Landscape context of habitat fragmentation and the diversity of plants, arthropods and snails on calcareous grasslands

Dissertation
zur Erlangung des Doktorgrades
der Fakultät für Agrarwissenschaften
der Georg-August-Universität Göttingen

vorgelegt von
Verena Rösch
geboren in Friedrichshafen am Bodensee
Göttingen, April 2015

1. Referent: Prof. Dr. Teja Tscharntke

2. Korreferent: Prof. Dr. Johannes Isselstein

Tag der mündlichen Prüfung: 22. 7. 2014

Contents

Chapter 1: Fragmentation of semi-natural habitats in agricultural landscapes

Calcareous grassland “Lengder Burg” near Göttingen (June 2013)

Introduction

Worldwide, habitat fragmentation, habitat loss and landscape modification are among the main drivers of biodiversity decline (Sala et al., 2000; Fahrig, 2003; Fischer & Lindenmayer, 2007). Several theories try to characterize the distribution of organisms in fragmented landscapes (MacArthur & Wilson, 1967; Forman, 1995; Hanski, 1998; Fahrig, 2013). The most important one may be the theory of island biogeography (MacArthur & Wilson, 1967). It assumes that small or isolated islands (e.g. habitat fragments in a ‘sea’ of intensively used agricultural matrix) are reached by fewer immigrants coming from a hypothetical mainland than large or connected ones, leading to lower species richness on these islands. Due to stochastic events, smaller fragments also face higher species extinction rates, while larger ones harbour more species due to a larger variety of habitat niches and greater apparency for dispersers (MacArthur & Wilson, 1967; Lomolino, 2000; Losos & Ricklefs, 2010). However, in fragmented landscapes a “mainland” is not necessarily present but only a set of larger and smaller fragments. These subdivide the so-called metapopulation of a species into subpopulations (Levins, 1970; Hanski, 1998), characterised by more or less frequent exchange between habitat fragments and recolonisations after stochastic extinction events. Decreasing habitat connectivity implies that a habitat fragment is surrounded by fewer, smaller and more distant neighbouring fragments (Hanski et al., 2000).

The type of landscape in between fragments (“matrix”) is crucial, since it may either facilitate or hinder the dispersal of organisms (Ewers & Didham, 2006; Prugh et al., 2008). Some types of matrix are more permeable for organisms than others and may be used as alternative habitat during dispersal or as alternative source of resources (Baum et al., 2004; Eycott et al., 2012; Öckinger et al., 2012). Arable land used for the production of annual crops is the matrix type that experiences the highest levels of disturbance and that displays the most unnatural habitat characteristics. Consequently, it is assumed to be the least permeable and most unwelcoming habitat type for dispersing and resident organisms as well as for organisms temporarily foraging there (Tscharntke et al., 2012). The percentage of arable land in a landscape has therefore been used as a measure for landscape complexity in numerous studies (e.g. Gagic et al., 2011; Rösch et al., 2013).

However, the way habitat fragmentation and the composition of the surrounding matrix are perceived is highly species specific and depends on a species’ habitat specialisation and mobility (Fischer & Lindenmayer, 2007). In contrast to generalist species, specialist species depend on the resources within a certain habitat type (e.g. for foraging, reproduction or nesting) and are unable to use the surrounding matrix (Henle et al., 2004; Ewers & Didham, 2006). In addition, mobile species, e.g. insects with strong flight abilities, will have less difficulty in bridging the gap between habitat fragments than less mobile or sedentary species. Mobile species are therefore likely to be less severely affected by habitat fragmentation (Jenkins et al., 2007; Sekar, 2012).

This thesis focuses on the effects of fragmentation on plants and invertebrates on calcareous grasslands, which are among the most species rich habitats in Central Europe, displaying an extraordinarily high diversity in specialised xero- and thermophilic plants and invertebrates (van Swaay, 2002; Boschi & Baur, 2008; Stoll et al., 2009; Ellenberg & Leuschner, 2010, Fig. 2, Fig. 3a,b,c). Originally, this type of grassland only occurred on rocky outcrops and other sites with shallow soils that made the growth of trees impossible (Wilmanns, 1993). Since the majority of today's calcareous grasslands have been developed through traditional land-use forms like grazing or mowing on sites that would naturally be covered by forest, they have to be considered as semi-natural (Hejcman et al., 2013).

Today, only a fraction of their historical extent remains (Riecken et al., 1994; WallisDeVries et al., 2002). For example, in the Swabian Alb in southern Germany more than 70 % of the calcareous grasslands that were present in the year 1900 have disappeared (Mattern et al., 1992). The main causes of their massive decline over the past century are changes in land use practices: on the one hand direct destruction due to the conversion to arable land or intensification through fertilisation, and on the other hand abandonment of traditional management and subsequent shrub encroachment (WallisDeVries et al., 2002). Furthermore, the cessation of transhumance shepherding has lead to isolation of fragments since large numbers of diaspores used to be transported by sheep (Poschlod & WallisDeVries, 2002). Fischer et al. (1996) reported up to 8500 diaspores from 85 plant species per sheep. Nevertheless, long-lived organisms like many plant species are able to persist for a longer period of time in fragmented, isolated habitats than short-lived organisms like most invertebrates, creating a so-called extinction debt that mirrors historical circumstances (Tilman et al., 1994; Piqueray et al., 2011). This makes it makes species' responses to the surrounding landscape more complicated to investigate.

In the study area (southern Lower Saxony in Central Germany, districts of Göttingen and Northeim, 51.5°N, 9.9°E), an area characterised by intensive agriculture (mainly cereals and fertile meadows), there are still more than 200 fragments of calcareous grassland, the majority of them smaller than 1 ha (Fig. 1). However, many of them – the small ones in particular – are in an unfavourable condition due to cessation of management by grazing or mowing and subsequent shrub encroachment and an increasing dominance of *Brachypodium pinnatum* or *Bromus erectus* (pers. obs.).

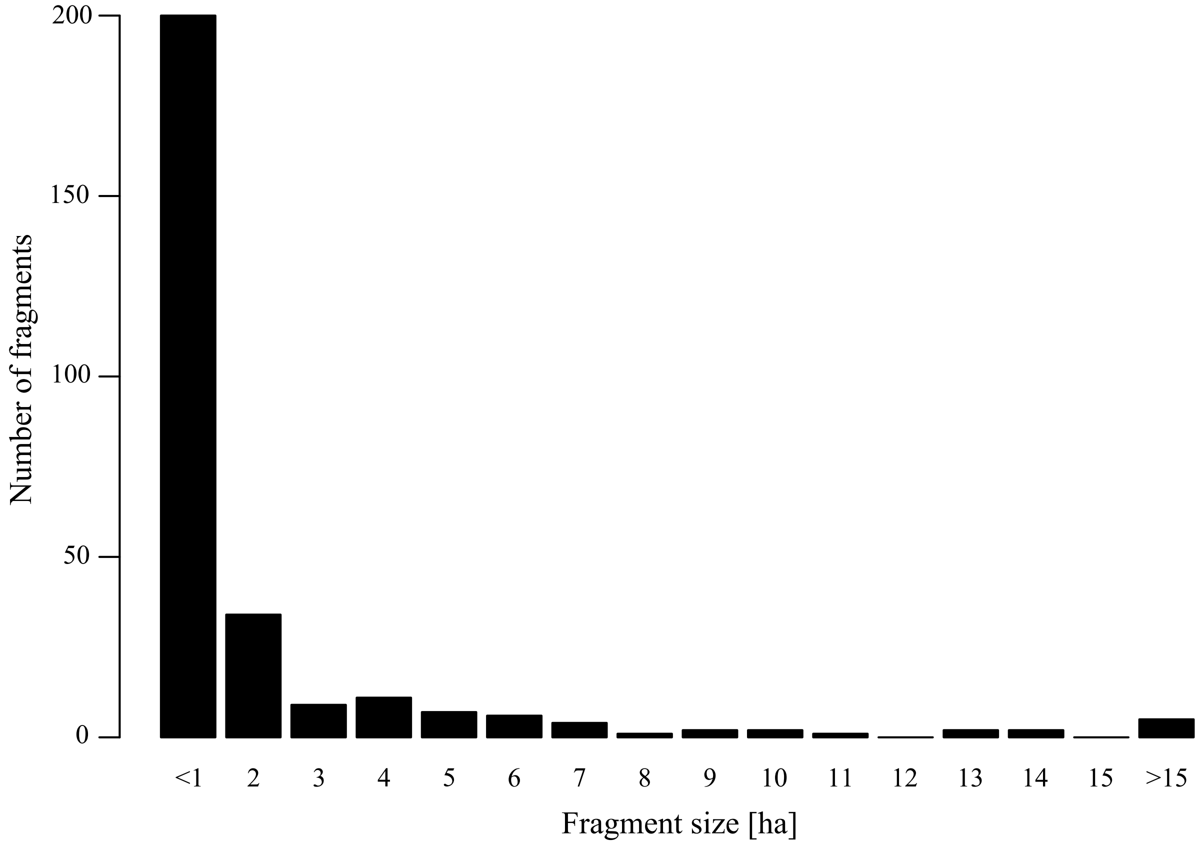


Fig. 1. Size distribution of calcareous grassland fragments in the study area.

Studies on calcareous grasslands in the area have shown a positive relationship between the species richness and abundance of butterflies, hoverflies and bees and landscape composition and as well as between species richness and habitat area (e.g. Krauss et al., 2003; Meyer et al., 2007).

Here, we study the effects of fragment size, habitat connectivity, landscape composition and local management on a broad range of organisms: plants, bees, butterflies, true bugs, leafhoppers, spiders, grasshoppers, rove beetles, hoverflies and snails (excluding slugs). Furthermore, we use plant species richness as a measure of resource availability. Many of the above mentioned taxa have only rarely or never been studied in this context (Biedermann, 2002; Zulka et al., 2013).

In the context of the conservation challenges of calcareous grasslands, this thesis addresses the following questions:

- How does habitat fragmentation affect species richness, abundance and community composition of plants and invertebrates on calcareous grasslands?
- Are species richness, abundance and community composition of plants and invertebrates linked to fragment size?
- Do connectivity and the composition of the surrounding landscape have an effect on species richness, abundance and community composition?
- Are specialist species more severely affected than generalist species?
- Do different taxa react differently to fragmentation and landscape modification?
- Are body size and Red List status important factors governing a species' reaction to habitat fragmentation?

Fig. 2. Close-up views of calcareous grasslands in the study area in June. Top: calcareous grassland with *Bromus erectus* and various herb species, below: calcareous grassland with *Linum leonii*.

Fig. 3a. Specialist plants and invertebrates on calcareous grasslands in the study area: *Setina irrorella, Potentilla neumanniana, Gentianella germanica, Linum leonii, Ophrys insectifera, Papilio machaon, Antennaria dioica, Galium pumilum, Cirsium acaule* (from top left to bottom right).

Fig. 3b. Specialist plants and invertebrates on calcareous grasslands in the study area: *Viola hirta, Platanthera chlorantha, Polygala comosa, Zygaena filipendulae, Hieracium pilosella, Orchis tridentata, Pimpinella saxifraga, Gentianella ciliata, Scabiosa columbaria* (from top left to bottom right).

Fig. 3c. Specialist plants and invertebrates on calcareous grasslands in the study area: *Veronica teucrium*, *Polyommatus icarus*, *Silene nutans*, *Callophrys rubi*, *Hippocrepis comosa*, *Briza media*, *Helicella itala*, *Salvia pratensis*, *Zygaena sp.* (from top left to bottom right).

Chapter outline

Chapter 2: *Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities*

This chapter explores the effects of fragment size (large or small), habitat connectivity and landscape composition on leafhopper communities in calcareous grasslands. We found that increasing habitat isolation reduced leafhopper species richness in simple (dominated by arable crops), but not in complex landscapes. Surprisingly, this effect was driven by generalist species. Moreover, we found that generalist species richness increased with increasing connectivity on small fragments, whereas it remained stable on large fragments. Finally, we found a steeper increase in generalist species richness with increasing plant species richness on connected than on isolated fragments, suggesting that more colonisers reach connected fragments and can subsequently use the available plant resources.

Our results show that insect biodiversity on fragmented calcareous grasslands does not depend only on habitat connectivity, but that it is interactively affected by the four factors habitat connectivity, landscape composition, habitat area and plant species richness. Isolated fragments that are either small or located in simple landscapes are less likely to receive immigrants after extinction events, leading to a gradual reduction in species richness over time. These patterns should not only apply to leafhoppers but to other insect groups as well (e.g. true bugs).

The results of Chapter 2 therefore stress that mitigating the negative effects of habitat fragmentation needs to take the surrounding landscape into account. Management should be prioritised towards increasing the connectivity of small, isolated fragments, of fragments in simple landscapes and towards management efforts that enhance dispersal by increasing the heterogeneity of both landscape composition and configuration.

Chapter 3: *Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments*

This chapter aims at contributing evidence to the resolution of the so-called “SLOSS”-debate (“Single Large Or Several Small”). In this manuscript, we test the hypothesis that both several small as well as single large habitat fragments in different landscape types contribute to biodiversity conservation. For the first time, we explore the relative importance of small vs. large habitats for overall species richness, richness of generalist vs. specialist species and for each species separately across four taxa (plants, leafhoppers, true bugs and snails) and in a landscape context. We found that species richness was substantially higher on several small fragments than on one or two large fragments of equal total size. However, community composition of large and small fragments differed and some of the rarest specialist species appeared to be confined to large fragments. The composition of the landscape surrounding the fragments only played a subordinate role for species richness and community composition but we found that true bug species richness, much like leafhopper species richness (Chapter 2), increased with increasing plant species richness on connected but not on isolated fragments.

The results of Chapter 3 therefore question the focus on either small or large fragments and call for a new intermediate habitat fragmentation strategy for biodiversity conservation since the protection of both single large and many small fragments is mandatory to sustain overall biodiversity. We hereby highlight the importance of thorough reconsideration of conservation measures in fragmented landscapes worldwide.

Chapter 4: *Local and landscape management affects trait-mediated biodiversity of nine taxa on small grassland fragments*

The fourth chapter examines the effects of landscape composition, habitat connectivity and local management (grazing, mowing or abandonment) on the species richness, community composition and trait-based responses (body size and Red List status) of nine taxa (plants, butterflies, bees, grasshoppers, hoverflies, spiders, true bugs, rove beetles and leafhoppers) on small fragments (<1 ha) of calcareous grassland. We found a negative effect of an increasing percentage of arable land in the surroundings of the fragments. It led to a 29 % loss of overall species richness. We assume that landscapes dominated by arable land offer less alternative habitat and resources for foraging or during migration, resulting in lower species richness. Habitat connectivity generally enhanced species richness across all taxa. This was more accentuated in the large species per taxon, which can be expected to be good dispersers. For small-bodied species, fragmentation in the study area may already be too great. Finally, grazing reduced species richness and abundance much more than mowing (once a year) or abandonment (for 5-15 years), in particular of red-listed species, presumably due to the greater damage caused, removing food resources for phytophagous insects. Furthermore, each of the three management types resulted in a different community composition of all taxa. Therefore, the preferential management strategy for small fragments of calcareous grassland should be an alternation between mowing and short-term abandonment combined with a diversification of the surrounding landscape.

Once again, the results of Chapter 4 stress the importance of the surrounding landscape for the conservation of plant and invertebrate communities on fragmented calcareous grasslands. Local management plays an important role, but must be complemented by a landscape perspective.

Conclusions

The results of the three studies show that the four factors fragment size, management, connectivity and landscape composition play a crucial role for species richness, abundance and community composition of plants, arthropods and snails living on calcareous grasslands.

The first study demonstrates that the influence of connectivity is different for large and small fragments of calcareous grassland and for fragments in simple and in complex landscapes, implying that landscapes should be diversified and that fragment sizes should not be decreased any further. The second study emphasises that even though less area is needed in order to reach a high number of species when focusing on small fragments, both large and small fragments are required to preserve full species diversity across taxa, since their community composition differs and the rarest specialists are confined to large fragments. Finally, the third study shows that the three management types grazing, mowing and abandonment result in differences in species richness, abundance and community composition. For organisms living on small fragments, the composition of the surrounding landscape is as important as connectivity between fragments.

Overall, we conclude that the widespread focus on large habitat fragments should be reconsidered, leading to the conservation of both large and small habitat fragments. When planning conservation measures for fragmented grassland habitats, a focus on local factors like fragment size and management is important but insufficient: landscape factors including habitat connectivity and landscape complexity need to be taken into account to ensure the long-term survival of plant and invertebrate populations.

Cicadetta montana (Cicadidae)

References

Baum, K.A., Haynes, K.J., Dillemuth, F.P., & Cronin, J.T. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**, 2671–2676.

Biedermann, B. (2002) Leafhoppers (Hemiptera, Auchenorrhyncha) in fragmented habitats. *Denisia 04*, **176**, 523–530.

Boschi, C. & Baur, B. (2008) Past pasture management affects the land snail diversity in nutrient-poor calcareous grasslands. *Basic and Applied Ecology*, **9**, 752–761.

Ellenberg, H. & Leuschner, C. (2010) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht.* Ulmer, Stuttgart.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., & Pullin, A.S. (2012) A meta-analysis on the impact of different matrix structures on species movement rates. *Landscape Ecology*, **27**, 1263–1278.

Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649–1663.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.

Forman, R.T.T. (1995) *Land mosaics: the ecology of landscapes and regions.* Cambridge University Press, New York.

Gagic, V., Tscharntke, T., Dormann, C.F., Gruber, B., Wilstermann, A., & Thies, C. (2011) Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. *Proceedings of the Royal Society B Biological sciences*, **278**, 2946–2953.

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

Hanski, I., Alho, J., & Moilanen, A. (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239–251.

Hejcman, M., Hejcmanová, P., Pavlů, V., & Beneš, J. (2013) Origin and history of grasslands in Central Europe - a review. *Grass and Forage Science*, **68**, 345–363.

Henle, K., Davies, K.F., Kleyer, M., Margules, C., & Settele, J. (2004) Predictors of Species Sensitivity to Fragmentation. *Biodiversity and Conservation*, **13**, 207–251.

Jenkins, D.G., Brescacin, C.R., Duxbury, C. V., Elliott, J.A., Evans, J.A., Grablow, K.R., Hillegass, M., Lyon, B.N., Metzger, G.A., Olandese, M.L., Pepe, D., Silvers, G.A., Suresch, H.N., Thompson, T.N., Trexler, C.M., Williams, G.E., Williams, N.C., & Williams, S.E. (2007) Does size matter for dispersal distance? *Global Ecology and Biogeography*, **16**, 415–425.

Krauss, J., Steffan-Dewenter, I., & Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography,* **30**, 889–900.

Levins, R. (1970) Extinction. *Lectures Notes in Mathematics and Life Sciences*, **2**, 75–107.

Lomolino, M. V. (2000) A call for a new paradigm of island biogeography. *Global Ecology & Biogeography*, **9**, 1–6.

Losos, J.B. & Ricklefs, R.E. (2010) *The Theory of Island Biogeography Revisited.* Princeton University Press, Princeton, New Jersey.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography.* Princeton University Press, Princeton, New Jersey.

Mattern, H., Mauk, J., & Kübler, R. (1992) Die Entwicklung der Heiden im Regierungsbezirk Stuttgart während des letzten Jahrzehnts (1980/1990). *Veröffentlichungen für Naturschutz und Landschaftspflege in Baden*-*Württemberg*, **67**, 127–135.

Meyer, B., Gaebele, V., & Steffan-Dewenter, I.D. (2007) Patch Size and Landscape Effects on Pollinators an Seed Set of the Horseshoe Vetch, Hippocrepis comosa, in an Agricultural Landscape of Central Europe. *Entomologia Generalis*, **30**, 173–185.

Öckinger, E., Lindborg, R., Sjödin, N.E., & Bommarco, R. (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, **35**, 259–267.

Piqueray, J., Cristofoli, S., Bisteau, E., Palm, R., & Mahy, G. (2011) Testing coexistence of extinction debt and colonization credit in fragmented calcareous grasslands with complex historical dynamics. *Landscape Ecology*, **26**, 823–836.

Poschlod, P. & WallisDeVries, M.F. (2002) The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. *Biological Conservation*, **104**, 361–376.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., & Brashares, J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 20770–20775.

Riecken, U., Ries, U., & Ssymank, A. (1994) Rote Liste der gefährdeten Biotoptypen der Bundesrepublik Deutschland. *Schriftenreihe Landschaftspflege und Naturschutz*, **41**, 1–184.

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2013) Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology*, **50**, 387–394.

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

Sekar, S. (2012) A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? *Journal of Animal Ecology*, **81**, 174–184.

Stoll, P., Oggier, P., & Baur, B. (2009) Population dynamics of six land snail species in experimentally fragmented grassland. *The Journal of Animal Ecology*, **78**, 236–246.

Van Swaay, C.A.M. (2002) The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, **104**, 315–318.

Tilman, D., May, R.M., Lehman, C.L., & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

WallisDeVries, M.F., Poschlod, P., & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, **104**, 265–273.

Wilmanns, O. (1993) *Ökologische Pflanzensoziologie, Eine Einführung in die Vegetation Mitteleuropas.* Quelle und Meyer, Heidelberg & Wiesbaden.

Zulka, K.P., Abensperg-Traun, M., Milasowszky, N., Bieringer, G., Gereben-Krenn, B.-A., Holzinger, W., Hölzler, G., Rabitsch, W., Reischütz, A., Querner, P., Sauberer, N., Schmitzberger, I., Willner, W., Wrbka, T., & Zechmeister, H. (2013) Species richness in dry grassland patches of eastern Austria: A multi-taxon study on the role of local, landscape and habitat quality variables. *Agriculture, Ecosystems & Environment*, **182**, 25–36.

Chapter 2: Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities

Stictocephala bisonia (Mebracidae)

Published as:
Rösch, V., Tscharntke, T., Scherber, C. & Batáry, P. (2013) Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology*, **50**, 387–394. doi: 10.1111/1365-2664.12056

Summary

1. Calcareous grasslands are among the most species rich habitats in Europe, but are increasingly threatened due to abandonment and fragmentation. Little is known about how the surrounding landscape influences fragmentation effects. Here we focus on the interaction between habitat fragmentation and landscape composition on leafhoppers, a highly diverse group of insects, including many species that are likely to be vulnerable to changes in their environment.

2. We selected 14 small and 14 large fragments of calcareous grassland in central Germany, differing in isolation from other calcareous grasslands and composition of the surrounding landscape. Leafhoppers, sampled by sweep netting, were either specialists that depended on calcareous grasslands or generalists that could use the landscape matrix, but still required low-productivity habitats.

3. Increasing habitat isolation reduced leafhopper species richness in simple (dominated by arable crops), but not in complex landscapes. This effect was driven by the generalist species. In simple landscapes, leafhoppers may find it more difficult to reach the next suitable fragment due to a lack of alternative resources during dispersal.

4. Moreover, we found that generalist species richness increased with increasing connectivity on small fragments, whereas it remained stable with increasing connectivity on large fragments. In small, isolated fragments, a higher extinction rate combined with a lower probability of recolonisation is thought to cause the reduced species richness.

