crops? (Chapter 4)*

While current studies mainly focus on how mobile organisms occurring in managed areas benefit from neighbouring natural habitats (e.g. Holzschuh et al. 2010, Rand et al. 2006) we provide information on organism spillover from managed crop fields to adjacent grassland reducing fruit set of wild mustard plants. Our results show that herbivore spillover and damage on wild plants was related to the amount of OSR at the 250 m scale and decreases (i) with increasing distance from crop fields and (ii) during mass-flowering peak of crops. This means benefits for wild Brassicacae budding at about the same time as mass-flowering crops appeared to be highest when occurring in the proximity of OSR fields. On the other hand when flowering beyond that period alternative host plants in the direct neighborhood of cropland suffer first and most strongly from increased herbivore spillover. In consequence of these spatial-temporal patterns shaping pest-induced damage to wild grassland plants we recommend not to fall below a minimum distance of 250 m between large crop monocultures and particularly plant species rich habitats like calcareous grasslands while following the seasonal crop rotation scheme. However, reduced herbivore damage of wild plants may in other situations be restricted by pollinator abundance and come at the cost of reduced pollination which is probably affected through pulsing availability of mass-flowering crops (Holzschuh et al. 2011) in a similar way as herbivore spillover.

GENERAL CONCLUSIONS

Taken together, the three studies presented in this thesis advance the understanding of responses of insect functional groups to land use intensification and interactions among plants, herbivores and predators. While herbivores generally respond negatively to land use intensification, in particular to increasing mowing frequency, predators were not directly affected by management, but indirectly controlled via herbivore availability. Hence increasing (non-pest) herbivore populations provide resources for higher trophic levels, insuring high predator diversity through bottom-up trophic cascades from plants via herbivores to predators (Fig. 2). In contrast to the negative effects of local management on grassland insect communities, single and highly specialized agricultural pest species profit from the expansion of monoculture crops. However, when crop resources get scarce, pest population spillover to noncrop areas can be a serious threat to wild plants through reducing their reproductive success. Since herbivore damage decreases with increasing distance from crop fields a minimum distance to crop monocultures should protect endangered plant species (e.g. in species rich habitats such as calcareous grasslands). We have also shown that even small and easily set up successional islets on meadows and pastures locally support insect diversities and

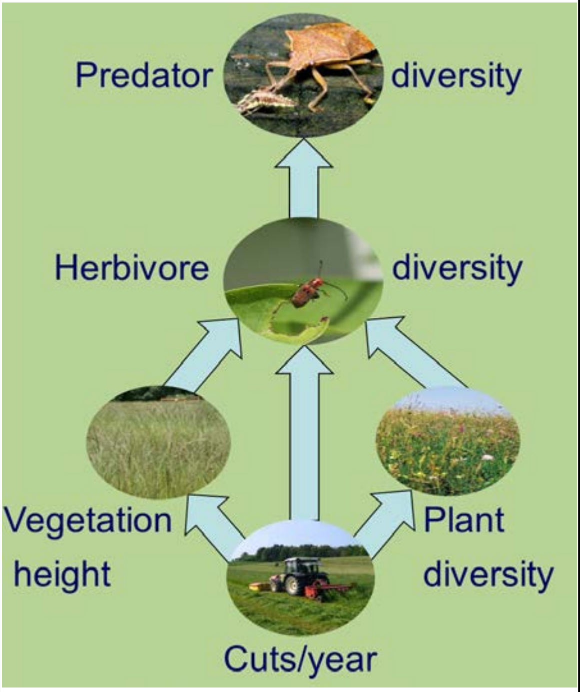


Fig. 2: Bottom-up effects on predator diversity.

promote associated ecosystem processes. Since the efficiency of this conservation practice increases with (i) land use intensity and (ii) duration, we assume the highest benefit of grassland set-asides on intensively managed grasslands (notably when several cuts per year are applied) within the first two years of succession. This low-cost and high-benefit conservation measure may provide suitable refuges from which insects can re-colonize sward islets on surrounding and intensively managed grasslands, despite of ever changing land use practices and environmental conditions. Further studies are needed to address the relationship between functional group diversity and performance in associated processes to sustain desirable levels of ecosystem services on local and landscape scales.

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Acknowledgements

Diese Doktorarbeit wäre nicht möglich gewesen ohne die Unterstützung zahlreicher Personen. Mein besonderer Dank gilt Prof. Dr. Teja Tscharntke für die freundliche Aufnahme in seine Arbeitsgruppe und sein Engagement bei Planung und Durchführung der einzelnen Projekte. Ebenfalls möchte ich mich herzlich bei Dr. Christoph Scherber bedanken, auf dessen Unterstützung, Motivation und Erfahrung ich mich auch während schwieriger Phasen meiner Dissertation immer verlassen konnte. Vielen Dank an Prof. Dr. Stefan Vidal und Prof. Dr. Stefan Scheu, die mein Prüfungskomitee vervollständigten.

Ein herzliches Dankeschön an alle Mitglieder der Abteilung Agrarökologie! Ich bin froh Teil dieser inspirierenden Gemeinschaft gewesen zu sein, in der immer eine gute Mischung aus persönlicher und professioneller Atmosphäre vorherrschte, was wesentlich zum Gelingen der Arbeit beitrug. Besonders danke ich dem Petri Jünger Jochen Fründ und T-Rex Sebastian Hänke, die mit mir auf diesem ereignisreichen Pfad wandelten und stets neue Herausforderungen an das „Zentrum für angewandte Chaos Theorie“ stellten. Ein grosses Dankeschön geht auch an Susanne Schiele, Susanne Jahn und Jutta Gilles für ihre effektive und unermüdliche Unterstützung bei organisatorischen und bürokratischen Problemen aller Art.

Weiterhin bedanke ich mich bei den Biodiversity-Exploratorern Juliane Steckel, Michaela Bellach, Carmen Börschig, Lars von Riedmatten, Nicole Wäschke, und Christine Herbst für die gute Kooperation im Feld und die interessanten Diskussionen auf unseren Treffen und Vollversammlungen. Bei meinen Assistenten Matthias Spiegler, Julia Dolezil, Sara Bauer, Kamini Barua, Kathrin Grahmann, Janna Gronefeld, Tim Koddenberg und Mareen Gollnow entschuldige ich mich für die widrigen Wetterbedingungen die sie meinetwegen draussen erdulden mussten.

Meiner Familie, insbesondere meiner Mom und meinem Dad danke ich für ihr Vertrauen und ihre fortwährende Unterstützung (sogar im Feld!), die es mir erst ermöglichte das alles zu erreichen. Dickes Busserl an meinen „gloan Hosn“, für deine Geduld und deinen Beistand während der letzten anstrengenden Wochen.

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Thesis declarations

Declaration of the author's own contribution to manuscripts with multiple authors

The Chapters 2 to 4 are a series of munuscripts that have or will be submitted to peer-reviewed journals. I am the overall author of all manuscripts presented in this thesis. Development of main ideas, data collection, statistical analysis and writing of the manuscripts is my original work. The respective co-authors contributed to various parts of the studies and provided comments to the manuscripts.

Declaration plagiarism

Herby I confirm that I have written this doctoral thesis independently, that I have not used other sources or facilities than the ones cited and acknowledged, that I have not used unauthorized assistance and that I have not submitted this thesis previously in any form for another degree at any university or institution.

Göttingen, Februar 2012

(Christoph Rothenwöhrer)