5. *Synthesis and applications.* Our results show for the first time that insect species richness can be negatively affected by increasing habitat isolation in simplified but not in complex landscapes, and in small but not in large fragments. We provide evidence that mitigating the negative effects of habitat fragmentation needs to take the surrounding landscape into account. Management efforts should prioritise (i) an increase in connectivity of small, isolated fragments, (ii) an increase in connectivity of fragments in simple landscapes and (iii) enhance dispersal by increasing heterogeneity of both landscape composition and configuration. Moreover, extensive management of fragments by grazing or mowing to increase local habitat quality for leafhoppers would benefit other insect groups as well.

Keywords: Auchenorrhyncha, connectivity, generalists, Germany, herbivores, isolation, leafhoppers, landscape context, matrix, specialists.

Introduction

Habitat fragmentation, habitat loss and landscape modification are the main drivers of biodiversity loss (Sala et al., 2000; Fahrig, 2003; Foley et al., 2005; Fischer & Lindenmayer, 2007). In Central Europe, semi-natural calcareous grasslands harbour an exceptional diversity of organisms, including plants (Ellenberg & Leuschner, 2010), insects (van Swaay, 2002; Krauss et al., 2003) and snails (Boschi & Baur, 2007). Unfortunately, since the onset of agricultural intensification and the abandonment of historic land use practices like extensive grazing (Poschlod & WallisDeVries, 2002) a large part of this highly diverse habitat type has been lost (for Germany: Riecken et al., 1994). For example in the Swabian Alb in southern Germany more than 70 % of the calcareous grasslands that were present in the year 1900 have disappeared (Mattern et al., 1992). Therefore, connectivity of the remaining sites has been reduced dramatically. For example, floral connectivity has decreased due to the abandonment of transhumance shepherding, which ensured the dispersal of plant propagules (Poschlod & WallisDeVries, 2002). Long-lived organisms like plants are able to persist for a longer period of time in fragmented, isolated habitats than short-lived organisms like most invertebrates ("extinction debt", Tilman et al., 1994; Piqueray et al., 2011). All these changes in management pose a severe threat for the specialised plant and invertebrate species confined to calcareous grasslands (Fischer & Stöcklin, 1997; Niemelä & Baur, 1998).

According to the theory of island biogeography, the species diversity of islands is determined by both extinction and immigration. Island habitats that are more isolated – in this case fragments of calcareous grassland in a 'sea' of intensively managed agricultural matrix – are less likely to receive immigrants from other islands. Smaller islands have a lower probability of receiving immigrants than larger ones and face higher extinction rates due to stochastic events (Whittaker, 1992), while larger islands harbour more species due to larger variety of (micro)habitats and enhanced apparency for dispersers. It nevertheless needs to be kept in mind that considering habitat fragments as surrounded by an entirely hostile matrix may be an oversimplification (Debinski, 2006; Ewers & Didham, 2006; Prugh et al., 2008). Eycott et al. (2012) and Öckinger et al. (2012) showed that different matrix types can either facilitate or hinder migration of organisms.

Within the study area (District Göttingen, Lower Saxony, Germany) there are still supposed to be more than 200 fragments of calcareous grassland. However, they only cover about 0.3 % of the area and frequently are of low quality due to a lack of management (pers. obs.). In the area there have been studies on butterflies, hoverflies and bees of calcareous grasslands (Krauss et al., 2003; Meyer et al., 2007), showing a positive relationship between habitat area and insect diversity as well as a positive effect of landscape diversity on both species richness and abundance.

In this study we focus on the effects of three landscape parameters: habitat area (large vs. small fragments), connectivity (measured by a connectivity index described by Hanski et al. (2000) and landscape composition (represented by the amount of arable land within a 500 m buffer around each site). Additionally, we use plant species richness as a surrogate for habitat quality and resource availability.

As study organisms we chose leafhoppers, planthoppers and froghoppers (Auchenorrhyncha, hereafter referred to as leafhoppers), a very diverse group of plant sucking insects highly influenced by vegetation structure and composition (Nickel, 2003). They include many specialist species that can be hypothesised to sensitively react to changing landscapes and fragmentation (Biedermann et al., 2005; Littlewood et al., 2012).This study is the first to test how habitat area, connectivity, and landscape composition interactively affect insect species richness (with a focus on leafhopper communities). We hypothesised that (1) there are fewer leafhopper species on isolated fragments than on connected ones, (2) increasing amount of arable land surrounding the fragments negatively influences leafhopper species richness, and (3) leafhopper species richness is higher on larger fragments (Tscharntke et al., 2012). (4) Specialist species are hypothesised to be more severely affected by decreasing connectivity and landscape compositional heterogeneity (i.e. increasing proportion of arable land) than generalists. This study has wider implications for other taxa with relatively low mobility since they can be expected to be affected by the landscape variables in a similar way.

Materials and methods

Study area

The study area was located in the vicinity of the city of Göttingen in southern Lower Saxony in central Germany (51.5°N, 9.9°E). The landscape is characterised by intensively managed agricultural areas with a dominance of cereal and rape fields and fertile meadows, interspersed with forests on hilltops and patchily distributed fragments of semi-natural habitats like calcareous grasslands, belonging to the plant association Mesobrometum erecti Koch 1926 (Ellenberg & Leuschner, 2010). These grasslands are frequently located on steep slopes and are managed by mowing or grazing with sheep, goats, cattle or horses. Many smaller fragments have been abandoned, leaving them to succession (pers. obs.).

Study design

By analysing digital maps (ATKIS-DLM 25/1 Landesvermessung und Geobasisinformationen Niedersachsen 1991–1996, Hanover, Germany) with the geographical information system ArcGIS 10.0 (ESRI Geoinformatik GmbH, Hanover, Germany) and subsequent extensive field surveys in the study area, we selected 14 small (0.1–0.6 ha) and 14 large (1.2–8.8 ha) fragments of calcareous grassland (for an overview of the study area see Appendix S1) along two orthogonal gradients: a landscape composition gradient, i.e. an increasing percentage of arable land within a radius of 500 m around the fragments (27–77 %, mean = 47 %), and a habitat connectivity gradient, measured by a connectivity index described by Hanski et al. (2000):

$$CI_i = \Sigma \exp(- \alpha d_{ij}) A_j^{\beta}$$

A_j is the area of the neighbouring fragment j (in m^2) and d_{ij} is the edge to edge distance (in m) from the focal fragment i to the neighbouring fragment j. α is a species specific parameter describing a species' dispersal ability and β is a parameter that describes the scaling of immigration. Since we applied the connectivity index to an entire community, both scaling parameters α and β were set to 0.5. The values of the connectivity index varied between 20 and 849 (mean = 244), with large values indicating high levels of connectivity. All calcareous grassland fragments within a radius of 2000 m around each study site were taken into account, to assure that for every fragment the connectivity index was greater than zero. In addition we measured the edge to edge distance to the nearest neighbouring fragment for each study fragment, which ranged from 30 to 1900 m. In order to be classified as separate, there had to be a distance of at least 30 m from the focal fragment to the nearest one. If the nearest fragment was smaller than 0.1 ha, the next nearest fragment larger than that was used. Both connectivity measures were strongly correlated (Spearman correlation, rho= 0.78, S = 6501.6, $P < 0.001$).

It was difficult to select fragments of similar quality, because management differed from fragment to fragment. Some were grazed, whereas on others, management had been abandoned. If fragments were mown, this could happen at different times throughout the season, although never before the first sampling, i.e. the beginning of June. Fragments that were managed for the conservation of rare plants (orchids in particular) were not cut before August to ensure that the seeds could fully ripen. In order to assure that the fragments exhibited the characteristics of calcareous grasslands, we only included fragments that harboured more than ten of the plant species that are typical for calcareous grasslands in the study area (Krauss et al., 2003). We did not try to avoid differences in habitat quality and management, since we intended to mirror the actual condition of calcareous grasslands in the study area.

Sampling methods

Leafhoppers were sampled by sweep netting (Heavy Duty Sweep Net, 7215HS, BioQuip, diameter: 38 cm) on six randomly distributed transects with homogeneous vegetation per fragment (20 sweeps each, i.e. 120 sweeps in total) in dry weather on three occasions in 2010 (at the beginning of June, at the end of July and at the beginning of September). Transects were approximately 10 m long, and were at least 3 m away from each other within a fragment.

The specimens caught were transferred into alcohol (70 % vol.) and identified to species level in the laboratory using Biedermann & Niedringhaus (2004) and Kunz et al. (2011). Specimens of species with woody host plants were excluded, except when saplings of a potential host tree were present on the transects. Otherwise it was assumed that they had been dislodged from their host tree by wind. If the species' larvae used herbs or grasses as host plants and only the imagines fed on trees, specimens were included in the analysis.

The identification to species level of female specimens of several genera is not possible (e.g. *Ribautodelphax, Anaceratagallia, Psammotettix*) (Biedermann & Niedringhaus, 2004; Kunz et al., 2011). Thus, if male specimens were present, female specimens were assumed to belong to the same species. If not, they were only identified to genus level. If males of more than one species of a genus were present, the number of females was assumed to mirror that of males.

All leafhopper species were classified into habitat specialists and generalists according to (i) their specific habitat requirements typical for calcareous grassland (i.e. warm and dry habitat conditions, short, grazed swards, open soil) and (ii) diet preferences (i.e. utilising plants that exclusively occur on calcareous grasslands) based on Nickel & Remane (2002) and Nickel (2003). A species was classified as a habitat specialist when conditions (i) and/or (ii) were fulfilled; it was classified as a generalist when neither (i) nor (ii) were fulfilled.

In addition, they were subdivided according to their ability to fly, i.e. the length of their wings, with Biedermann & Niedringhaus (2004). If a species was wing dimorphic, i.e. it could be both long and short winged, the predominant wing type was used for categorisation.

At the beginning of June the vegetation (only vascular plants) of each transect was recorded in botanical plots (one 1 x 5 m plot per transect) according to Wilmanns (1993).

Plant species identification and nomenclature follow Seybold (2009). The plant species were subdivided into habitat specialists and generalists according to Krauss et al. (2003).

Statistical analyses

Both leafhopper and plant species richness of the six transects per fragment were summed up. The leafhoppers were also summed over the three sampling occasions. Statistical analyses were conducted with R, version R 2.15.1 (R Development Core Team 2012).

For analysis of overall leafhopper species richness and species richness of specialist and generalist leafhoppers we used generalised linear models using Poisson errors with the following explanatory variables: (1) the percentage of arable land in a 500 m buffer around each fragment, (2) fragment size (in ha, taken as a factor, either ‘large’ or ‘small’), (3) habitat connectivity, measured by a connectivity index described by Hanski et al. (2000) ($\log_{10}$-transformed to achieve a better fit of the models), and (4) plant species richness per site. The explanatory variables were essentially uncorrelated (Table S1).

In the full models two way interactions between all the explanatory variables were included. For all three models we performed an automated stepwise model selection by AIC (function ‘stepAIC’ in the package ‘MASS’ (Venables & Ripley, 2002)). In all analyses there was no indication of overdispersion.

Results

In the 28 fragments of calcareous grassland we found 77 leafhopper species (Table S2), from 65 genera with 7073 adult specimens (with 3454 specimens caught on the small sites and 3619 specimens caught on the large sites), representing 13 % of the German leafhopper fauna (Biedermann & Niedringhaus, 2004; Kunz et al., 2011). Species richness ranged from 14 to 31 species per fragment (Table S2, S3). Separation into habitat specialists and generalists resulted in 29 specialist and 48 generalist species. The four most abundant specialist leafhopper species were *Turrutus socialis* (18.3 % of total abundance), *Doratura stylata* (8.5 %), *Adarrus multinotatus* (7.5 %), and *Neophilaenus albipennis* (3.5 %). The four most abundant generalist species were *Arocephalus longiceps* (5.7 %), *Philaenus spumarius* (5.1 %), *Mocydia crocea* (4.1 %) and *Verdanus abdominalis* (3.2 %) (Table S2). In the botanical surveys we recorded 167 plant species from 123 genera, comprising 65 specialist and 102 generalist species (including 22 tree and shrub species as saplings), with a minimum of 25 and a maximum of 65 species per site.

Table 1. Mean ± SEM leafhopper and plant species richness on small (n = 14) *vs*. large (n = 14) sites.

	Small	Large
Leafhopper SpR	22.9 ± 1.2	22.4 ± 1.6
specialists	8.6 ± 0.8	9.5 ± 0.9
generalists	14.2 ± 1.2	12.9 ± 1.0
Leafhopper abundance	246.7 ± 22.5	258.5 ± 29.3
specialists	138.6 ± 18.1	160.8 ± 23.5
generalists	108.1 ± 19.4	97.7 ± 20.7
Plant SpR	47.6 ± 3.3	55.1 ± 1.7
specialists	23.8 ± 2.1	28.8 ± 1.1
generalists	23.8 ± 2.0	26.3 ± 2.0

In the analysis of overall leafhopper species richness we found an interaction between habitat connectivity and landscape composition. An increase in habitat isolation caused a reduction in leafhopper species richness in simple (high percentage of arable land), but not in complex landscapes (low percentage of arable land) (Table 2, Fig. 1a). Subsequent analysis of generalist and specialist leafhopper species richness separately revealed that this interaction was driven by the generalist leafhoppers (Table 2, Fig. 1b). The latter showed the same pattern as the overall species richness. The generalist leafhoppers showed an additional interaction: species richness on small fragments increased with increasing habitat connectivity, whereas it remained stable on large fragments (Table 2, Fig. 1c). There was an increase in generalist species richness with increasing plant species richness on both isolated and connected fragments. This increase, however, was steeper on connected fragments (Fig. 1d). Specialist leafhopper species richness was not affected by connectivity, landscape context or fragment size. Generalist species richness per site was highly correlated with the number of long winged (macropterous) species (Pearson correlation, r = 0.83, t = 7.58, d.f. = 26, P < 0.001), while the same was true for specialist species richness per site and short winged (brachypterous) species (Pearson correlation, r = 0.61, t = 3.93, d.f. = 26, P < 0.001).

Fig. 1. Interaction plots showing the relationship between (generalist) leafhopper species richness (y-axis) and the landscape parameters (x-axis). Effect of habitat isolation (measured by a connectivity index (Hanski et al., 2000), $\log_{10}$-transformed) on a) leafhopper species richness and b) generalist species richness in conjunction with landscape composition (Complex: 27–46 % arable land, Simple: 47–77 % arable land). c) Effect of habitat isolation on generalist leafhopper species richness in conjunction with fragments type (Small: 0.1–0.6 ha, Large: 1.2–8.6 ha). d) Effect of plant species richness on generalist leafhopper species richness in conjunction with habitat isolation (Isolated: values of the connectivity index from 19–155, Connected: values from 180–849). The dashed lines show mean squares fits (for illustration). The graphs were made with the lattice package (Sarkar, 2008) in R.

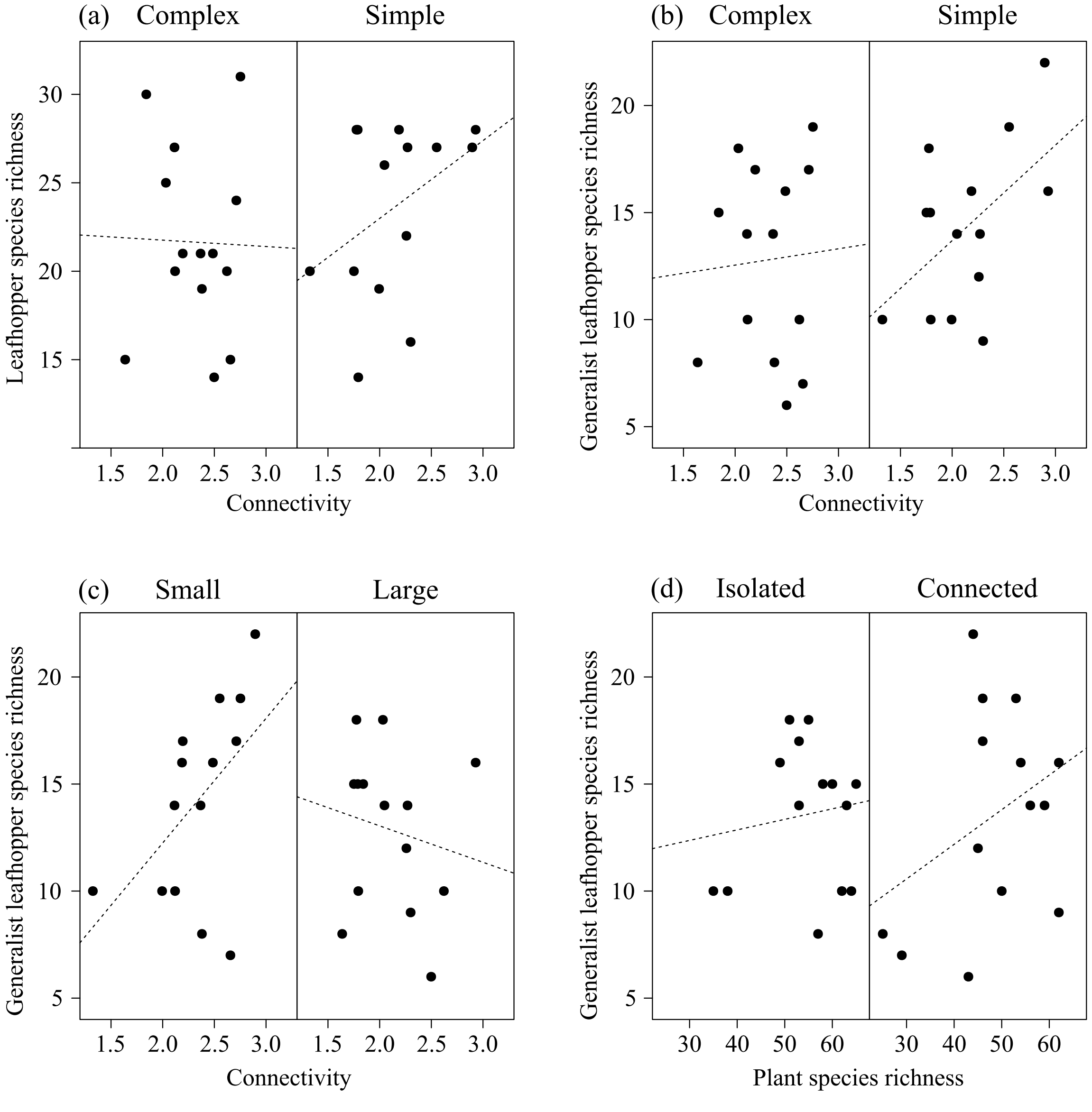


Table 2. Generalised linear models on the effects of landscape context (% arable land), fragment type (large or small), connectivity ($\log_{10}$(CI+1), a connectivity index described by Hanski et al. (2000), $\log_{10}$-transformed) and plant species richness on (1) overall leafhopper species richness, (2) generalist leafhopper species richness and (3) specialist leafhopper species richness. Only variables included in the final models are shown. *P*-values < 0.05 are depicted in bold characters.

	SpR				Generalists				Specialists			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	11.01	3.56	3.10	**0.002**	14.59	4.71	3.10	**0.002**	2.21	0.06	35.14	**<0.001**
% arable land (Ar)	-0.08	0.03	-2.39	**0.017**	-0.11	0.04	-2.40	**0.016**	–	–	–	–
Fragment type (Type)	-1.07	0.76	-1.40	0.161	-2.47	0.98	-2.54	**0.011**	–	–	–	–
log10(CI+1) (Conn)	-3.55	1.48	-2.39	**0.017**	-5.49	1.97	-2.79	**0.005**	–	–	–	–
Plant SpR	-0.07	0.05	-1.52	0.128	-0.12	0.06	-1.94	0.052	–	–	–	–
Ar × Conn	0.04	0.01	2.49	**0.013**	0.05	0.02	2.52	**0.012**	–	–	–	–
Type × Conn	0.48	0.32	1.50	0.133	1.14	0.41	2.76	**0.006**	–	–	–	–
Conn × plant SpR	0.03	0.02	1.60	0.110	0.05	0.03	2.10	**0.036**	–	–	–	–

Discussion

In this study we found that generalist but not specialist leafhoppers are interactively affected by connectivity, landscape composition (complex or simple) and fragment size (large or small). Generalist leafhopper species richness increased with decreasing isolation in simple but not in complex landscapes and on small but not on large fragments.

Habitat isolation

According to our results we assume that the specialists persist on the fragments of calcareous grassland without much exchange between them, especially since many species have limited dispersal abilities due to their short wings. Therefore they do not seem to be affected by decreasing connectivity. In accordance with this result, Schuch et al. (2012) found no decrease in leafhopper species richness (but a marked decrease in abundance) in protected dry grasslands in Eastern Germany over the last 50 years.

Generalist leafhoppers can be assumed to move more between fragments, especially since they are more likely to be long-winged than specialists. However, the dispersal abilities of macropterous leafhoppers seem to be species dependent. In a mark and recapture experiment, Biedermann (1997) found that the froghopper *Neophilaenus albipennis*, even though able to fly, rarely moved more than 20 m from the original point of capture. Other leafhopper species are able to fly and bridge greater distances, or get passively dispersed by air currents (Waloff, 1973; Nickel, 2003).

Despite being referred to as generalists here, a large proportion of the species recorded in this study require low-productivity habitats, i.e. they cannot cope with the conditions that prevail in today’s intensified agricultural landscapes. Only few species are able to breed in arable fields or intensified meadows and pastures, colonising them anew every year (Nickel, 2003). This leads to the assumption that calcareous grasslands are an important refuge for many leafhopper species, regardless of their degree of specialisation. So where fragments of calcareous grassland are few and scattered, even these generalist species are likely to find it difficult to locate and subsequently colonise the next suitable fragment, explaining the decrease in generalist species richness with decreasing connectivity.

Landscape composition

Increasing isolation caused a decrease in both overall and generalist leafhopper species richness in simple (high percentage of arable land) but not in complex landscapes. In simple landscapes, leafhoppers may find it difficult to reach the next suitable site, being unable to find suitable alternative resources or habitats with a similar vegetation type or structure during dispersal. Similar to our results, Baum et al. (2004) found that dispersal of the planthopper *Prokelisia crocea* depended on the surrounding matrix habitat (pure stands of *Bromus inermis* vs. mudflat). These contrasting matrices may be comparable to arable fields vs. more natural habitats. This implies that the permeability of simple landscapes dominated by arable land may be reduced compared to more complex landscapes (Eycott et al., 2012). The reduced permeability of the matrix may become more problematic with increasing distance between suitable habitat fragments, and may explain the reduction in leafhopper species richness with decreasing connectivity in simple landscapes.

Fragment size

We found that generalist species richness increased with decreasing isolation in small but not in large fragments. In small fragments, a higher extinction rate due to stochastic effects in combination with a lower probability of recolonisation with increasing isolation may cause the decline in generalist species richness (Hanski et al., 2000). Recolonisation of larger fragments is more probable (for a beetle species see Matter, 1996), and fewer extinctions occur. Cronin (2003) found that immigration of the planthopper *P. crocea* into host plant patches decreased with decreasing patch size. Nevertheless, since distances between habitat patches were much lower (up to 50 m) than in this study, immigration was not limited by increasing isolation.

In contrast to our results, Krauss et al. (2003) and Meyer et al. (2007) found a strong positive relationship between fragment size and species richness of butterflies, hoverflies and bees. Butterflies as well as hoverflies and bees have more complex habitat and resource requirements than leafhoppers. This appeared to be the reason why they need larger habitat fragments. Resource requirements of butterflies and bees change during their life cycle: adult butterflies feed on nectar, whereas the caterpillars feed on plant tissue (Ebert & Rennwald, 1991). Bees require nectar and pollen, both as food for themselves and to provision their brood cells, they need hollow or pithy plant stems, empty snail shells or cavities in the ground as nesting sites and nesting material like leaves, clay, small stones and plant resin (Westrich, 1989). In other words, they need different resources that are often spatially separated. In contrast, leafhoppers lay their eggs directly onto the host plant and all life stages feed on plant sap, which is an ample resource throughout the growing season (Nickel, 2003). This life history strategy enables them to potentially stay on the same plant stem for all their life, which is likely to reduce the minimum fragment size required for persistence. Thus, the threshold for a decrease in generalist species richness with fragment size alone might not have been reached within the range of fragment sizes chosen for this study (smallest fragment: 0.1 ha). It seems that many leafhopper species are able to cope with small fragment sizes as long as a sufficient amount of their host plant is present.

This is in accordance with Biedermann (1997) who showed a clear but species-dependent relationship between host plant patch size and the occurrence of three leafhopper species. So if a dispersing individual reaches the next fragment but the host plant patch is too small – which is more likely to be the case in small fragments – it will not be able to establish a stable population there, causing the lower species richness of specialists on small fragments we observed in this study.

Usually, a focus on large fragments is recommended (e.g. Krauss et al., 2003) but according to our results, both large and small fragments deserve to be maintained since at least for generalist leafhoppers we found no generally negative effect of small fragment size, but only in combination with decreasing connectivity.

Plant species richness

Generalist leafhopper species richness increased with plant species richness on both connected and isolated fragments, but the increase was more pronounced on the connected ones. As mentioned above, leafhoppers live in close association with their host plants (Nickel, 2003), spanning from strictly monophagous to highly polyphagous species (Nickel & Remane, 2002). Host plants provide feeding resources, shelter and oviposition sites and are also used for the transmission of bioacoustic signals (Nickel, 2003). We therefore assume that the more plant species occur per site, the more leafhopper species can occur since the appropriate host plant for more species will be provided. This finding is in accordance with Siemann et al. (1998) and Scherber et al. (2010) who found an increase in herbivore diversity when the number of plants in their experimental setups increased. So even if suitable plant resources are available, isolated fragments are less likely to be colonised than connected ones, resulting in an increase in leafhopper species richness with plant species richness that is less steep than the one on connected fragments.

Conclusion

Our results are the first to show that insect biodiversity on fragmented calcareous grasslands not only depends on habitat connectivity but that it is interactively affected by the four factors habitat connectivity, landscape composition, habitat area and plant species richness. Isolated fragments that are either small or located in simple landscapes are less likely to receive immigrants after extinction events, leading to a gradual reduction in species richness over time. These patterns should not only apply to leafhoppers but to other insect groups as well.

Mitigating the negative effects of habitat fragmentation therefore needs to take the surrounding landscape into account. Management should be prioritised towards increasing the connectivity (i) of small, isolated fragments, (ii) of fragments in simple landscapes and (iii) towards management efforts that enhance dispersal by increasing heterogeneity of both landscape composition and configuration. Moreover, extensive management of fragments by grazing or mowing, both relatively late in the season, to increase habitat quality for leafhoppers would benefit other insect groups as well.

Acknowledgements

We would like to thank Andrea Rösch, Éva M. Szegő and Felix Weiß for their help with data collection in the field. Sebastian Schuch gave an introduction into leafhopper identification to VR. Urs Kormann, Lorenzo Marini, Herbert Nickel and Laura Sutcliffe provided helpful comments on earlier versions of this manuscript. Laura Sutcliffe helped to improve the English. We thank Nick A. Littlewood and one anonymous referee for their valuable comments. PB was supported by the Bolyai Research Fellowship of the Hungarian Academy of Sciences and by the German Research Foundation (DFG BA4438/1-1). Financial support by the MWK graduate school "Biodiversität und Gesellschaft" to VR is acknowledged.

References

Baum, K.A., Haynes, K.J., Dillemuth, F.P., & Cronin, J.T. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**, 2671–2676.

Biedermann, R. (1997) *Populationsökologische Untersuchungen an Zikaden (Homoptera, Auchenorrhyncha): zum Einfluß von Habitatqualität, Habitatgröße und Isolation auf das Vorkommen und Überleben von Populationen.* Dissertation, Johannes Gutenberg-Universität, Mainz.

Biedermann, R., Achtziger, R., Nickel, H., & Stewart, A.J.A. (2005) Conservation of Grassland Leafhoppers: A Brief Review. *Journal of Insect Conservation*, **9**, 229–243.

Biedermann, R. & Niedringhaus, R. (2004) *Die Zikaden Deutschlands - Bestimmungstafeln für alle Arten.* WABV Fründ, Scheeßel.

Boschi, C. & Baur, B. (2007) Effects of management intensity on land snails in Swiss nutrient-poor pastures. *Agriculture, Ecosystems & Environment*, **120**, 243–249.

Cronin, J.T. (2003) Movement and spatial population structure of a prairie planthopper. *Ecology*, **84**, 1179–1188.

Debinski, D.M. (2006) Forest fragmentation and matrix effects: the matrix does matter. *Journal of Biogeography*, **33**, 1791–1792.

Ebert, G. & Rennwald, E. (1991) *Die Schmetterlinge Baden-Württembergs.* Ulmer, Stuttgart.

Ellenberg, H. & Leuschner, C. (2010) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht.* Ulmer, Stuttgart.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., & Pullin, A.S. (2012) A meta-analysis on the impact of different matrix structures on species movement rates. *Landscape Ecology*, **27**, 1263–1278.

Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.

Fischer, M. & Stöcklin, J. (1997) Local Extinctions of Plants in Remnants of Extensively Used Calcareous Grasslands 1950 – 1985. **11**, 727–737.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.

Hanski, I., Alho, J., & Moilanen, A. (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239–251.

Krauss, J., Steffan-Dewenter, I., & Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, **30**, 889–900.

Kunz, G., Nickel, H., & Niedringhaus, R. (2011) *Fotoatlas der Zikaden Deutschlands.* WABV Fründ, Scheeßel.

Littlewood, N.A., Pakeman, R.J., & Pozsgai, G. (2012) Grazing impacts on Auchenorrhyncha diversity and abundance on a Scottish upland estate. *Insect Conservation and Diversity*, **5**, 67–74.

Matter, S.F. (1996) Interpatch movement of the red milkweed beetle, Tetraopes tetraophthalmus: individual responses to patch size and isolation. *Oecologia*, **105**, 447–453.

Mattern, H., Mauk, J., & Kübler, R. (1992) Die Entwicklung der Heiden im Regierungsbezirk Stuttgart während des letzten Jahrzehnts (1980/1990). *Veröffentlichungen für Naturschutz und Landschaftspflege in Baden*-*Württemberg*, **67**, 127–135.

Meyer, B., Gaebele, V., & Steffan-Dewenter, I.D. (2007) Patch Size and Landscape Effects on Pollinators an Seed Set of the Horseshoe Vetch, Hippocrepis comosa, in an Agricultural Landscape of Central Europe. *Entomologia Generalis*, **30**, 173–185.

Nickel, H. (2003) *The Leafhopper and Planthoppers of Germany (Hemiptera, Auchenorrhyncha): Patterns and strategies in a highly diverse group of phytophagous insects.* Pensoft and Goecke & Evers, Sofia, Moscow and Keltern.

Nickel, H. & Remane, R. (2002) Artenliste der Zikaden Deutschlands mit Angabe von Nährpflanzen, Nahrungsbreite, Lebenszyklus, Areal und Gefährdung (Hemiptera, Fulgoromorpha et Cicadomorpha). *Beiträge zu Zikadenkunde*, **64**, 27–64.

Niemelä, J. & Baur, B. (1998) Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in the Swiss Jura mountains. *Biodiversity and Conservation*, **7**, 1407–1416.

Öckinger, E., Lindborg, R., Sjödin, N.E., & Bommarco, R. (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, **35**, 259–267.

Piqueray, J., Cristofoli, S., Bisteau, E., Palm, R., & Mahy, G. (2011) Testing coexistence of extinction debt and colonization credit in fragmented calcareous grasslands with complex historical dynamics. *Landscape Ecology*, **26**, 823–836.

Poschlod, P. & WallisDeVries, M.F. (2002) The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. *Biological Conservation*, **104**, 361–376.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., & Brashares, J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 20770–20775.

Riecken, U., Ries, U., & Ssymank, A. (1994) Rote Liste der gefährdeten Biotoptypen der Bundesrepublik Deutschland. *Schriftenreihe Landschaftspflege und Naturschutz*, **41**, 1–184.

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

Sarkar, D. (2008) *Lattice: Multivariate Data Visualization with R.* Springer, New York.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., Bessler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A. m., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Müller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V.M., & Tscharntke, T. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553–556.

Schuch, S., Bock, J., Krause, B., Wesche, K., & Schaefer, M. (2012) Long-term population trends in three grassland insect groups: a comparative analysis of 1951 and 2009. *Journal of Applied Entomology*, **136**, 321–331.

Seybold, S. (2009) *Schmeil-Fitschen: Flora von Deutschland und angrenzender Länder.* Quelle & Meyer, Heidelberg & Wiesbaden.

Siemann, E., Tilman, D., Haarstad, J., & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, **152**, 738–50.

Van Swaay, C.A.M. (2002) The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, **104**, 315–318.

Tilman, D., May, R.M., Lehman, C.L., & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S.* Springer, New York.

Waloff, N. (1973) Dispersal by flight of leafhoppers (Auchenorrhyncha: Homoptera). *Journal of Applied Ecology*, **10**, 705–730.

Westrich, P. (1989) *Die Wildbienen Baden-Württembergs. Allgemeiner Teil: Lebensräume, Verhalten, Ökologie und Schutz.* Ulmer, Stuttgart.

Whittaker, R.J. (1992) Stochasticism and determinism in island ecology. *Journal of Biogeography*, **19**, 587–559.

Wilmanns, O. (1993) *Ökologische Pflanzensoziologie, Eine Einführung in die Vegetation Mitteleuropas.* Quelle und Meyer, Heidelberg & Wiesbaden.

Supporting information

Appendix S1. Location of the 28 grasslands, with the city of Göttingen in the centre of the map. Large grasslands are marked with 'L', small grasslands with 'S', both with a subsequent site number (see Table S3).

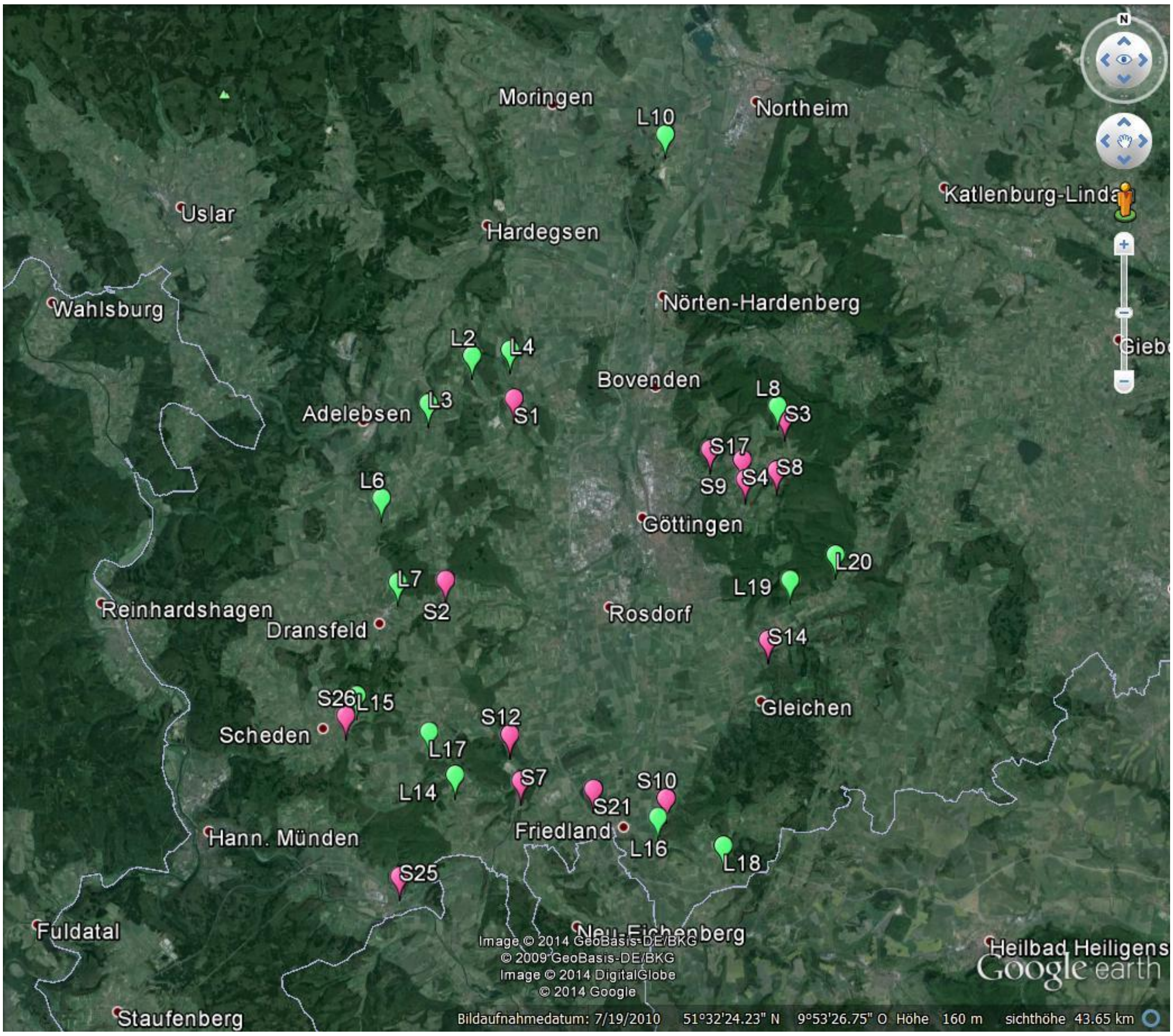


Table S1. Correlations between explanatory variables (Spearman's rho). If |rho| ≥ 0.6, a strong correlation between two variables can be assumed. Distance: the distance (in km) to the nearest neighbouring fragment, Conn. Index: a connectivity index described by Hanski et al. (2000), % arable: landscape composition, i.e. the percentage of arable land within a 500 m buffer around each fragment, Plant SpR: plant species richness per fragment, Fragment type: small or large fragment, Fragment size: Size of the fragments in ha.

	Distance	Conn. Index	% arable	Fragment size	Fragment type
Distance					
Conn. Index	-0.78				
% arable	0.21	-0.17			
Fragment size	0.27	-0.33	0.19		
Fragment type	0.16	-0.20	0.22	0.87	
Plant SpR	0.42	-0.32	-0.10	0.30	0.24

Table S2. List of the 77 leafhopper species that were recorded on the 28 fragments. Frequencies and abundances of the species of large (L) and small (S) sites are shown separately. Freq. = frequency, i.e. the number of sites occupied, Abu. = abundance, s/g = habitat specialist / generalist, WL = wing length, b = brachypterous, m = macropterous, information on host plants and habitat specialisation derived from Nickel (2003) and Nickel & Remane (2002), information on wing length derived from Biedermann & Niedringhaus (2004).

	Freq.		Abu.				
Species	L	S	L	S	s/g	WL	Host plants
Acanthodelphax denticauda	0	1	0	1	g	b	*Deschampsia cespitosa*
Acanthodelphax spinosa	8	8	25	104	g	b	*Festuca rubra, F. ovina*
Adarrus multinotatus	13	12	206	324	s	m	*Brachypodium pinnatum*
Allygus mixtus	0	1	0	1	g	m	nymphs on grasses and herbs, adults on trees
Anakelisia perspicillata	9	6	42	24	s	m	*Carex flacca*
Anaceratagallia ribauti	9	3	42	30	g	m	mainly *Plantago lanceolata*
Anaceratagallia venosa	7	3	100	62	s	m	*L. corniculatus, Thymus sp., H. comosa*
Aphrophora alni	8	11	27	100	g	m	nymphs on herbs, adults on shrubs and trees
Aphrodes sp.	11	5	61	16	g	m	
Arocephalus longiceps	7	7	34	367	g	m	various grasses
Arocephalus punctum	0	1	0	2	s	m	mainly *F. ovina*
Arthaldeus pascuellus	2	5	2	49	g	m	various grasses
Asiraca clavicornis	1	3	1	4	g	m	unknown
Athysanus argentarius	4	6	9	14	g	m	various grasses
Balclutha punctata	3	2	4	2	g	m	grasses, in winter on coniferous trees
Batracomorphus irroratus	1	0	10	0	s	m	*Helianthemum nummularium*
Cercopis vulnerata	1	8	1	17	g	m	tall herbs and grasses
Chlorita paolii	1	0	1	0	s	m	*Achillea millefoilum, Artemisia vulgaris*
Cicadula persimilis	0	5	0	15	g	m	*Dactylis glomerata*
Cicadella viridis	0	2	0	2	g	m	rushes, sedges, grasses, probably also dicotyledons
Criomorphus albomarginatus	2	4	6	7	g	m	various grasses
Deltocephalus pulicaris	1	0	1	0	g	m	various grasses
Delphacinus mesomelas	0	1	0	1	s	b	*F. ovina, F. rubra*
Dicrantropis hamata	2	2	2	2	g	m	various grasses
Diplocolenus bohemani	1	1	10	123	s	m	*Calamagrostis spp., Bromus erectus*
Ditropsis flavipes	7	8	64	87	s	b	*Bromus erectus*
Doratura stylata	13	10	301	299	s	b	fine-leaved grasses
Elymana sulphurella	5	3	25	17	g	m	various grasses
Emelyanoviana mollicula	4	6	63	14	s	m	mainly Lamiaceae, but also other families
Errastunus ocellaris	0	2	0	30	g	m	taller growing grasses
Eupelix cuspidata	4	3	8	5	s	m	*F. ovina*
Eupteryx notata	13	6	117	21	g	m	various dicotyledonous herbs
Euscelis incisus	7	5	142	15	g	m	*Fabaceae, Poaceae*
Evacanthus acuminatus	0	2	0	5	g	m	various dicotyledonous herbs
Evacanthus interruptus	1	4	1	10	g	m	various dicotyledonous herbs
Fieberiella septentrionalis	1	2	1	6	g	m	*Prunus spinosa, Rosa* sp.
Forcipata citrinella	2	4	5	17	g	m	*Carex flacca, C. nigra* and others
Goniagnathus brevis	5	0	7	0	s	m	*Thymus pulegioides, Th. praecox*
Graphocraerus ventralis	2	0	2	0	g	m	various grasses

Table S2 continued.

Species	Freq. L	S	Abu. L	S	s/g	WL	Host plants
Hephathus nanus	1	0	2	0	s	m	*Cirsium acaule?*
Hesium domino	0	3	0	8	g	m	nymphs on grasses, adults on trees
Hyledelphax elegantula	1	3	1	7	g	b	*B. pinnatum* and other grasses
Idiodonus cruentatus	0	1	0	12	g	m	woody plants and dwarf shrubs
Jassidaeus lugubris	1	0	1	0	s	b	*F. ovina agg*
Javesella pellucida	6	12	31	89	g	m	various grasses, Juncaceae, Cyperaceae
Kelisia irregulata	8	9	60	85	s	m	*Carex flacca*
Kosswigianella exigua	7	4	48	19	s	b	*F. ovina agg.*
Macrosteles laevis	0	1	0	2	g	m	grasses, sedges, rushes, dicotyledonous herbs
Megophthalmus scanicus	4	4	4	4	g	m	various species of Fabaceae
Megadelphax sordidula	4	3	55	19	g	b	*Arrhenatherum elatius*
Mocydiopsis attenuata	0	1	0	1	s	m	*F. ovina agg, F. rubra, F. heterophylla*
Mocydia crocea	12	12	99	190	g	m	various tall grasses
Neophilaenus albipennis	4	7	105	142	s	m	*B. pinnatum*
Neophilaenus campestris	4	2	28	13	g	m	various grasses
Neophilaenus lineatus	2	2	7	9	g	m	Poaceae, Cyperaceae, Juncaceae
Neoaliturus fenestratus	2	0	3	0	s	m	*Asteraceae,* notably *Leontodon spp.*
Oncopsis flavicollis	0	2	0	7	g	m	*Betula pendula, B. pubescens*
Philaenus spumarius	6	8	319	38	g	m	extremely polyphagous
Platymetopius major	2	0	2	0	s	m	nymphs among low vegetation, adults on trees
Psammotettix alienus	7	3	15	9	g	m	various grasses
Psammotettix cephalotes	11	4	222	23	s	m	*Briza media*
Psammotettix confinis	3	1	16	3	g	m	various grasses
Psammotettix helvolus	9	9	148	29	g	m	various grasses
Psammotettix kolosvarensis	0	1	0	1	g	m	*Puccinellia distans, Elymus repens*
Rhopalopyx adumbrata	3	6	13	28	s	m	*F. rubra, F. ovina*
Rhopalopyx preyssleri	2	4	5	33	s	m	*Poa pratensis, P. angustifolia*
Rhopalopyx vitripennis	1	1	13	1	s	m	*F. ovina agg*
Rhytistylus proceps	2	2	3	3	s	m	*F. ovina*
Ribautodelphax albostriata	3	7	10	91	s	b	*Poa angustifolia*
Ribautodelphax pungens	9	7	69	118	s	b	*B. pinnatum*
Speudotettix subfusculus	0	1	0	1	g	m	nymphs on sedges and grasses, adults on trees
Stenocranus minutus	6	7	11	27	g	m	*Dactylis glomerata*
Streptanus marginatus	3	3	7	40	g	b	*Deschampsia flexuosa, F. ovina*
Thamnotettix confinis	0	1	0	2	g	m	nymphs in herbaceous vegetation, adults on trees
Turrutus socialis	11	11	867	424	s	m	various grasses
Verdanus abdominalis	10	10	92	136	g	m	*Holcus lanatus* and other grasses
Zyginidia scutellaris	11	9	25	15	g	m	*Festuca, Poa, Dactylis* and others

Table S3. Fragment type (small (S) / large (L)), fragment size [ha], percentage of arable land in a 500 m radius around the sites, values of a connectivity index (Hanski et al., 2000), distance to the next fragment [km], (specialist) leafhopper species richness and abundance and (specialist) plant species richness of the 28 fragments of calcareous grassland.

Site	Type	Size [ha]	% arable land	Conn. index	Distance to next fragment [km]	Leafhopper SpR	Specialist SpR	Abundance	Specialist abundance	Plant SpR	Plant specialist SpR
S01	S	0.54	33.8	130.9	1.53	20	9	175	87	64	36
S02	S	0.57	77.4	97.8	1.43	19	8	245	67	35	15
S03	S	0.31	44.4	565.0	0.09	31	11	257	123	53	30
S04	S	0.22	45.1	515.2	0.03	24	6	327	218	46	23
S07	S	0.13	48.9	153.0	0.85	28	11	283	142	49	26
S08	S	0.28	40.7	231.9	1.13	21	6	105	37	59	22
S09	S	0.32	67.3	355.3	0.29	27	8	207	84	46	22
S10	S	0.26	43.7	305.2	0.61	21	5	135	65	62	34
S12	S	0.45	37.1	129.2	0.86	27	12	291	219	63	36
S14	S	0.06	33.8	155.5	0.40	21	4	342	159	53	21
S17	S	0.6	39.3	451.8	0.10	15	7	224	177	29	20
S21	S	0.37	55.6	20.1	1.52	20	9	419	112	38	23
S25	S	0.24	27.4	238.9	0.32	19	10	184	98	25	11
S26	S	0.27	51.3	786.5	0.07	27	5	260	54	44	14
L02	L	4.08	48.1	198.5	0.06	16	6	227	129	62	26
L03	L	1.50	51.8	58.6	0.68	28	9	246	92	51	26
L04	L	4.29	68.0	185.1	1.55	27	12	269	220	56	38
L06	L	8.76	40.7	314.3	0.15	14	7	147	78	43	27
L07	L	1.54	51.3	110.3	1.75	26	12	289	211	53	32
L08	L	2.56	34.1	417.5	0.41	20	9	303	250	50	29
L10	L	6.15	46.7	180.4	0.09	22	9	392	261	45	26
L14	L	2.45	58.4	61.1	1.89	14	3	232	5	62	22
L15	L	5.45	59.0	848.9	0.24	28	11	546	251	54	30
L16	L	6.38	40.8	68.4	0.61	30	14	239	114	65	29
L17	L	3.55	47.7	60.3	1.89	28	12	240	110	58	25
L18	L	1.24	30.6	106.5	1.08	25	6	143	50	55	28
L19	L	2.28	45.9	42.4	1.84	15	6	105	76	57	33
L20	L	1.78	50.0	55.3	1.84	20	4	241	103	60	32

Chapter 3: Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments

Xerocrassa geyeri (Hygromiidae, photo by Urs Kormann)

In press as:
Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*.

Abstract

Agricultural intensification has been shown to reduce biodiversity through processes such as habitat degradation and fragmentation. We tested whether several small or single large habitat fragments (re-visiting the "SLOSS" debate) support more species across a wide range of taxonomic groups (plants, leafhoppers, true bugs, snails).

Our study comprised 14 small (< 1 ha) and 14 large (1.5 – 8 ha) fragments of calcareous grassland in Central Germany along orthogonal gradients of landscape complexity and habitat connectivity. Each taxon was sampled on six plots per fragment.

Across taxa, species richness did not differ between large and small fragments, whereas species-area accumulation curves showed that both overall and specialist species richness, was much higher on several small fragments of calcareous grassland than on few large fragments. On average, 85 % of the overall species richness was recorded on all small fragments taken together (4.6 ha), whereas the two largest ones (15.1 ha) only accounted for 37 % of the species. This could be due to the greater geographic extent covered by many small fragments. However, community composition differed strongly between large and small fragments, and some of the rarest specialist species appeared to be confined to large fragments. The surrounding landscape did not show any consistent effects on species richness and community composition.

Our results show that both single large and many small fragments are needed to promote landscape-wide biodiversity across taxa. We therefore question the focus on large fragments only and call for a new diversified habitat fragmentation strategy for biodiversity conservation.

Keywords: calcareous grasslands, community composition, habitat fragmentation, invertebrates, isolation, landscape composition, plants, SLOSS debate, species richness

Introduction

Habitat fragmentation and land-use change have been found to be major drivers of biodiversity loss (Foley et al 2005; Fischer and Lindenmayer 2007), resulting in a mosaic of habitat remnants of different sizes. In this context, there is an ongoing debate on whether biodiversity conservation should focus on single or few large habitat fragments, or whether the protection of many small fragments (covering the same habitat area in a landscape) is of equal or even greater importance (“SLOSS” – Single Large Or Several Small, e.g. Maiorano et al. 2008; Tjørve and Tjørve 2008; Tjørve 2010; Tscharntke et al. 2012, for a review see Ovaskainen 2002). The main argument in favour of several small fragments is that they usually cover a wider geographic range and therefore greater environmental heterogeneity than a single or few large fragments of equal total area (Qian and Shimono 2012). This provides greater differences in community composition, increasing beta-diversity (community dissimilarity) and thereby supporting more species in total (Tscharntke et al 2012). In contrast, large fragments have the advantage that their species are less prone to extinction due to more stable habitat conditions, larger population sizes and higher immigration rates (MacArthur and Wilson 1967). Furthermore, highly specialised species tend to be area-sensitive and hence are mostly confined to large fragments (Bender et al 1998; Lasky and Keitt 2013). Since the debate is far from being resolved, empirical evidence across different taxa and landscape types is urgently needed.

Apart from fragment size, connectivity among fragments is highly important for species richness and community composition since it affects extinction-immigration dynamics (Losos and Ricklefs 2010), i.e. fragments that are more isolated are less likely to be colonised. In addition, different landscape types surrounding the fragments may facilitate or hinder dispersal (Öckinger et al 2012; Eycott et al 2012). Habitat fragments in a ‘sea’ of intensively managed agricultural matrix therefore receive fewer immigrants from the surrounding landscape.

In this study, we analyse landscape-wide fragmentation effects of calcareous grasslands, which are among the most species-rich habitats in Central Europe (Poschlod and WallisDeVries 2002; Ellenberg and Leuschner 2010). They have declined at an alarming rate due to their conversion to arable land or the abandonment of historic land-use forms like extensive grazing (Poschlod and WallisDeVries 2002). For example, in Southwestern Germany more than 70 % of the calcareous grasslands that were present in the year 1900 have disappeared (Mattern et al 1992). Thereby, connectivity of the remaining fragments has been reduced dramatically.

Within the study area (districts of Göttingen and Northeim, Lower Saxony, Germany, 2391.5 km^2) there are still more than 200 fragments of calcareous grassland, covering about 0.3 % of the area. The vast majority (70 %) of these fragments are smaller than 1 ha, but some large fragments are present as well (see Fig. S1 in Electronic supplementary material). They differ in connectivity and landscape complexity, making the study area highly appropriate for studying relative effects of fragment size and surrounding landscape matrix on species richness and community composition (Tscharntke et al 2002; Scherber et al 2012).

We focus on the effects of three landscape metrics: fragment size (large vs. small fragments), connectivity (measured by a connectivity index described by Hanski et al., 2000) and landscape composition (represented by the amount of arable land within a 500-m buffer around each site) on species richness and community composition of four taxa covering different trophic and organisational levels: (1) plants, (2) leafhoppers, planthoppers and froghoppers (Auchenorrhyncha, hereafter referred to as leafhoppers), (3) true bugs (Heteroptera) and (4) snails (Mollusca). In addition, for leafhoppers and true bugs we used plant species richness as a surrogate for habitat quality and resource availability. Habitat specialist and generalist species were analysed separately in order to test whether their species richness and community composition were affected differently by landscape parameters.

Studies often focus on large, attractive or mobile invertebrate taxa like bees, butterflies and hoverflies (e.g. Krauss et al., 2003; Schüepp et al., 2011), whereas the use of taxa with small body size and therefore restricted mobility like leafhoppers, true bugs and snails is far less common (but see Boschi and Baur 2007; Kőrösi et al. 2012). Due to their restricted mobility, the latter are likely to be much more affected by fragment size, connectivity and landscape complexity (Greenleaf et al 2007; Stoll et al 2009; Marini et al 2012). Therefore they are most suitable for shedding light on the “SLOSS” debate and testing the hypothesis that both several small and single large habitat fragments substantially contribute to biodiversity conservation in human-dominated landscapes.

In detail, we hypothesize that

(1) Many small habitat fragments support more species than few large fragments of similar habitat area, while community composition on small and large fragments is different.

(2) Species richness and community composition of plants and invertebrates are affected by decreasing landscape complexity (represented by increasing amount of arable land) and habitat connectivity. Furthermore, we hypothesize a positive relationship between plant species richness and true bug species richness.

(3) Specialist species of all taxa are more severely affected by fragment size than generalists.

(4) Very rare and area-sensitive species predominantly occur on large fragments.

Methods

Study area

The study area was located around the city of Göttingen in southern Lower Saxony in central Germany (51.5°N, 9.9°E, see Fig. 1). The landscape is characterised by intensively managed agricultural areas with a dominance of cereal, maize and rape fields and fertile meadows, interspersed with forests and patchily distributed fragments of calcareous grasslands (Fig. 1), belonging to the plant association *Mesobrometum erecti* Koch 1926 (Ellenberg and Leuschner 2010). These grasslands are managed by mowing or by grazing with livestock like sheep, goats, cattle or horses.

Study design

The study was conducted between April and September 2010. By analysing digital maps (ATKIS-DLM 25/1 Landesvermessung und Geobasisinformationen Niedersachsen 1991–1996, Hannover, Germany) with the geographical information system ArcGIS 10.0 (ESRI Geoinformatik GmbH, Hannover, Germany) and subsequent extensive field surveys in the study area, we selected 14 small (0.1–0.6 ha) and 14 large (1.2–8.8 ha) fragments of calcareous grassland (Fig 1). The threshold of 1 ha was chosen since the majority (70 %) of fragments in the study area is smaller than 1 ha and only few larger fragments exist (Fig. S1, Krauss et al. 2003). The fragments were chosen along two orthogonal gradients (Fig. S2): 1) a landscape composition gradient, i.e. an increasing percentage of arable land within a radius of 500 m around the fragments (27–77 %, mean = 47 %). We chose a radius of 500 m since we expected all four chosen taxa to be highly dispersal limited so that the close surroundings of the fragments would be most important for them, and 2) a habitat connectivity gradient, measured by a connectivity index (CI) described by Hanski et al. (2000):

$$CI_i = \Sigma \exp(- \alpha d_{ij}) A_j^{\beta}$$

Aj is the area of the neighbouring fragment j (in m2) and dij is the edge to edge distance (in m) from the focal fragment i to the neighbouring fragment j. α is a species specific parameter describing a species' dispersal ability and β is a parameter that describes the scaling of immigration. Since we applied the connectivity index to an entire community with several taxa, both scaling parameters α and β were set to the commonly used value of 0.5 (e.g. Brückmann et al., 2010). The values of the connectivity index ranged between 20 and 849 (mean = 244) with large values indicating high levels of connectivity. To assure that for no fragment the connectivity index was equal to zero, all calcareous grassland fragments with a minimum size of 50 m^2 within a radius of 2000 m around each study site were taken into account. Roadsides and field margins with plant species typical for calcareous grasslands (Krauss et al 2003) were uncommon and were not taken into account. The rationale behind choosing a radius of 500 m for the local variable of arable land and a radius of 2000 m for the landscape variable connectivity was that we specifically wanted to compare local (fragment size) with landscape effects at different spatial scales (landscape composition of the matrix around fragments and connectivity of the fragments). The values of the connectivity index for different spatial scales between 500 and 2000 m were highly correlated (see Table S7).

It was difficult to select fragments of similar habitat quality, because management differed from fragment to fragment. Some were grazed or mown, while on some, management had been abandoned. Mowing was done at different times throughout the year, although never before the first insect sampling, i.e. the beginning of June. Fragments that were managed for the conservation of rare plants (orchids in particular) were not cut before August to ensure that the seeds could fully ripen. In order to ensure that the fragments exhibited the characteristics of calcareous grasslands, we only included fragments that harboured more than ten of the plant species that are typical for calcareous grasslands in the study area (Krauss et al 2003).

Sampling methods

At the beginning of June 2010, we recorded the vegetation (only vascular plants) on six plots per fragment (1 × 5 m). The plots were at least 3 m away from each other and located in the centre of the fragments. The plant species were subdivided into habitat specialists and generalists according to Krauss et al. (2003).

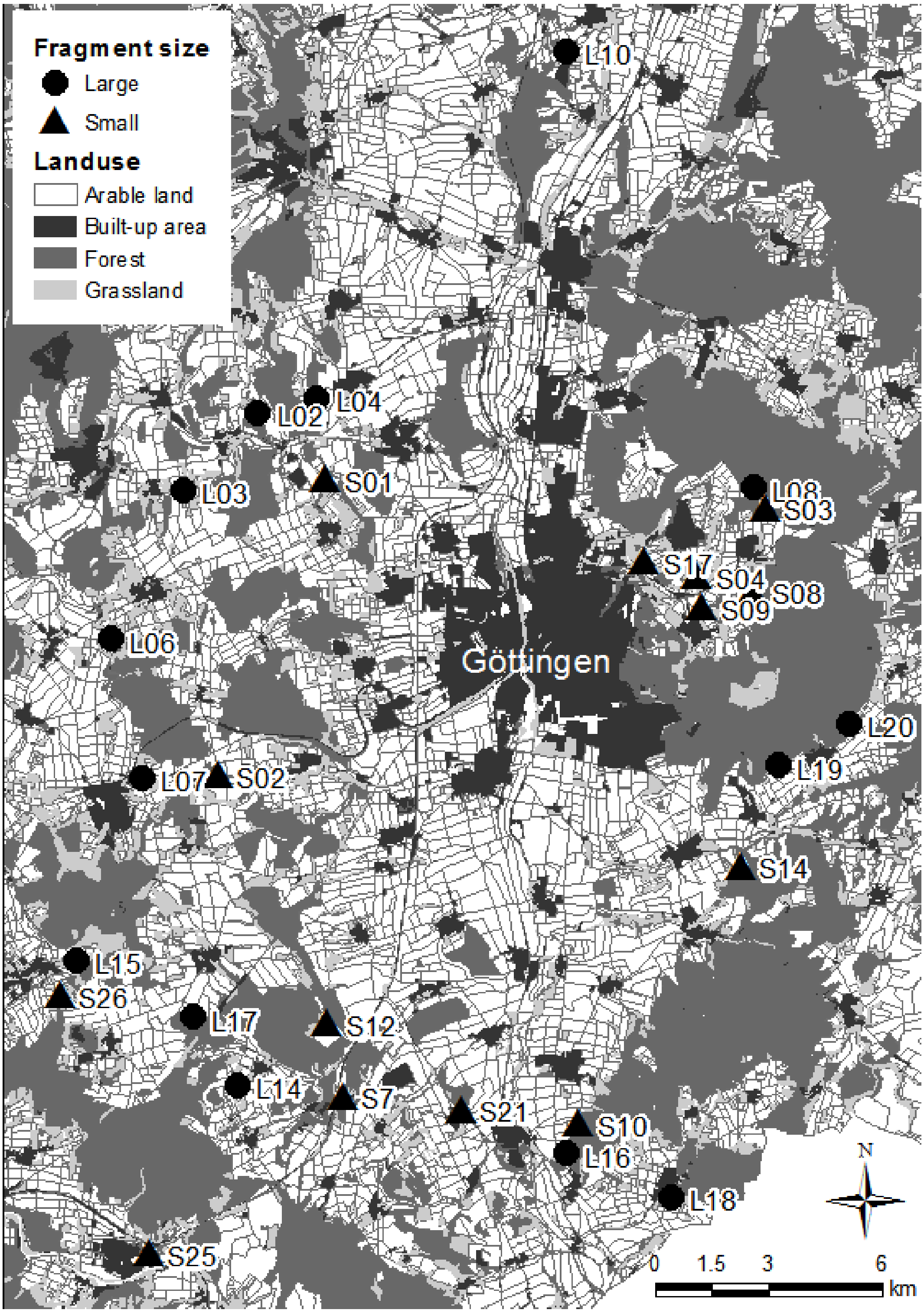
Leafhoppers and true bugs were sampled by sweep netting (Heavy Duty Sweep Net, 7215HS, BioQuip, diameter: 38 cm) on the botanical plots (20 sweeps each, i.e. 120 sweeps in total) in dry weather on three occasions in 2010 (at the beginning of June, at the end of July and at the beginning of September). These plots exceeded the botanical plots and were approximately 10 m long. The specimens of leafhoppers and true bugs caught were transferred into ethanol (70 % vol.) and subsequently identified to species level. Species with woody host plants were excluded, except when saplings of a potential host tree had been recorded in the botanical plots. Otherwise it was assumed that they had been dislodged from their host tree by wind. If the species' larvae used herbs or grasses as host plants and only the imagines fed on trees, specimens were included in the analysis.

The identification to species level of female specimens of several leafhopper genera was not possible (*Ribautodelphax, Anaceratagallia, Psammotettix, Rhopalopyx*) (Biedermann and Niedringhaus 2004). Thus, if male specimens were present, female specimens were assumed to belong to the same species (we used this in the case of 84 specimens, which represented around 1 % of the total abundance). If not, they were only identified to genus level. If males of more than one species of a genus were present, the number of females was assumed to mirror that of males.

All leafhopper and true bug species were classified into habitat specialists and generalists according to (i) their specific habitat requirements typical for calcareous grassland (i.e. warm and dry habitat conditions, short, grazed swards, open soil) and (ii) diet preferences (i.e. only being able to utilise plants that exclusively occur on calcareous grasslands) based on Nickel (2003) and Wachmann et al. (2004, 2006, 2007, 2008) and expert opinions (H. Nickel (Göttingen), M. Goßner (Fronreute)). A species was classified as a habitat specialist if conditions (i) and/or (ii) were fulfilled; it was classified as a generalist if neither (i), nor (ii) were fulfilled.

In September 2010, land snails (excluding slugs) were sampled by taking soil samples on the six botanical plots on each fragment (11.2 × 11.2 × 5 cm, approximately 0.6 l each) (method modified after Koordinationsstelle Biodiversitäts-Monitoring Schweiz, 2010). In addition, in order to sufficiently record the shells of larger species, we thoroughly searched the botanical plots (modified after Boschi and Baur (2007) and K. Groh (Hackenheim), pers. comm.). The soil samples were washed through sieves of four different mesh sizes (4 mm, 2 mm, 1 mm, 0.5 mm). The remaining fine plant material was checked for snail shells under a magnifying lens. Specimens were identified to species level and were subdivided into four classes of weathering. Class 1 included specimens that had been alive at the time of collection (with the remains of the soft parts still visible inside the shells), shells in class 2 were fresh but the snail had already been dead at the time of collection, shells in class 3 were slightly weathered and in class 4 all the periostracum had weathered away. Only the specimens from class 1 to 3 were included in the analyses since it could be expected that these species still occurred on the fragments. Like the other taxa, the snails were subdivided into grassland specialists and generalists (Kerney et al 1983; Boschi and Baur 2007).

Fig. 1. Location of the 28 grasslands, with the city of Göttingen in the centre of the map. Large grasslands are marked with 'L', small grasslands with 'S', both with a subsequent site number (see Table S2).



We determined the Red List status of all species and subsequently determined those specialist species that exclusively occurred either on large or on small fragments. For plants, true bugs and snails Red Lists for Lower Saxony were used (Melber 1999; Garve 2004; Teichler and Wimmer 2007), for leafhoppers only a Red List for all of Germany was available (Remane et al 1997). Nomenclature follows Seybold (2009) (plants), Biedermann and Niedringhaus (2004) (leafhoppers), Wachmann et al. (2004, 2006, 2007, 2008) (true bugs) and Teichler and Wimmer (2007) (snails).

Species richness of the six plots per fragment for each taxon was pooled for all statistical analyses. Furthermore, species richness of leafhoppers and true bugs was pooled over the three sampling occasions.

Statistical analyses

We estimated the number of species, which we would have been able to attain with a three times higher sampling effort (i.e. 18 instead of six plots per fragment) with EstimateS (version 9.1.0, Colwell, 2013), using 100 randomisations, randomising the individuals without replacement. We found that with our actual sampling effort we captured between 47 and 100 % of species (plants: mean = 84.2 % of overall species richness (87.5 % of specialists), leafhoppers: mean = 77.2 % (78.0 %), true bugs: mean = 66.7 % (77.4 %), snails: mean = 78.9 % (90.0 %)). There was no difference in sampling efficiency between large and small fragments (Table S2, Table S3, Fig. S2).

Species-area accumulation curves were established by starting with the smallest fragment going to the largest one, progressively adding the species that had not occurred on the previous fragment. We then employed the same procedure again, starting with the largest fragment going to the smallest one. The summed fragment sizes on a $\log_{10}$-scale were placed on the x-axis.

When comparing several small with few large fragments, we had to control for differences in sampling intensity with respect to fragment size. We therefore randomly selected pairs of two large fragments (i.e. 12 plots) and in addition selected 12 plots originating from 12 different small fragments. This procedure was then repeated ten times, resulting in a new data set with ten times two large fragments (N=10) and ten sets of 12 randomly selected plots from small fragments (N=10). We then created sample-based rarefaction curves for each taxon for both overall species richness and specialist species richness with EstimateS (version 9.1.0, Colwell 2013), using 100 randomisations, randomising the individuals without replacement. For plants we analysed presence-absence data. We used nonlinear mixed-effects models (R package *nlme*, Pinheiro et al 2014) to fit Michaelis-Menten models to the rarefaction curves (as suggested by Gotelli and Colwell (2011)). In these models, the response variable was rarefied species richness and the explanatory variable was the number of individuals. Models contained fragment size as fixed effect and for site (N=20) random effect. Starting values for the parameters were estimated using the *SSmicmen* function in R package *nlme* (Pinheiro et al 2014).

To detect differences in species composition, redundancy analyses (RDAs) with each of the explanatory variables (fragment size (large or small), connectivity, percentage of arable land and plant species richness (for leafhoppers and true bugs)) were performed with function *rda* from R package *vegan* (Oksanen et al 2013). Interactions between explanatory variables were not tested. Prior to analysis, the community data matrices were Hellinger-transformed, thereby giving lower weights to rare species (Legendre and Gallagher 2001). A permutation test with 999 permutations with function *permutest* from R package *vegan* (Oksanen et al 2013) was used to assess statistical significance of the similarity in community composition.

In order to detect similarities between the species composition of the four taxa, Mantel tests (based on Pearson's product-moment correlation) with 999 permutations (Mantel 1967) were conducted using the function *mantel* from R package *vegan* (Oksanen et al 2013) with distance matrices using Bray-Curtis indices created with function *vegdist* from R package *vegan* (Oksanen et al 2013).

Species richness was analysed using generalized linear models with negative binomial errors (*glm.nb,* R package *MASS* (Venables and Ripley 2002)) or Poisson errors (for generalist snails, R package *MASS* (Venables and Ripley 2002)) with the following explanatory variables: (1) fragment size (taken as a factor, either ‘large’ or ‘small’), (2) habitat connectivity, measured by a connectivity index described by Hanski et al. (2000), (3) the percentage of arable land in a 500 m-buffer around each fragment ($\log_{10}$-transformed to achieve a better fit of the models) and (4) plant species richness per site (only for leafhoppers and true bugs). The families and link functions used in generalized linear models were selected based on residual deviance. The explanatory variables were uncorrelated (Table S4) and no collinearity (Smith et al 2009) was detected (function vif from R package *usdm* (Naimi 2014), Table S5). We started off with full models containing two-way interactions between all the explanatory variables. These models were then simplified using an automated stepwise model selection procedure based on AICc (function *stepAICc* based on function *stepAIC* (R package *MASS* (Venables and Ripley 2002), but corrected for small sample sizes by CS, see URL: http://wwwuser.gwdg.de/~cscherb1/stepAICc.txt).

To account for spatial autocorrelation we conducted Mantel tests (based on Pearson's product-moment correlation) with 999 permutations (Mantel 1967) using Bray-Curtis indices created with function *vegdist* from R package *vegan* (Oksanen et al 2013). With the resulting distance matrices we then performed Mantel tests with the function *mantel* from R package *vegan* (Oksanen et al 2013). There was no sign of correlation of the geographic fragment location with species richness or community composition (see Table S6).

All statistical analyses were conducted with R version 2.15.3 (R Development Core Team 2012).

Results

In the 28 fragments of calcareous grassland we recorded 167 plant species, comprising 65 specialist and 102 generalist species (including 21 tree and shrub species as saplings), with a minimum of 25 and a maximum of 65 species per site. We found 77 leafhopper species (29 specialists and 48 generalists), with 7073 adult specimens. Species richness ranged from 14 to 31 species per fragment. There were 76 true bug species (21 specialists and 55 generalists), with 2117 adult specimens with a range of species richness between 7 and 29 species per fragment. In the first three shell age classes we recorded 28 snail species (10 specialists and 18 generalists) with 7199 specimens. Species richness ranged from 5 to 16 species per fragment (see Table S2, Table S6).

The species-area accumulation curves showed a similar pattern for all four taxa (Fig. 2a). The accumulated area of all 14 small fragments resulted in a much higher total species richness than if only few large fragments of similar area were considered. Specifically, an average of 85 % of the overall species richness was recorded on all small fragments taken together (4.6 ha), whereas the two largest ones (15.1 ha) only accounted for 37 % of the species. This effect was the same for both overall species richness and the species richness of habitat specialists (Fig. 2b). The 14 small fragments covered a wider geographic range (264 km^2) than few large fragments of similar area (on average, three large fragments taken together only covered 56 km^2, see Fig. 1).

When controlling for sampling effort on small vs. large fragments, we found that the accumulated species richness of 12 plots from 12 different small fragments resulted in a significantly higher species richness than 12 plots from two large fragments. On average, the attained species richness was 30 % higher (Fig. 3, Table S8). This was not only true for overall species richness but also for specialist species richness of plants and leafhoppers (species richness was 23 % higher).

We found a significant effect of fragment size on the species composition of all four taxa (Table 2, Fig. 4). In most cases, both specialist and generalist species were affected by fragment size. In addition, the community composition of true bugs (all species and generalists) was influenced by plant species richness. Leafhopper community composition (all species and generalists) was affected by the percentage of arable land surrounding the sites (Table 2). The community composition of the other taxa was not influenced by connectivity or landscape composition.

The community composition of plants, leafhoppers and true bugs on the 28 fragments of calcareous grassland was highly significantly correlated (Mantel tests, Table S1). Snail community composition, however, was not correlated with plant and true bug community composition and only weakly correlated with leafhopper community composition.

In the case of leafhoppers and true bugs, a number of red-listed specialist species occurred on large fragments exclusively (Table 1). In the case of plants and snails, red-listed specialists occurred on both large and small fragments but the occurrence of the most threatened plant and snail species was restricted to large fragments.

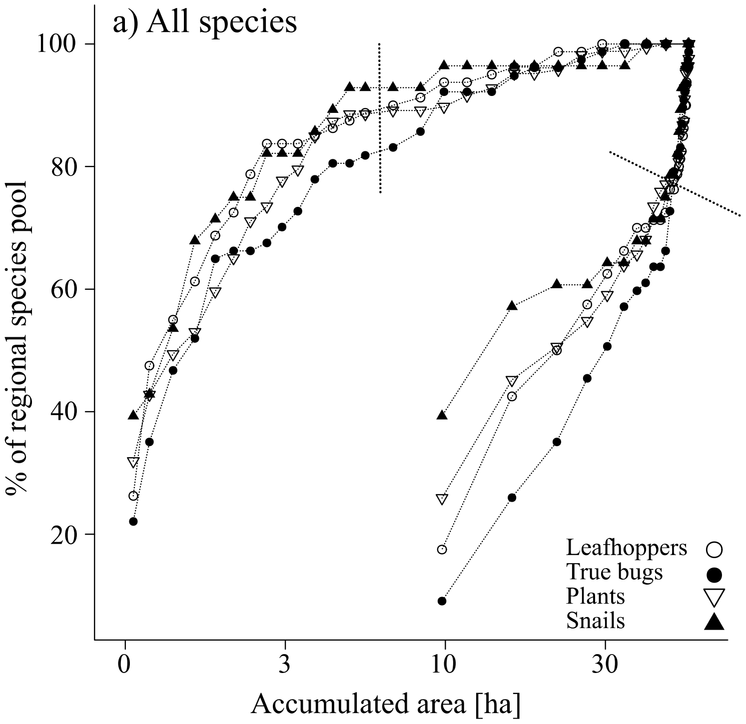
We found no effect of fragment size on the species richness of plants, true bugs and snails (Table 3). For leafhoppers there was an interaction of fragment size with habitat connectivity (Rösch et al 2013).

With increasing connectivity, plant species richness remained stable in simple landscapes (dominated by arable crops), whereas it decreased with increasing connectivity in complex landscapes (Table 3, Fig. 5a). For overall and generalist true bug species richness we found an increase in species richness with increasing plant species richness on connected but not on isolated fragments (Table 3, Fig. 5b). Snail species richness was not significantly influenced by any of the chosen landscape parameters (Table 3).

Table 1. Specialist species of plants, leafhoppers, true bugs and snails that exclusively occurred on either large (L) or on small (S) fragments. Red list status (RL status) derived from Remane et al. (1997), Melber (1999), Garve (2004) and Teichler & Wimmer (2007). Categories: 1 – critical, 2 – endangered, 3 – vulnerable, 4 – near threatened.

		RL Status	Fragment size	Occupied fragments	Cover (%) / individuals
Plants	*Genista tinctoria*	4	L	4	4.33
	Filipendula vulgaris	2	L	1	0.22
	Ophrys apifera	3	L	4	0.25
	Ophrys insectifera	3	L	4	0.65
	Orchis tridentata	2	L	2	5.83
	Vincetoxicum hirundinaria		L	1	0.08
	Orchis mascula	3	S	2	0.10
	Clinopodium vulgare		S	1	3.33
	Dactylorhiza maculata	3	S	1	0.33
	Melampyrum arvense	2	S	1	0.57
	Platanthera chlorantha	3	S	1	0.02
	Silene nutans	4	S	2	0.03
Leafhoppers	*Batracomorphus irroratus*	2	L	1	10
	Chlorita paolii		L	1	1
	Goniagnathus brevis	2	L	5	7
	Hephathus nanus	2	L	1	2
	Jassidaeus lugubris	3	L	1	1
	Neoaliturus fenestratus	3	L	2	3
	Platymetopius major	3	L	2	2
	Arocephalus punctum		S	1	2
	Delphacinus mesomelas		S	1	1
	Mocydiopsis attenuata		S	1	1
True bugs	*Lygaeus equestris*	3	L	1	1
	Phymata crassipes	3	L	2	5
	Phytocoris varipes		L	3	23
	Dicyphus annulatus		S	1	1
	Legnotus picipes		S	1	1
	Oncochila simplex		S	2	2
	Orthops kalmii		S	1	2
Snails	*Candidula unifasciata*	2	L	1	98
	Xerocrassa geyeri	1	L	1	36

Fig. 2. Fig. 2. Species-area accumulation curves of overall and specialist species richness of plants, leafhoppers, true bugs and snails: the cumulative number of species of the regional species pool (in percent, y-axis) in relation to cumulative grassland area (in ha) (x-axis) of the 14 small and 14 large calcareous grassland fragments. The first set of lines (left) sums the species from the smallest to the largest of the 28 fragments; the second set of lines (right) sums the species from the largest to the smallest fragment. The thresholds between large and small fragments are marked by the grey dashed lines. These results indicate that on a landscape scale many small fragments include more species than few large fragments.



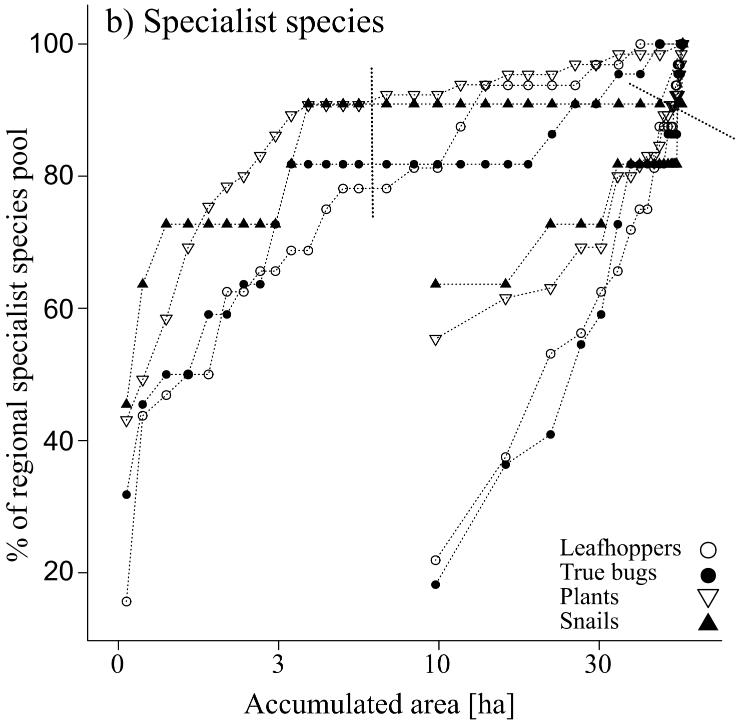


Fig. 3. Sample-based rarefaction curves showing the estimated species richness (SpR) against the number of individuals per sampling plot of 12 plots originating from either (i) 12 different small fragments (10 curves of randomly selected fragments and plots) vs. (ii) 12 plots originating from each two randomly selected large fragments. For plants the analysis was based on presence-absence data. Note that this sampling was replicated 10 times at random (10 curves of randomly selected fragments). Lines represent the average curve for the 10 randomly selected curves per fragment size category.

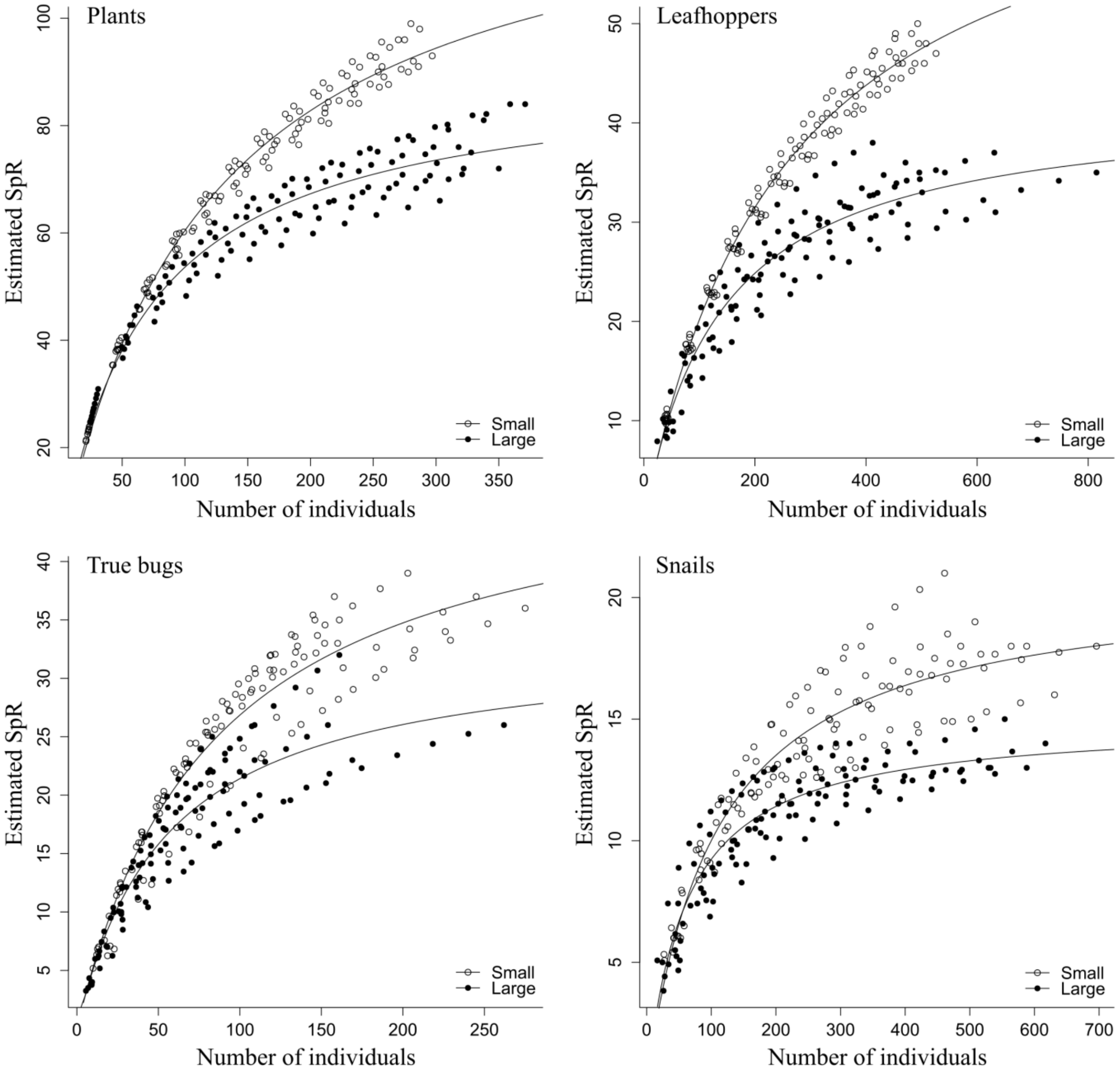


Fig. 4. RDA plots for species composition of specialist plants, generalist true bugs, specialist and generalist leafhoppers and specialist and generalist snails showing the effect of fragment size with minimum convex polygons. Closed circles (L): large fragments, open circles (S): small fragments.

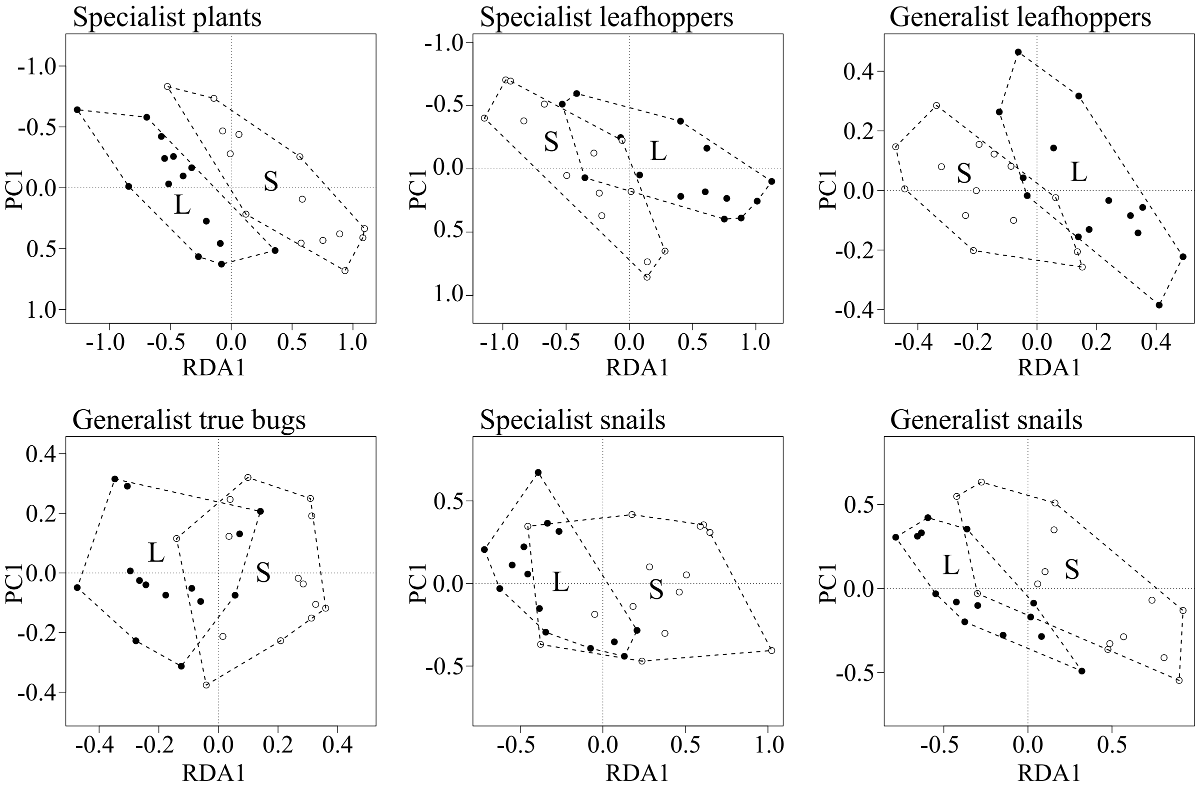


Fig. 5. Interaction plots showing the relationship between plant species richness/true bug species richness (y-axis) and the landscape parameters (x-axis). Effect of landscape composition and habitat isolation (measured by a connectivity index (Hanski et al., 2000), $\log_{10}$-transformed) on plant species richness (complex: 27 – 46 % of arable land in 500 m buffer, simple: 47 – 77 % of arable land), Effect of increasing plant species richness on true bug species richness in conjunction with habitat isolation (connected: values of the connectivity index from 180 – 849, isolated: values from 19 – 155).

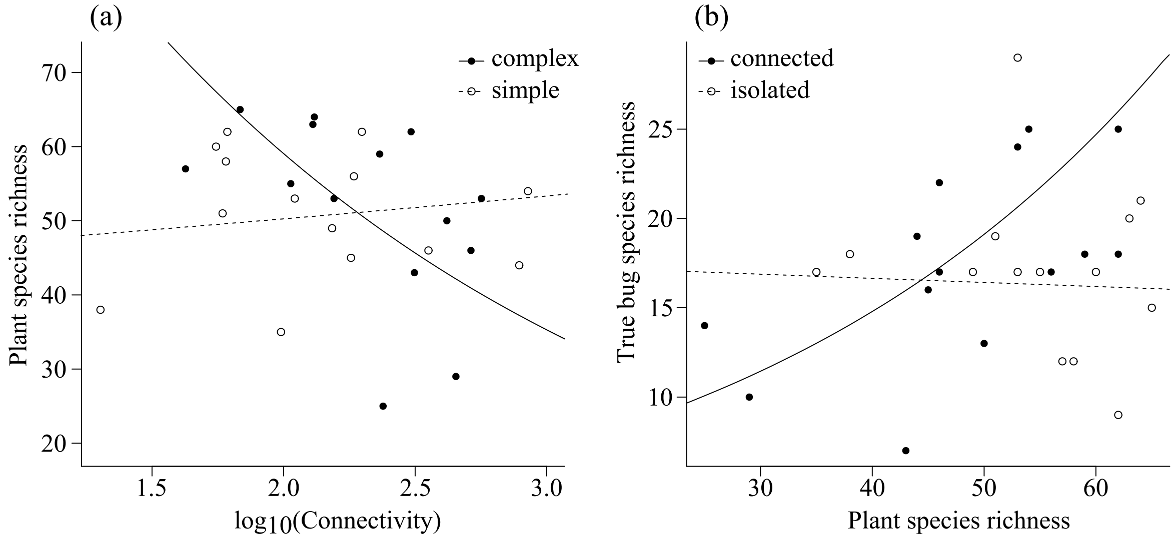


Table 2. Results of RDA analyses: influence of fragment size (large/small), landscape composition (% arable), connectivity (a connectivity index described by Hanski et al. (2000), $\log_{10}$-transformed) and plant species richness (for leafhoppers and true bugs) on the community composition of plants, leafhoppers, true bugs and snails. *P*-values < 0.05 are depicted in bold characters.

		All species			Specialists			Generalists		
		partial RDA % of variation	F	*P*	partial RDA % of variation	F	*P*	partial RDA % of variation	F	*P*
Plants	Type	5.7	1.58	**0.017**	6.5	1.85	**0.025**	4.7	1.28	0.150
	% arable	4.0	1.11	0.275	4.3	1.22	0.206	3.6	0.99	0.431
	Connectivity	3.6	1.02	0.393	4.0	1.12	0.277	3.3	0.89	0.612
	Total	14.1	1.32	**0.024**	15.5	1.47	**0.024**	12.5	1.14	0.170
Leafhoppers	Type	6.2	1.82	**0.008**	6.3	1.79	**0.047**	6.2	1.84	**0.024**
	% arable	5.8	1.68	**0.019**	5.0	1.44	0.119	6.4	1.90	**0.009**
	Connectivity	4.8	1.40	0.070	5.3	1.50	0.105	4.4	1.30	0.139
	plant SpR	4.2	1.23	0.170	3.6	1.02	0.438	4.8	1.43	0.087
	Total	21.0	1.53	**0.001**	19.1	1.36	**0.042**	22.6	1.68	**0.001**
True bugs	Type	7.1	2.06	**0.003**	5.0	1.33	0.182	7.8	2.32	**0.003**
	% arable	3.8	1.10	0.318	2.5	0.67	0.778	4.2	1.25	0.158
	Connectivity	3.9	1.12	0.295	2.4	0.65	0.804	4.4	1.31	0.146
	plant SpR	5.9	1.71	**0.016**	4.3	1.15	0.315	6.6	1.95	**0.004**
	Total	20.4	1.48	**0.003**	14.1	0.95	0.584	22.7	1.68	**0.001**
Snails	Type	8.6	2.47	**0.001**	9.0	2.51	**0.022**	8.3	2.44	**0.013**
	% arable	4.1	1.18	0.271	2.4	0.67	0.693	5.6	1.64	0.076
	Connectivity	3.0	0.88	0.627	3.9	1.10	0.364	2.3	0.68	0.767
	Total	16.5	1.58	**0.015**	14.3	1.34	0.146	18.4	1.80	**0.014**

Table 3. Generalized linear models on the effects of landscape context (% arable land), fragment size (large or small), connectivity (a connectivity index described by Hanski et al. (2000), $\log_{10}$-transformed) and plant species richness (for true bugs) on the species richness of plants, true bugs and snails. Only variables included in the final models are shown. P-values < 0.05 are depicted in bold characters.

		All species				Specialists				Generalists			
		Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Plants	Intercept	7.87	1.19	6.64	**<0.001**	6.94	1.59	4.37	**<0.001**	7.47	1.86	4.01	**<0.001**
	% arable land (Ar)	-0.07	0.02	-3.14	**0.002**	-0.07	0.03	-2.20	**0.028**	-0.08	0.04	-2.15	**0.032**
	Connectivity (Conn)	-1.73	0.53	-3.29	**0.001**	-1.60	0.70	-2.28	**0.023**	-1.88	0.83	-2.27	**0.023**
	Ar × Conn	0.03	0.01	3.10	**0.002**	0.03	0.01	2.16	**0.031**	0.03	0.02	2.13	**0.033**
True bugs	Intercept	6.45	1.42	4.55	**<0.001**	1.41	0.09	15.15	**<0.001**	5.98	1.65	3.62	**<0.001**
	Connectivity (Conn)	-1.84	0.64	-2.89	**0.004**	–	–	–	–	-1.81	0.74	-2.45	**0.014**
	Plant SpR	-0.08	0.03	-2.91	**0.004**	–	–	–	–	-0.08	0.03	-2.41	**0.016**
	Conn × plant SpR	0.04	0.01	3.24	**0.001**	–	–	–	–	0.04	0.01	2.78	**0.005**
Snails	Intercept	2.42	0.06	42.96	**<0.001**	1.74	0.08	21.90	**<0.001**	2.26	0.73	3.08	**0.002**
	Fragment size (Type)	–	–	–	–	–	–	–	–	-1.29	1.01	-1.28	0.202
	Connectivity (Conn)	–	–	–	–	–	–	–	–	-0.36	0.35	-1.01	0.312
	Type × Conn	–	–	–	–	–	–	–	–	0.74	0.45	1.63	0.103

Discussion

Our results show that even though per fragment species richness did not differ between large and small fragments, 87 % of the overall species richness was recorded on all small fragments taken together (4.6 ha), whereas the two largest ones (15.1 ha) only accounted for 41 % of the species. This did not only hold for overall species richness, but also for specialist species richness. Even when controlling for sampling effort in comparison of several small with few large fragments, several small fragments resulted in a much higher species richness than the few large ones. In addition, community similarity was high between plants, leafhoppers and true bugs, whereas snail community composition correlated only with that of leafhoppers. However, community composition of large and small fragments differed greatly and some of the rarest specialist species appeared to be mostly confined to large fragments.

The cumulative area of the 14 small fragments resulted in a higher species richness of all four taxa than few large fragments, showing a highly similar pattern for both overall species richness and the species richness of habitat specialists. The observed shape of the species-area accumulation curves supports published findings from the species richness of small and large habitat fragments (Tscharntke et al. 2002; Fahrig 2013, for a theoretical approach see Tjørve 2010). The 14 small fragments covered a wider geographic range (264 km^2) than few large fragments of similar area (on average, three large fragments taken together only covered 56 km^2, also see Fig. 1). Due to the considerable geographic distance between fragments, each fragment - both large and small - was different in terms of connectivity, surrounding landscape matrix (driving immigration patterns), local management and management history (Tscharntke et al 2012), which led to a specific plant species composition, influencing the composition of the associated invertebrate species. This was confirmed by the result of Mantel tests which showed that the species composition of plants, leafhoppers and true bugs on each fragment was highly correlated (Su et al., 2004, but see Dormann et al., 2007). In contrast, snail community composition was only weakly correlated with that of leafhoppers, presumably because of the high dispersal limitation in snails (Götmark et al 2008). Also, since the fragments did not display a nested species composition, i.e. the small fragments not only contained subsets of the species occurring on large fragments but distinct communities, there were more species on several small fragments taken together than on few large ones (Simberloff 1988). In general, all taxa chosen here are relatively dispersal limited, albeit not as limited as snails (Poschlod et al 1998; Jenkins et al 2007; Littlewood et al 2007). This dispersal limitation can also be assumed to have played a crucial role in creating distinct communities on each fragment, making the chosen taxa highly suitable for the study of the SLOSS question.

Even though across taxa many more species could be preserved on less area with the "several small fragments" approach, the species composition of small and large fragments differed strongly, and red-listed specialist species were mostly restricted to large fragments. It was only in the case of plants and snails that some red-listed specialists occurred on small fragments as well. This could at least partly be due to an unpaid extinction debt on small fragments resulting from long generation times of most plant species (Helm et al 2006; Hylander and Ehrlén 2013). In line with our results, Fukamachi et al. (1996) found that the maximum number of plant species in Japanese forest reserves could be achieved by pursuing the "several small" strategy, but the rarest species were confined to large fragments. Similarly, Godefroid and Koedam (2003) found that several forest specialist plants in Belgian forest remnants predominantly occurred in the largest fragment they investigated. So obviously there is a trade-off between the protection of the few very rare species and the increase of overall species richness (including habitat specialists) in an area (Tjørve 2010).

We chose the four taxa since they can all be assumed to be dispersal limited and thus dependent on connectivity and the composition of the surrounding landscape. Nevertheless, except for leafhopper community composition, which was affected by landscape composition, community composition of the other taxa was not affected by connectivity or landscape composition. The effect of landscape composition on leafhopper community composition can be explained by changed immigration and dispersal patterns in landscapes dominated by arable land (Eycott et al 2012) and is in line with our former findings, i.e. an increase in leafhopper species richness with connectivity in simple but not in complex landscapes (high vs. low amount of arable land) (Rösch et al 2013).

Fragment size (large vs. small) did not affect species richness of plants, snails and true bugs. For plants, this is in line with Helm et al. (2006), who found no effect of current grassland size on plant species richness in Estonian calcareous grasslands, explaining this by an unpaid extinction debt. For snails, the size of the fragments chosen here may have been above a threshold value (Stoll et al 2009), i.e. many species would have been able to persist on even smaller fragments and so, no effect on species richness became apparent. True bugs show a relatively low degree of specialisation (Wachmann et al. 2004, 2006, 2007, 2008). Therefore, the surrounding landscape seems to offer sufficient alternative habitat, rendering the size of the focal fragment less important. Leafhoppers, however, showed an interaction of fragment size with connectivity (Rösch et al 2013), implying that in their case connectivity is more important for small, isolated fragments.

Plant species richness decreased with increasing connectivity, albeit only in complex and not in simple landscapes. This is contrary to theoretical assumptions, predicting increased species richness with increasing connectivity due to enhanced dispersal and colonisation (MacArthur and Wilson 1967) and also contrary to findings of similar studies (e.g. Brückmann et al. 2010). However, time-lag effects like an extinction debt may currently obscure these processes (e.g. Hylander and Ehrlén 2013). Contrastingly, an increase in connectivity has also been shown to cause a decrease in the persistence of species, e.g. through changes in predator-prey networks (as discussed in Fahrig 2003; Ethier and Fahrig 2011), but to our knowledge this has not been reported for plants yet.

Overall and generalist true bug species richness increased with increasing plant species richness in connected but not in isolated fragments, which is similar to the pattern in generalist leafhoppers (Rösch et al 2013). True bugs frequently feed on plant sap, although most species are not as highly specialised as the majority of leafhopper species (Nickel 2003; Wachmann et al. 2004, 2006, 2007, 2008). In comparison to leafhoppers, this is reflected in the lower proportion of true bug species that were classified as habitat specialists. More plant species per site increase (i) the probability that an appropriate host plant per species is present (sampling effect) and (ii) the heterogeneity of the food resource (complementarity effect). This finding is in accordance with Scherber et al. (2010), who found an increase in herbivore diversity when the number of grassland plants in their experimental setup increased. Immigration increases with increasing connectivity (MacArthur and Wilson 1967), so even if suitable plant resources are available, isolated fragments are less frequently colonised than connected ones. This explains the observed increase in true bug species richness with plant species richness in connected but not in isolated fragments. The close relationship of true bugs with plants was also reflected in the change in true bug community composition with increasing plant species richness.

Snail species richness was not affected by connectivity or landscape composition. This can be explained by their low mobility, making connectivity and the surrounding landscape less important for them. They can be expected to be more influenced by local habitat factors like management and management history (Boschi and Baur 2007; but see Götmark et al. 2008).

Conclusion

Our results demonstrate that a much less area is needed to accumulate a large number of species, also including habitat specialists, when combining several small habitat fragments across landscapes, showing the need to maintain many fragmented communities to protect as many species as possible. Although this is even true for the richness of specialist species, the conservation of small fragments must not be an exclusive conservation strategy since (1) large and small fragments differed in their community composition across taxa and (2) red-listed specialist species were mostly, and a few particularly rare species completely, confined to large fragments. Connectivity and landscape complexity (even when choosing a steep gradient as in this study) showed effects on species richness and community composition of all taxa, but they were not as consistent as the effects of fragment size. This leads to the conclusion that across landscapes both many small fragments as well as a few large fragments are needed for successful biodiversity conservation, especially in situations, where the majority of fragments has already been lost. Such a diversified habitat fragmentation strategy should be considered when setting priorities for conservation management in fragmented landscapes worldwide.

Acknowledgements

We would like to thank Andrea Rösch, Boris M. Hillmann, Éva M. Szegő and Felix Weiß for their help with data collection in the field. Furthermore, we would like to thank Sebastian Schuch who gave an introduction into leafhopper identification to V.R, Walter Wimmer and Ira Richling who both helped with snail identification and Laura Sutcliffe who helped to improve the English and gave valuable comments on earlier versions of the manuscript. We thank Adam C. Smith and one anonymous referee for their valuable comments. P.B. was supported by the German Research Foundation (DFG BA4438/1-1). Support to VR by the MWK graduate school “Biodiversität und Gesellschaft” and the DFG Research Training Group 1644 (Scaling Problems in Statistics) is acknowledged.

References

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79**:517–533. doi: 10.2307/176950

Biedermann R, Niedringhaus R (2004) Die Zikaden Deutschlands - Bestimmungstafeln für alle Arten. WABV Fründ, Scheeßel

Boschi C, Baur B (2007) Effects of management intensity on land snails in Swiss nutrient-poor pastures. *Agric Ecosyst Environ* **120**:243–249. doi: 10.1016/j.agee.2006.09.008

Brückmann SV, Krauss J, Steffan-Dewenter I (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *J Appl Ecol* **47**:799–809. doi: 10.1111/j.1365-2664.2010.01828.x

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Permanent URL: http://purl.oclc.org/estimates.

Dormann CF, Schweiger O, Augenstein I, Bailey D, Billeter R, de Blust G, DeFilippi R, Frenzel M, Hendrickx F, Herzog F, Klotz S, Liira J, Maelfait J-P, Schmidt T, Speelmans M, van Wingerden WKRE, Zobel M (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Glob Ecol Biogeogr* **16**:774–787. doi: 10.1111/j.1466-8238.2007.00344.x

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht, 6th edn. Ulmer, Stuttgart

Ethier K, Fahrig L (2011) Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Landsc Ecol* **26**:865–876. doi: 10.1007/s10980-011-9614-2

Eycott AE, Stewart GB, Buyung-Ali LM, Bowler DE, Watts K, Pullin AS (2012) A meta-analysis on the impact of different matrix structures on species movement rates. *Landsc Ecol* **27**:1263–1278. doi: 10.1007/s10980-012-9781-9

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *J Biogeogr* **40**:1649–1663. doi: 10.1111/jbi.12130

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. *Annu Rev Ecol Evol Syst* **34**:487–515. doi: 10.1146/annurev.ecolsys.34.011802.132419

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Glob Ecol Biogeogr* 16:265–280. doi: 10.1111/j.1466-8238.2006.00287.x

Foley JA, Defries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. *Science* (80-) **309**:570–574. doi: 10.1126/science.1111772

Fukamachi K, Iida S, Nakashizuka T (1996) Landscape patterns and plant species diversity of forest reserves in the Kanto region, Japan. *Vegetatio* **124**:107–114. doi: 10.1007/BF00045149

Garve E (2004) Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen - 5. Fassung, Stand 1.3. 2004. *Informationsdienst Naturschutz Niedersachsen* **1**:1–76.

Godefroid S, Koedam N (2003) How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Glob Ecol Biogeogr* **12**:287–298. doi: 10.1046/j.1466-822X.2003.00035.x

Gotelli NJ, Colwell RK (2011) Estimating Species Richness. In: Magurran AE, McGill BJ (eds) Biological Diversity. Oxford University Press, New York, pp 39–53

Götmark F, Von Proschwitz T, Franc N (2008) Are small sedentary species affected by habitat fragmentation? Local vs. landscape factors predicting species richness and composition of land molluscs in Swedish conservation forests. *J Biogeogr* **35**:1062–1076. doi: 10.1111/j.1365-2699.2008.01882.x

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia* **153**:589–596. doi: 10.1007/s00442-007-0752-9

Hanski I, Alho J, Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* **81**:239–251. doi: 10.1890/0012-9658(2000)081[0239:ETPOSA]2.0.CO;2

Helm A, Hanski I, Pärtel M (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecol Lett* **9**:72–77. doi: 10.1111/j.1461-0248.2005.00841.x

Hylander K, Ehrlén J (2013) The mechanisms causing extinction debts. *Trends Ecol Evol* **28**:341–346. doi: 10.1016/j.tree.2013.01.010

Jenkins DG, Brescacin CR, Duxbury C V., Elliott JA, Evans JA, Grablow KR, Hillegass M, Lyon BN, Metzger GA, Olandese ML, Pepe D, Silvers GA, Suresch HN, Thompson TN, Trexler CM, Williams GE, Williams NC, Williams SE (2007) Does size matter for dispersal distance? *Glob Ecol Biogeogr* **16**:415–425. doi: 10.1111/j.1466-8238.2007.00312.x

Kerney MP, Cameron RAD, Jungbluth JH (1983) Die Landschnecken Nord- und Mitteleuropas. Paul Parey, Hamburg & Berlin.

Koordinationsstelle Biodiversitäts-Monitoring Schweiz (2010) Anleitung für die Feldarbeit zum Indikator « Z9-Mollusken », Bundesamt für Umwelt, Bern www.biodiversitymonitoring.ch/pdfs/downloads/737%20Anleitung%20Z9-Moll%20Feldv10.pdf%20.

Kőrösi Á, Batáry P, Orosz A, Rédei D, Báldi A (2012) Effects of grazing, vegetation structure and landscape complexity on grassland leafhoppers (Hemiptera: Auchenorrhyncha) and true bugs (Hemiptera: Heteroptera) in Hungary. *Insect Conserv Divers* **5**:57–66. doi: 10.1111/j.1752-4598.2011.00153.x

Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *J Biogeogr* **30**:889–900. doi: 10.1046/j.1365-2699.2003.00878.x

Lasky JR, Keitt TH (2013) Reserve size and fragmentation alter community assembly, diversity, and dynamics. *Am Nat* **182**:E142–E160. doi: 10.1086/673205

Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**:271–280. doi: 10.1007/s004420100716

Littlewood NA, Pakeman RJ, Woodin SJ (2007) Isolation of habitat patches limits colonisation by moorland Hemiptera. *J Insect Conserv* **13**:29–36. doi: 10.1007/s10841-007-9114-5

Losos JB, Ricklefs RE (2010) The Theory of Island Biogeography Revisited. Princeton University Press, Princeton, New Jersey.

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

Maiorano L, Falcucci A, Boitani L (2008) Size-dependent resistance of protected areas to land-use change. *Proc R Soc B Biol Sci* **275**:1297–1304. doi: 10.1098/rspb.2007.1756

Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* **27**:209–220.

Marini L, Öckinger E, Battisti A, Bommarco R (2012) High mobility reduces beta-diversity among orthopteran communities - implications for conservation. *Insect Conserv Divers* **5**:37–45. doi: 10.1111/j.1752-4598.2011.00152.x

Mattern H, Mauk J, Kübler R (1992) Die Entwicklung der Heiden im Regierungsbezirk Stuttgart während des letzten Jahrzehnts (1980/1990). *Veröffentlichungen für Naturschutz und Landschaftspflege Baden-Württembergs* **67**:127–135.

Melber A (1999) Rote Liste der in Niedersachsen und Bremen gefährdeten Wanzen mit Gesamtartenverzeichnis, 1. Fassung, Stand 31.12.1998. *Informationsdienst Naturschutz Niedersachsen* **5**:1–44.

Naimi B (2014) usdm: Uncertainty analysis for species distribution models, R package version 1.1-12, http://usdm.r-forge.r-project.org/, http://r-gis.net

Nickel H (2003) The Leafhopper and Planthoppers of Germany (Hemiptera, Auchenorrhyncha): Patterns and strategies in a highly diverse group of phytophagous insects. Pensoft and Goecke & Evers, Sofia-Moscow and Keltern

Öckinger E, Lindborg R, Sjödin NE, Bommarco R (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography (Cop)* **35**:259–267. doi: 10.1111/j.1600-0587.2011.06870.x

Oksanen J, Blanchet FG, Kindt R, Minchin PR, Hara RBO, Simpson GL, Sólymos P, Stevens MHH, Wagner H (2013) vegan: Community Ecology Package. R package version 2.0-9, http://cran.r-project.org/package=vegan%20.

Ovaskainen O (2002) Long-term persistence of species and the SLOSS problem. *J Theor Biol* **218**:419–433. doi: 10.1006/yjtbi.3089

Pinheiro J, Bates D, DebRoy S, Sarkar D, R-Core-Team (2014) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-116, http://CRAN.R-project.org/package=nlme

Poschlod P, Kiefer S, Tränkle U, Fischer S, Bonn S (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Appl Veg Sci* **1**:75–91. doi: 10.2307/1479087

Poschlod P, WallisDeVries MF (2002) The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. *Biol Conserv* **104**:361–376. doi: 10.1016/S0006-3207(01)00201-4

Qian H, Shimono A (2012) Effects of geographic distance and climatic dissimilarity on species turnover in alpine meadow communities across a broad spatial extent on the Tibetan Plateau. *Plant Ecol* **213**:1357–1364. doi: 10.1007/s11258-012-0095-4

Remane R, Achtziger R, Fröhlich W, Nickel H, Witsack W (1997) Rote Liste der Zikaden in der Bundesrepublik Deutschland (Homoptera, Auchenorrhyncha). *Cicadina* **1**:243–249.

Rösch V, Tscharntke T, Scherber C, Batáry P (2013) Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *J Appl Ecol* **50**:387–394. doi: 10.1111/1365-2664.12056

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze E-D, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, et al (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**:553–556. doi: 10.1038/nature09492

Scherber C, Lavandero B, Meyer K, Perovic D, Visser U, Wiegand K, Tscharntke T (2012) Scale effects in biodiversity and biological control: methods and statistical analysis. In: Gurr GM, Wratten SD, Snyder WE, Read DMY (eds) Biodivers. Insect Pests Key Issues Sustain. Manag., First Edit. John Wiley & Sons, Ltd., Chichester, pp 123–138

Schüepp C, Herrmann JD, Herzog F, Schmidt-Entling MH (2011) Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia* **165**:713–721. doi: 10.1007/s00442-010-1746-6

Seybold S (2009) Schmeil-Fitschen: Flora von Deutschland und angrenzender Länder, 93rd edn. Quelle & Meyer, Heidelberg & Wiesbaden

Simberloff D (1988) The Contribution of Population and Community Biology to Conservation Science. *Annu Rev Ecol Syst* **19**:473–511.

Smith AC, Koper N, Francis CM, Fahrig L (2009) Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. *Landsc Ecol* **24**:1271–1285. doi: 10.1007/s10980-009-9383-3

Stoll P, Oggier P, Baur B (2009) Population dynamics of six land snail species in experimentally fragmented grassland. *J Anim Ecol* **78**:236–246. doi: 10.1111/j.1365-2656.2008.01478.x

Su JC, Debinski DM, Jakubauskas ME, Kindscher K (2004) Beyond species richness: community similarity as a seasure of cross-taxon congruence for coarse-filter conservation. *Conserv Biol* **18**:167–173. doi: 10.1111/j.1523-1739.2004.00337.x

Teichler K-H, Wimmer W (2007) Liste der Binnenmollusken Niedersachsens, http://niedersachsen.nabu.de/imperia/md/content/niedersachsen/schnecken/1.pdf

Tjørve E (2010) How to resolve the SLOSS debate: lessons from species-diversity models. *J Theor Biol* **264**:604–612. doi: 10.1016/j.jtbi.2010.02.009

Tjørve E, Tjørve KMC (2008) The species-area relationship, self-similarity, and the true meaning of the z-value. *Ecology* **89**:3528–3533. doi: 10.1890/07-1685.1

Tscharntke T, Steffan-Dewenter ID, Kruess A, Thies C (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol Appl* **12**:354–363. doi: 10.1890/1051-0761(2002)012[0354:COSHFT]2.0.CO;2

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, et al (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol Rev* **87**:661–685. doi: 10.1111/j.1469-185X.2011.00216.x

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, 4th edn. Springer, New York.

Wachmann E, Melber A, Deckert J (2004) Wanzen 2 - Tierw. Deutschlds., **75**: 1-294. Goecke & Evers, Keltern

Wachmann E, Melber A, Deckert J (2006) Wanzen 1 - Tierw. Deutschlds., **77**: 1-263. Goecke & Evers, Keltern

Wachmann E, Melber A, Deckert J (2007) Wanzen 3 - Tierw. Deutschlds., **78**: 1-272. Goecke & Evers, Keltern

Wachmann E, Melber A, Deckert J (2008) Wanzen 4 - Tierw. Deutschlds., **81**: 1-230. Goecke & Evers, Keltern

Supporting information

Fig. S1. Size frequency histogram of the fragments of calcareous grassland in the study area (districts of Göttingen and Northeim, Lower Saxony, Germany), based on Biotopkartierung Niedersachsen (1999).

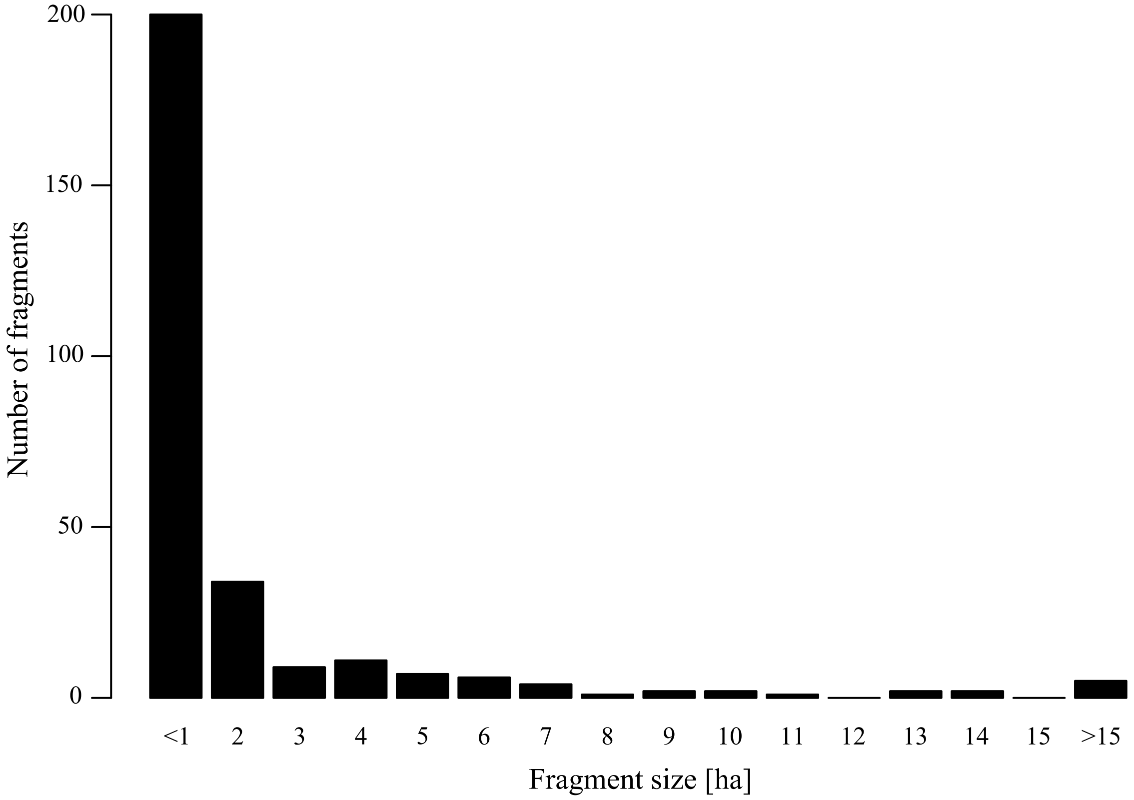


Fig. S2. Relationship between estimated (y-axis) and (specialist) species richness determined in the field (x-axis) of plants, leafhoppers, true bugs and snails on the 28 fragments of calcareous grassland. Closed circles: large fragments, open circles: small fragments. Estimated and determined species richness were highly correlated (see Table S2).

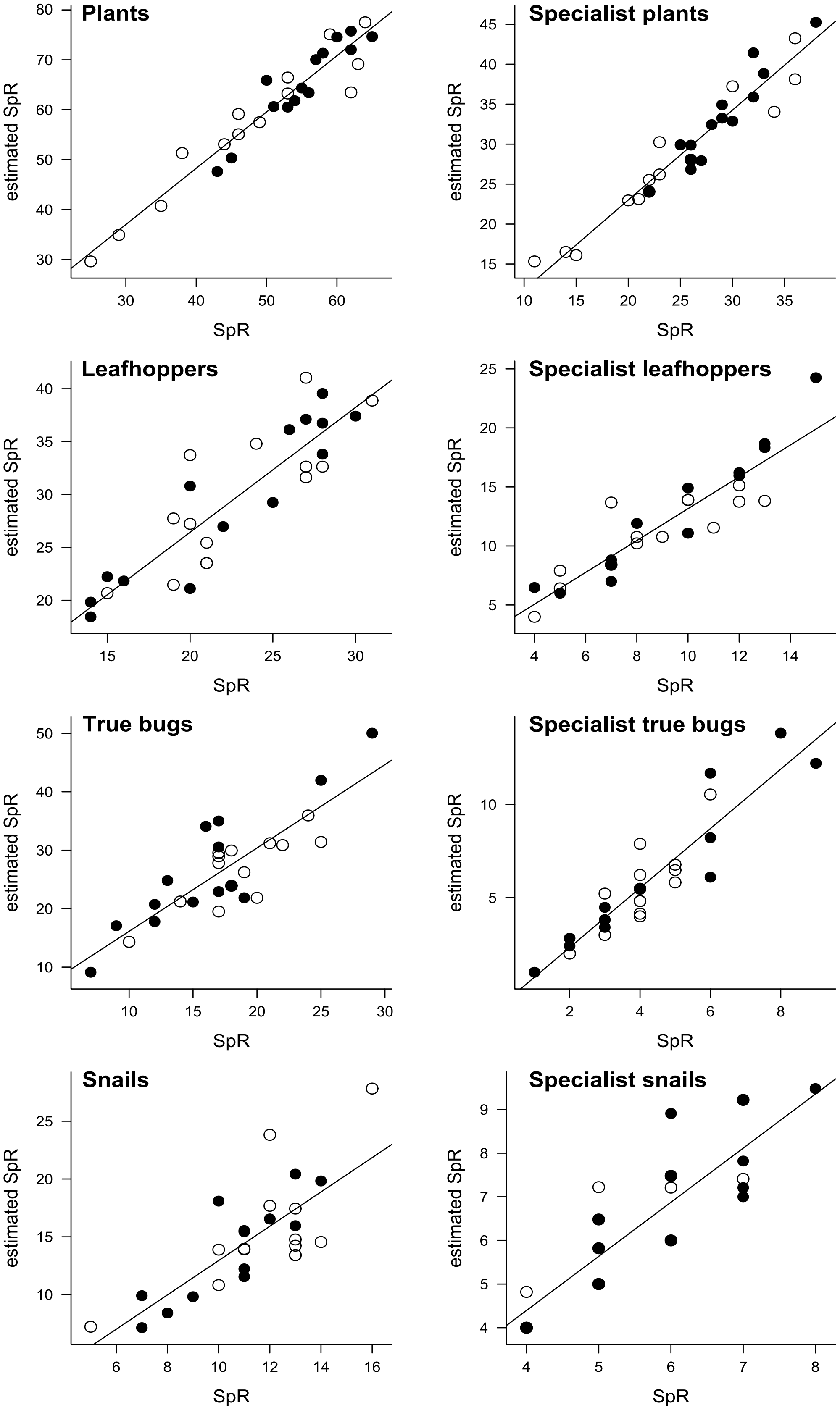


Fig. S3. Gradients of the explanatory variables used in the glms and RDAs.

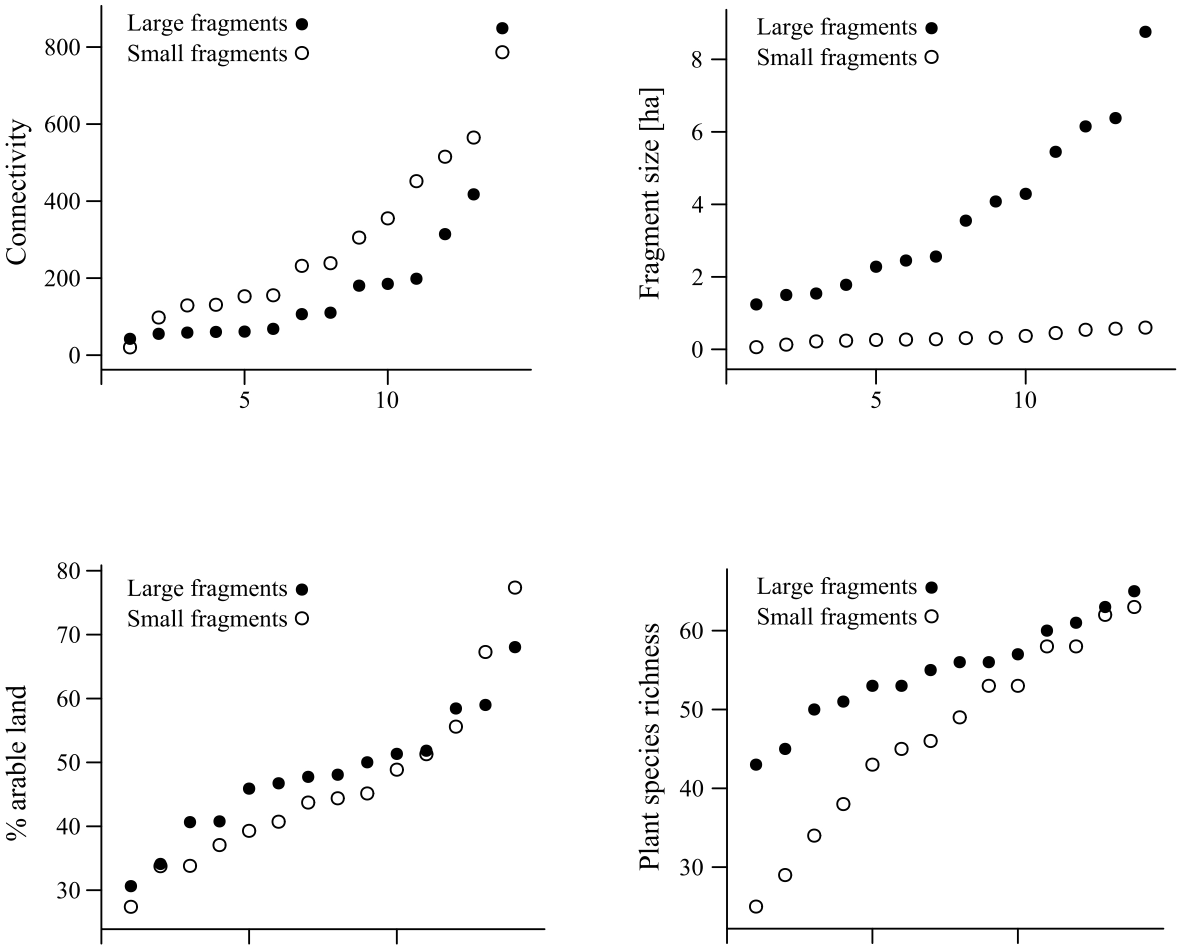


Table S1. Correlation matrix of community similarities between plants, leafhoppers, true bugs and snails (Mantel tests based on Pearson's product moment correlation). *P*-values <0.05 are depicted in bold characters and indicate significant similarity in community composition.

	Plants	Leafhoppers	True bugs	Snails
Plants				
Leafhoppers	**0.343**			
True bugs	**0.298**	**0.274**		
Snails	0.006	**0.193**	0.064	

Table S2. Fragment type (small (S) / large (L)), fragment size [ha], values of a connectivity index (Hanski et al., 2000), distance to the nearest fragment [km], percentage of arable land in a 500 m radius around the sites, (specialist) species richness of plants, leafhoppers, true bugs and snails and the corresponding percentage of the estimated SpR of the four taxa of the 28 fragments of calcareous grassland.

			Plants				Leafhoppers				True bugs				Snails			
Site	Fragment type	Size [ha]	overall SpR	% of estim. SpR	Specialist SpR	% of estim. SpR	overall SpR	% of estim. SpR	Specialist SpR	% of estim. SpR	overall SpR	% of estim. SpR	Specialist SpR	% of estim. SpR	overall SpR	% of estim. SpR	Specialist SpR	% of estim. SpR
L02	L	4.08	62	86.1	26	87.0	16	73.3	7	100.0	18	75.3	3	78.5	10	55.3	6	67.3
L03	L	1.50	51	84.1	26	92.7	28	76.2	10	67.1	19	86.9	6	98.4	11	89.9	7	97.1
L04	L	4.29	56	88.3	38	84.0	27	72.8	13	70.9	17	74.2	6	51.4	12	72.6	7	89.5
L06	L	8.76	43	90.3	27	96.7	14	70.6	8	67.2	7	76.7	3	67.0	11	95.2	6	100.0
L07	L	1.54	53	87.6	32	89.2	26	72.0	12	75.2	29	58.0	9	73.7	14	70.6	8	84.4
L08	L	2.56	50	75.9	29	83.0	20	94.7	10	90.3	13	52.4	3	78.5	11	70.8	7	75.9
L10	L	6.15	45	89.4	26	96.9	22	81.6	10	90.1	16	46.9	2	70.9	7	98.0	5	100.0
L14	L	2.45	62	81.8	22	91.5	14	75.9	4	61.7	9	52.7	2	70.9	8	95.1	7	100.0
L15	L	5.45	54	87.4	30	91.3	28	70.8	12	74.0	25	59.6	8	57.8	9	91.6	6	100.0
L16	L	6.38	65	87.1	29	87.2	30	80.2	15	61.9	15	71.0	1	100.0	13	63.7	6	80.2
L17	L	3.55	58	81.3	25	83.6	28	82.8	13	69.6	12	57.9	2	83.0	7	70.6	4	100.0
L18	L	1.24	55	85.5	28	86.3	25	85.5	7	83.2	17	55.6	6	73.0	11	71.2	5	77.2
L19	L	2.28	57	81.4	33	85.0	15	67.5	7	79.4	12	67.5	4	73.0	13	81.5	5	85.9
L20	L	1.78	60	80.5	32	77.2	20	64.9	5	83.3	17	48.6	3	88.0	12	72.6	6	100.0
S01	S	0.54	64	82.6	36	83.2	20	59.3	10	71.9	21	67.3	4	83.0	13	91.4	7	97.1
S02	S	0.57	35	85.9	15	93.1	19	68.5	9	83.6	17	58.7	4	64.3	16	57.5	7	75.9
S03	S	0.31	53	83.8	30	80.6	31	79.7	12	87.3	24	66.8	5	77.2	13	96.9	5	100.0
S04	S	0.22	46	83.5	23	87.8	24	69.0	7	83.2	17	61.2	4	83.0	12	50.4	5	77.2
S07	S	0.13	49	85.2	26	92.7	28	85.8	12	79.3	17	87.1	4	96.6	10	92.4	4	100.0
S08	S	0.28	59	78.6	22	91.5	21	89.3	7	51.2	18	75.3	4	100.0	13	74.5	5	85.9
S09	S	0.32	46	77.8	22	86.2	27	65.8	8	74.3	22	71.2	5	73.9	11	79.1	6	80.2
S10	S	0.26	62	97.7	34	99.9	21	89.3	5	78.0	25	79.6	4	73.0	13	88.0	4	100.0
S12	S	0.45	63	91.1	36	94.4	27	82.7	13	94.1	20	91.5	6	56.9	14	96.2	7	94.5
S14	S	0.06	53	79.7	21	90.8	21	82.5	4	100.0	17	57.5	3	100.0	11	78.8	4	100.0
S17	S	0.60	29	83.0	20	87.1	15	72.5	8	78.3	10	69.8	3	57.5	10	72.0	5	69.3
S21	S	0.37	38	74.0	23	76.0	20	73.4	10	72.0	18	60.1	4	50.7	5	69.3	4	83.0
S25	S	0.24	25	84.4	11	71.8	19	88.5	11	95.2	14	65.9	5	85.9	13	96.9	5	100.0
S26	S	0.27	44	82.9	14	84.8	27	85.4	5	63.2	19	72.4	2	100.0	12	67.9	6	100.0
	mean L		55.1	84.7	28.8	88.0	22.4	76.3	9.5	76.7	16.1	63.1	4.1	76.0	10.6	78.5	6.1	89.8
	mean S		47.6	83.6	23.8	87.1	22.9	78.0	8.6	79.4	18.5	70.3	4.1	78.7	11.9	79.4	5.3	90.2

Table S3. Correlations (Spearman's rho) between estimated and determined species richness for large and small fragments respectively.

Large fragments	**rho**	**S**	***P***
Plant SpR	0.91	40.54	< 0.001
Specialist plant SpR	0.91	40.26	< 0.001
Leafhopper SpR	0.91	39.25	< 0.001
Specialist leafhopper SpR	0.97	15.14	< 0.001
True bug SpR	0.80	93.01	< 0.001
Specialist true bug SpR	0.98	10.15	< 0.001
Snail SpR	0.82	83.25	< 0.001
Specialist snail SpR	0.81	87.44	< 0.001

Small fragments	**rho**	**S**	***P***
Plant SpR	0.97	15.03	< 0.001
Specialist plant SpR	0.98	8.53	< 0.001
Leafhopper SpR	0.69	140.18	0.006
Specialist leafhopper SpR	0.84	70.96	< 0.001
True bug SpR	0.76	108.79	0.002
Specialist true bug SpR	0.75	112.89	0.002
Snail SpR	0.56	198.43	0.036
Specialist snail SpR	0.90	45.78	< 0.001

Table S4. Correlations between explanatory variables (Spearman's rho). If |rho| ≥ 0.6, a strong correlation between two variables can be assumed. Distance: the distance (in km) to the nearest neighbouring fragment, Conn. Index: a connectivity index described by Hanski et al. (2000), % arable: landscape composition, i.e. the percentage of arable land within a 500 m radius around each fragment, Plant SpR: plant species richness per fragment, Fragment type: small or large fragment, Fragment size: Size of the fragments in ha.

	Distance	Conn. Index	% arable	Fragment size	Fragment type
Distance					
Conn. Index	-0.78				
% arable	0.21	-0.17			
Fragment size	0.27	-0.33	0.19		
Fragment type	0.16	-0.20	0.22	0.87	
Plant SpR	0.42	-0.32	-0.10	0.30	0.24

Table S5. Variance inflation factors (VIFs) of the four explanatory variables used in the models (Fragment type: small or large fragment, Conn. Index: a connectivity index described by Hanski et al. (2000), % arable: landscape composition, i.e. the percentage of arable land within a 500 m radius around each fragment, Plant SpR: plant species richness per fragment). A VIF greater than 10 is a signal that the model has a collinearity problem.

Expl. variables	VIF
Frangment type	1.20
Conn. Index	1.09
% arable	1.02
Plant SpR	1.20

Table S6. Test for spatial autocorrelation between location of study site and species richness (SpR) and between location of study site and community composition (Mantel tests based on Pearson's product-moment correlation). There is no indication for spatial autocorrelation. Shown are r- and *P*-values.

	location vs. SpR		location vs. community composition	
	r	*P*	r	*P*
Plants	-0.010	0.829	0.039	0.201
Leafhoppers	-0.054	0.986	0.064	0.119
True bugs	-0.115	0.481	0.096	0.234
Snails	0.000	0.434	-0.049	0.695

Table S7. Correlations between values of the connectivity index at different spatial scales.

	500 m	1000 m	1500 m	2000 m
500 m				
1000 m	0.90			
1500 m	0.89	0.97		
2000 m	0.91	0.96	0.98	

Table S8. Asymptotic species richness in large and small fragments for specialist and generalist species. We fitted nonlinear mixed-effects Michaelis-Menten models to individual-based rarefied species richness data for large and small calcareous grasslands. Asymptote, the estimate of asymptotic species richness (for large numbers of individuals); constant, the Michaelis-Menten constant (i.e. the number of individuals for which half of the asymptotic species richness value is reached). Δ, the difference in parameter values between large and small fragments. Positive values of Δ indicate more species in small fragments. Estimate, the estimated number of species; SE, 1 standard error of the mean.

		All Species					Specialists				
		Estimate	SE	DF	t-value	*P*	Estimate	SE	DF	t-value	*P*
Plants	Asymptote (Large)	89.39	2.19	217	40.92	**<0.001**	42.93	1.14	217	37.79	**<0.001**
	Δ Asymptote (Small)	42.07	3.13	217	13.42	**<0.001**	14.18	1.62	217	8.76	**<0.001**
	Constant (Large)	65.97	2.18	217	30.32	**<0.001**	27.94	1.27	217	22.07	**<0.001**
	Δ Constant (Small)	51.42	3.24	217	15.86	**<0.001**	19.19	1.84	217	10.42	**<0.001**
Leafhoppers	Asymptote (Large)	45.75	1.26	217	36.20	**<0.001**	19.97	1.33	217	15.08	**<0.001**
	Δ Asymptote (Small)	26.87	1.80	217	14.94	**<0.001**	6.29	1.87	217	3.36	**0.001**
	Constant (Large)	178.00	10.94	217	16.27	**<0.001**	89.29	8.86	217	10.08	**<0.001**
	Δ Constant (Small)	84.39	15.51	217	5.44	**<0.001**	21.61	12.54	217	1.72	0.086
True bugs	Asymptote (Large)	43.08	2.13	217	20.19	**<0.001**	10.92	1.64	217	6.66	**<0.001**
	Δ Asymptote (Small)	14.57	3.01	217	4.84	**<0.001**	3.64	2.23	217	1.63	0.104
	Constant (Large)	92.32	8.47	217	10.90	**<0.001**	20.88	9.52	217	2.19	**0.029**
	Δ Constant (Small)	26.37	11.96	217	2.21	**0.029**	24.19	13.78	217	1.76	0.08
Snails	Asymptote (Large)	16.34	0.80	217	20.48	**<0.001**	7.92	0.19	217	41.65	**<0.001**
	Δ Asymptote (Small)	5.15	1.13	217	4.56	**<0.001**	0.05	0.27	217	0.20	0.843
	Constant (Large)	91.58	10.24	217	8.95	**<0.001**	41.26	5.84	217	7.06	**<0.001**
	Δ Constant (Small)	29.09	14.48	217	2.01	**0.046**	10.74	8.27	217	1.30	0.196

Chapter 4: Local and landscape management affects trait-mediated biodiversity of nine taxa on small grassland fragments

Graphosoma lineatum (Pentatomidae)

Published as:
Kormann, U., Rösch, V., Batáry, P., Tscharntke, T., Orci, K.M., Samu, F., & Scherber, C. (2015) Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. *Diversity and Distributions*. doi: 10.1111/ddi.12324

Abstract

Aim Biodiversity across the globe is heavily eroded by intensified management, at local and landscape scales. Species communities of calcareous grasslands, which are among Europe’s most diverse habitats, are severely threatened by the cessation of appropriate traditional management, loss of habitat connectivity and simplification of the surrounding landscape. However, our understanding of these often interrelated factors remains limited, in particular for trait-mediated responses across taxa. Here, we test the independent effects of local management (grazing, mowing and abandonment), habitat connectivity (measured by a connectivity index) and landscape complexity (indicated by the percentage of arable land) on nine taxa: plants, butterflies, bees, grasshoppers, hoverflies, spiders, true bugs, rove beetles and leafhoppers on small semi-natural calcareous grassland remnants (< 1 ha).

Location Central Germany

Methods We use a joint analysis across taxa to identify general and trait-mediated responses (body size and Red List status) in species richness, abundance and community composition.

Results We identified three key drivers of local diversity patterns: First, an increasing proportion of arable land from 10 % to 80 % led to a 29 % loss of overall species richness. Second, despite differences between taxa, increasing habitat connectivity generally enhanced species richness. Connectivity effects were more accentuated in the large species per taxon, which can be expected to be good dispersers. Finally, grazing reduced species richness and abundance much more than annual mowing or short-term abandonment (5–15 years), in particular for red-listed species. We attribute this to plant resource removal through overgrazing and trampling.

Main conclusions For the conservation management of small calcareous grasslands, we advocate an alternating strategy of mowing or lenient grazing and short-term abandonment, prioritizing connected fragments surrounded by diverse landscapes. Despite taxon-specific responses, our study across nine taxa demonstrates universal, trait-mediated effects of management, landscape complexity and connectivity on local biodiversity in fragmented communities.

Keywords: Calcareous grasslands, community dissimilarity, connectivity, habitat fragmentation, landscape composition, multitaxon approach

Introduction

Habitat fragmentation, habitat loss and agricultural intensification are major reasons for biodiversity decline worldwide (Sala et al., 2000; Fahrig, 2003; Fischer & Lindenmayer, 2007), causing reductions in habitat area and connectivity. Small or isolated fragments are reached by fewer immigrants than large or connected ones (MacArthur & Wilson, 1967; Losos & Ricklefs, 2010). Furthermore, small fragments may experience higher extinction rates. The type of land use between fragments (matrix) also affects dispersal and persistence of species in fragmented landscapes. Simple landscapes with high proportions of arable land are a hostile matrix for many organisms (Ewers & Didham, 2006; Prugh et al., 2008). However, matrix types may influence permeability (Eycott et al., 2012; Öckinger et al., 2012), as shown e.g. for mass flowering crops (Holzschuh et al., 2013).

In fragmented landscapes, surprisingly little is known about the effects of landscape factors like habitat connectivity and matrix complexity on invertebrate communities across taxa (Prugh et al., 2008). Previous studies focussed on few taxa with a bias on butterflies and bees (e.g. van Swaay, 2002; Krauss et al., 2003; Brückmann et al., 2010, but see Zulka et al., 2013) and were rarely designed to distinguish between local management, connectivity and landscape complexity (but see Sjödin et al., 2007; Pöyry et al., 2009). This lack of knowledge is particularly accentuated for trait-mediated patterns across taxa (Öckinger et al., 2010). These may be life history traits like body size or conservation-relevant characteristics such as Red List status. Body size can mediate the response of species to habitat loss, predicting dispersal capability in many taxa (Jenkins et al., 2007; Öckinger et al., 2010; Sekar, 2012).

In Central Europe, calcareous grasslands are among the most species-rich habitat types for both plants and invertebrates. Over centuries, calcareous grasslands have been maintained through traditional extensive (sheep) grazing and, less frequently, by mowing (Wilmanns, 1993). With increasing agricultural intensification, management has become progressively uneconomical for farmers. Therefore, up to 90 % of calcareous grasslands have been lost over the past decades due to changed management (Poschlod & WallisDeVries, 2002). As a result, the distribution of the remaining habitat patches is nowadays highly fragmented. Accordingly, many species occurring on these grasslands have been categorised as threatened in Red Lists (Binot-Hafke et al., 2011). The current conservation of calcareous grasslands primarily focuses on local habitat management, aimed at mimicking traditional management. As rotational shepherding has become scarce, the remnants are often kept open by grazing, mowing or shrub removal. Contrastingly, the composition of the landscape surrounding a habitat fragment is often disregarded (Zulka et al., 2013).

In the study area (southern Lower Saxony, Central Germany) the landscape surrounding calcareous grasslands is intensively managed. More than 70 % of all fragments are small (<1 ha, Fig. S1), yet of high conservation value due to their high biodiversity (Tscharntke et al., 2002; Rösch et al., 2013) and their potential role as stepping stones (Saura et al., 2014). Therefore, in order to avoid the confounding influence of differences in fragment size, we here focus on small fragments (<1 ha). We set up a landscape-scale mensurative experiment to disentangle the effects of local management, landscape complexity and connectivity on nine taxa (plants, butterflies, bees, grasshoppers, hoverflies, spiders, true bugs, rove beetles and leafhoppers).

In particular, we test the following hypotheses:

1) Species richness, abundance and community composition change with the composition and connectivity of the surrounding landscape and depend on the type of local management.
2) Body size (as a proxy for dispersal capacity) indicates the sensitivity to landscape scale factors, i.e. the larger species of a taxon can benefit more from connectivity than the smaller ones.
3) Negative effects of management cessation, decreasing connectivity and landscape simplification are more pronounced in red-listed species.

Methods

Study area

The study area was situated in Central Germany, southern Lower Saxony (51.5°N, 9.9°E, see Map S1 in Supporting Information) in the districts of Göttingen and Northeim.

About 30 % of the area is intensively managed arable land, with wheat, maize, sugar beet and oilseed rape grown in crop rotation. Forest fragments and grasslands make up another 40 % of the landscape. For the present study, we focused on fragments of calcareous grasslands (*Mesobrometum erecti* Koch 1926 (Ellenberg & Leuschner, 2010)) that are patchily distributed across the landscape (mainly on South-facing slopes). These grasslands are either mown or extensively grazed, or management has been abandoned. Mowing occurs once a year, usually in autumn or winter to ensure successful ripening of plant seeds. Grasslands are grazed predominantly by ruminants such as sheep and goats, but to a lesser extent also by horses or cattle, starting in the middle of June at the earliest. Grazing frequently results in trampling, areas of open soil and in the removal of a large proportion of the available plant material. Management of abandoned fragments used in our study ceased between five and 15 years ago. We did not include fragments that had been abandoned for longer, since they did not display the characteristics of calcareous grasslands anymore.

Study design

The study was conducted between April and September 2011. A total of 30 small fragments of calcareous grasslands (0.045 – 0.69 ha, mean = 0.3 ha) were selected from a total pool of about 200 potential fragments using digital maps (ATKIS-DLM 25/1 Landesvermessung und Geobasisinformationen Niedersachsen 1991–1996, Hanover, Germany) in ArcGIS 10.0 (ESRI Geoinformatik GmbH, Hanover, Germany) and extensive field surveys in the study area. Sites were selected to be either grazed, mown or abandoned (10 each). Fragments were grazed by single species (sheep, goats, cows, highland cattle, ponies or horses). For the type of livestock used on the grazed fragments see Table S3. Grazing intensity varied greatly from a few days to months.

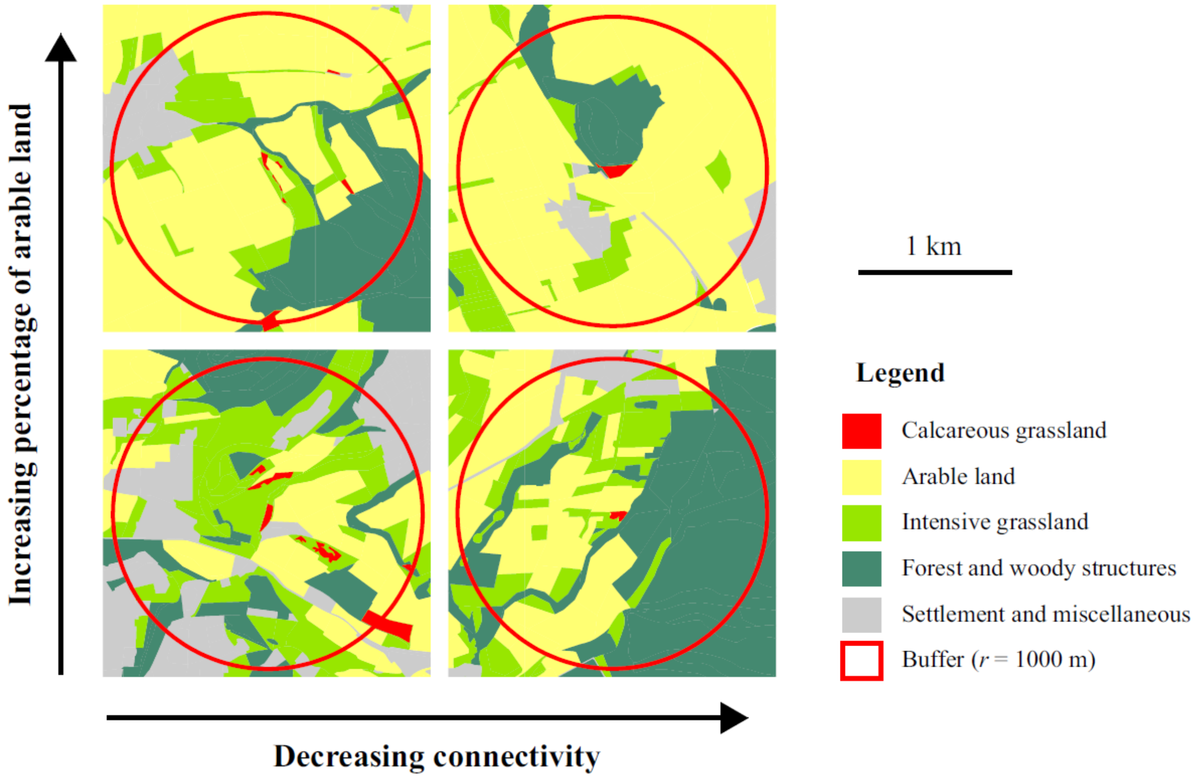
The fragments were selected with randomization along two orthogonal gradients (Fig. 1, Fig. S2, Table S3): (1) A landscape composition gradient, i.e. increasing percentage of arable land within a radius of 1000 m around fragments (9 – 78 %, mean = 44 %). We chose a radius of 1000 m since we expected some taxa to be dispersal limited (e.g. leafhoppers, plants, true bugs) so that the close surroundings of the fragments would be most important for them. Several previous studies have shown that the percentage of arable land (used here) is highly correlated with landscape Shannon diversity in the study region (e.g. Thies et al., 2003; Roschewitz et al., 2005). (2) A gradient in habitat connectivity, measured by a connectivity index (CI) as described in Hanski et al. (2000):

$$CI_i = \Sigma \exp(- \alpha d_{ij}) A_j^{\beta} \quad \text{(equation 1)}$$

where A_j is the area (in m^2) of the j^{th} neighbouring fragment and d_{ij} is the edge-to-edge distance (in m) between focal fragment i and neighbouring fragment j. α is a species-specific parameter describing species' dispersal ability and β is a parameter describing the scaling of immigration. Since we applied the connectivity index to entire communities containing many taxa, both scaling parameters α and β were set to the commonly used value of 0.5 (e.g. Brückmann et al., 2010). Connectivity indices calculated with $\alpha = 0.5$ or $\alpha = 1$ were highly correlated (Spearman's rho = 0.997, p = <0.001). We included all fragments of calcareous grassland that were located a radius of 1000 m around the focal fragment. If only part of a fragment was inside the 100 m buffer and it continued outside it, we included the whole fragment area, weighted by the shortest distance to the central fragment. Roadsides and field margins with plant species typical for calcareous grasslands (Krauss et al., 2003) were uncommon and were not taken into account. To ensure that fragments exhibited the characteristics of calcareous grasslands, we only included fragments that harboured more than five of the plant species that are characteristic for calcareous grasslands in the study area (Krauss et al., 2003). The values of the connectivity index ranged between 0 and 443 (mean = 121) with larger values indicating higher levels of connectivity.

The explanatory variables habitat connectivity and landscape complexity were weakly, but non-significantly correlated (following Dancey and Reidy (2004), Pearson correlation, r = -0.19, t = -1.05, d.f. = 28, *P* = 0.303, Fig. S2).

Fig. 1. Illustration of the study design, showing calcareous grasslands with high (left) and low (right) levels of habitat connectivity and low (above) and high (below) levels of landscape complexity (measured as percentage of arable land).



Sampling methods

At the beginning of June 2011, we recorded the vegetation (only vascular plants) in four botanical plots per fragment (1 × 5 m). The plots were well spread across the fragments, about 10-15 m away from each other within a fragment (minimum distance 3 m); fragment edges were avoided.

Leafhoppers (Hemiptera: Auchenorrhyncha), true bugs (Hemiptera: Heteroptera) and spiders (Arachnida) were sampled by suction sampling (modified SH 56 leaf blower, Stihl, Waiblingen, Germany) on the botanical plots (20 suction pulses per plot, i.e. 80 pulses per fragment) in dry weather on three occasions in 2011 (early June, late July, early September). Transects were located on the botanical plots but exceeded them (length approximately 10 m). Spiders were sampled by both suction sampling and pitfall trapping (see below) to improve coverage of species sampled (Standen, 2000).

Hoverflies (Diptera: Syrphidae) and bees (Hymenoptera: Apiformes) were surveyed with three pan traps per fragment during two three-day rounds (mid June, mid July). Each trap consisted of a yellow plastic cup (23 cm diameter, filled with salt water), treated with UV-reflecting paint and mounted at vegetation height to maximize trapping efficiency (Stephen & Rao, 2005; Westphal et al., 2008). Traps were separated by at least 15 m from the next trap and from the fragment edge (Westphal et al., 2008), to minimize potential interactions between traps and edge effects.

We sampled butterflies (Lepidoptera: Hesperiidae, Papilionidae and Zygaenidae) using standardized visual transect walks (Krauss et al., 2003). Fragments were visited four times (late May – early September) under suitable weather (temperature > 18 ° C, wind speed < 4 Beaufort, < 50 % cloud cover, 10:00 – 17:30). Transects on each fragment were 180 m long and divided into three non-overlapping 60-m subtransects. Butterflies were sampled during four minutes per subtransect using a butterfly net within a 5-m wide band, identified and released immediately or collected for identification.

We recorded grasshoppers (Orthoptera: Caelifera, Ensifera) during their peak density in late summer. Each fragment was sampled on two occasions (late July, late August) under dry and warm conditions (> 22 ° C, cloud cover < 50 %, 10:00 – 18:00). We applied a box-quadrat procedure for sampling, using a foldable wooden construction (1 x 1 m) with gauze sides (70 cm high) that was repeatedly placed onto the vegetation. This method yields more consistent and unbiased abundance estimates than sweep netting (Gardiner et al., 2005; Gardiner & Hill, 2006). Grasshoppers were collected in five 1 × 1 m squares near each botanical plot, resulting in 40 1 × 1 m squares per fragment in total. Only adult specimens were determined to species level and incorporated into further analyses.

Rove beetles (Coleoptera: Staphylinidae) and spiders were sampled twice with pitfall traps for seven days each, in early August and in late August/early September. We employed three pitfall traps per fragment (plastic cups filled with salt water & detergent, 12 cm diameter, plastic roof) with >15 m distance from each other and >15 m away from the fragment edge.

All specimens caught (except butterflies released after identification) were transferred into ethanol (70 % vol.) and identified to species level. Only adult specimens were determined and used for later analyses.

For leafhoppers and true bugs, species feeding on woody host plants were excluded, except if host tree saplings were present in botanical plots. Species feeding on woody plants whose larvae fed on herbs or grasses were included in the analysis.

For species with morphologically similar female specimens (e.g. *Ribautodelphax, Anaceratagallia, Psammotettix*) (Biedermann & Niedringhaus, 2004), species identity was inferred from male specimens; if this was not possible, identification stopped at genus level. If males of more than one species of a genus were present, the number of females was assumed to mirror that of males.

Specification of traits

All taxa were subdivided into habitat specialists and generalists, except for rove beetles for which no suitable literature was available. Plant habitat specialization was defined following Krauss et al. (2003). Arthropod habitat specialization was derived from (i) habitat requirements typical for calcareous grasslands (i.e. warm, dry habitat conditions; short, grazed swards; open soil) and (ii) diet preferences (i.e. host plants occurring exclusively on calcareous grasslands), based on published work and expert opinions (see References S1). Species were classified as habitat specialists if conditions (i) and/or (ii) were fulfilled, whereas it was classified as a generalist if neither (i), nor (ii) were fulfilled.

Body sizes of species was defined as body length (from head to end of abdomen) taken from published literature (Supplementary References S1). For species with sexually dimorphic body sizes, we used the mean body size of both sexes. For butterflies, we used median forewing length as this was a better indicator of dispersal ability. Species larger than the taxon-specific median body size were considered large; all others were considered small. The Red List status was based on the most recent and regional Red List available (Remane et al., 1997; Melber, 1999; Garve, 2004; Binot-Hafke et al., 2011; Westrich et al., 2011).

Statistical analyses

Species richness and abundance of the nine taxa were summed over transects, vegetation plots and pan traps. Arthropod species richness and abundance were summed over the sampling occasions.

We performed four types of analyses: (1) Analysis of species richness and abundance for every taxon separately and cumulated over all taxa. (2) Redundancy analysis for all taxa separately to assess changes in community composition. (3) A hierarchical analysis including all taxa simultaneously to determine general trends in species richness and abundance. (4) Two hierarchical analyses including all taxa simultaneously to determine if richness patterns are generally modified by relative body size and Red List status, respectively.

(1) Species richness and abundance were analysed for every taxon separately and cumulated over all taxa (additive species richness). Depending on the distribution of the response variables (assessed using R package *fitdistrplus,* URL: http://cran.r-project.org/web/packages/fitdistrplus/index.html), we fitted either generalized linear models with negative binomial or Poisson errors (*glm.nb* or *glm*, R package *MASS* (Venables & Ripley, 2002)) or linear models (see Table S1), starting with the following explanatory variables: (1) habitat connectivity, measured as described in Equation 1, (2) the percentage of arable land in a 1000-m buffer around each fragment and (3) habitat management (abandonment, grazing or mowing), including an interaction between connectivity and arable land. The families and link functions used in generalized linear models were selected based on residual deviance. In addition, we divided residual deviance by residual degrees of freedom to assess overdispersion. Model selection was then done using an automated stepwise selection procedure based on AICc (function *stepAICc* based on function *stepAIC* (R package *MASS* (Venables & Ripley, 2002), but corrected for small sample sizes, see URL: http://wwwuser.gwdg.de/~cscherb1/stepAICc.txt). Multiple comparisons between management types were conducted using the *glht* function in R package *multcomp* (Hothorn et al., 2008). Models showed no spatial autocorrelation of the residuals (i.e. Moran's I was > 0.05).

(2) For the nine taxa, partial redundancy analyses (RDAs) with all three explanatory variables (management, connectivity and percentage of arable land) were performed with function *rda* from R package *vegan* (Oksanen et al., 2013). We performed four RDAs: one with each of the explanatory variables, with the two remaining ones as conditional variables, and an ordinary RDA including all three variables. Interactions between explanatory variables were not tested. Prior to analysis, community data matrices were Hellinger-transformed, weigting rare species lower (Legendre & Gallagher, 2001). A permutation test with 999 permutations with function *permutest* from R package *vegan* (Oksanen et al., 2013) was used to asses statistical significance.

(3) To identify general patterns of species richness across all taxa, we ran linear mixed models (Pinheiro et al., 2014) including all taxa simultaneously. In such a joint analysis, all taxa contribute equally to identify general responses, independent of overall species richness. This is in contrast to the analysis of cumulated species richness described above, which is strongly influenced by species-rich taxa.

We standardized species richness per taxon by dividing it by the taxon's mean species richness across all fragments. The resulting value reflects the relative increase in species richness, compared to the average species richness of the taxon, and can be compared between taxa. We fitted linear mixed-effects models to standardized species richness (function *lme*, R package *nlme* (Pinheiro et al., 2014)), using fragment as a random factor. Note that because taxon was the lowest level in the hierarchy, it was not included in the random-effects part of the model as this would have saturated the model with random effects. Taxon was included as a fixed factor into the maximal model. Heteroscedasticity was accounted for by an exponential variance function, where the variance was an exponential function of the fitted values (weights = varexp()). Models with and without variance function were fitted using restricted maximum likelihood; AICc values indicated that variance functions considerably improved model fit.

In the fixed-effects part of the models, we started model selection with the same set of explanatory variables as for the taxon-specific models, but included interactions with taxon. Model selection was done using *stepAICc* for models fit by maximum likelihood.

(4) Finally, we fitted two linear mixed effects models to test if explanatory variables affected species richness differently for small vs. large species of a taxon, and red-listed vs. unthreatened species of a taxon. Standardisation of species richness per taxon and model selection were performed as described above. In addition to management, connectivity and proportion of arable land, we included interactions of size class (large/small) or Red List status (red-listed/unthreatened) with all other explanatory variables and their interactions. Fragment was treated as a random factor. Taxon was included as a fixed and not as a random factor. We ran additional models including a spatial correlation structure of the form "correlation=corCompSymm(form=~X+Y)". However, these models showed similar parameter values to those without correlation structure. Further, models with spatial correlation had consistently higher AICc values than those without (deltaAICc > 2).

For consistency, we opted to not include fragment area in any of our analyses, as some of the models did not converge when fragment area was included.

Results

On the 30 calcareous grassland fragments we recorded 604 species (154 specialists, 360 generalists) with 19696 arthropod individuals (8016 specialists, 11680 generalists) within the nine taxa. The most species-rich taxon was plants with 148 species, followed by spiders (83 species), bees and true bugs (82 and 80 species, respectively). The least diverse taxon was grasshoppers with only 10 species (Table S2).

In the analysis of abundance and species richness of all taxa combined and of each of the nine taxa individually we found that increasing the percentage of arable land always tended to negatively affect species richness (all nine taxa) and in most cases abundance (all arthropod taxa except hoverflies and rove beetles) (Table 1, Fig. S3, Table S4).

Management significantly changed community composition of all taxa combined as well as for most taxa individually (except for grasshoppers, rove beetles and hoverflies, Fig. 2, Table 2). In particular, the three management types harboured three distinct communities, both for habitat generalists and habitat specialists. Except for hoverflies, where the abundance of species with aphidophagous larvae was increased in landscapes with a high proportion of arable land, the surrounding landscape did not have an effect on community composition.

Among the three management types, grazing tended to reduce both species richness and abundance across arthropod taxa (Fig 3a, Table 3). The only case where grazing had a positive effect compared to abandonment was for bee species richness and abundance. In some arthropod taxa (butterflies, true bugs, spiders, leafhoppers), species richness and/or abundance were increased by abandonment (Table 1, Fig. S3, Table S4). Plant species richness was not affected by management.

Accumulated species richness was strongly reduced in simplified landscapes (-29 %, Table 1, Fig. S3). Similarly, standardized species richness per taxon decreased in simplified landscapes (Fig. 3b, Table 4). Furthermore, standardized species richness also generally increased with connectivity, but this effect depended on the taxon (Fig. 3c, Table 3). In contrast to all other taxa, species richness of hoverflies and leafhoppers slightly decreased with increasing connectivity (Fig. 3c). Furthermore, the connectivity effect was modified by body size: The number of large-bodied species within each taxon significantly increased with increasing connectivity, whereas the number of small-bodied species per taxon did not (Fig. 4a, Table 4). Finally, grazing had a much stronger negative effect on red-listed species than on unthreatened species (Fig. 4b, Table 5). Interactions between management, proportion of arable land and connectivity was never retained in the best models in any analysis.

Table 1. Generalized linear models showing effects of landscape context (% arable land), connectivity (Equation 1) and management on the abundance and species richness of all species, specialists and generalists. For management, successive differences between treatment levels are shown (g: grazed, m: mown, a: abandoned). The table shows parameter estimates on the scale of the linear predictor. Note that differences between management types are Tukey's pairwise comparisons (ignoring covariates) calculated using the glht function (R package multcomp (Hothorn et al., 2008)). Only variables included in the final models are shown. P-values < 0.05 are depicted in bold characters.

Abundance	All taxa				Specialists				Generalists			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	6.49	0.06	110.00	**<0.001**	6.24	0.32	19.64	**<0.001**	5.73	0.08	73.66	**<0.001**
% Arable land					-0.02	0.01	-2.24	**0.025**				
Connectivity												
Management g-a									-0.35	0.11	-3.14	**0.005**
Management m-a									-0.05	0.11	-0.49	0.878
Management m-g									0.29	0.11	2.65	**0.022**

Species richness	All taxa				Specialists				Generalists			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	5.15	0.07	68.75	**<0.001**	3.98	0.14	29.07	**<0.001**	4.59	0.08	55.56	**<0.001**
% Arable land	-0.01	0.002	-3.08	**0.002**	-0.005	0.003	-1.65	0.099	-0.01	0.002	-2.98	**0.003**
Connectivity												
Management g-a												
Management m-a												
Management m-g												

Fig. 2. RDA plots for species composition of all species, specialists and generalists showing the effect of management with minimum convex polygons (dashed lines). Closed circles: abandoned fragments, open circles: grazed fragments, triangles: mown fragments. Plants: Brapin - *Brachypodium pinnatum*, Brimed - *Briza media*, Fesovi - *Festuca ovina*, Leohis - *Leontodon hispidus*, Leuvul - *Leucanthemum vulgare*, Medlup - *Medicago lupulina*, Thypul - *Thymus pulegioides*, Bees: Andnig - *Andrena nigroaena*, Lascal - *Lasioglossum calceatum*, Laspau - *Lasioglossum pauxillum*, Butterflies: Aphhyp - *Aphantopus hyperantus*, Manjur - *Maniola jurtina*, Melgal - *Melanargia galathea*, Pienap - *Pieris napi*, Zygcar - *Zygaena carniolica*, Zyglon - *Zygaena lonicerae*, True bugs: Bersig - *Berytinus signoreti*, Copscu - *Coptosoma scutellatum*, Halapt - *Halticus apterus*, Myrmir - *Myrmus miriformis*, Spiders: Aulalb - *Aulonia albimana*, Euofro - *Euophrys frontalis*, Ozypul - *Ozyptila pullata*, Hoverflies: Euplun - *Eupeodes luniger*, Scapyr - *Scaeva pyrastri*, Leafhoppers: Acaspi - *Acanthodelphax spinosa*, Adamul - *Adarrus multinotatus*, Anaper - *Anakelisia perspicillata*, Arolon - *Arocephalus longiceps*, Eupnot - *Eupteryx notata*, Kelirr - *Kelisia irregulata*, Moccro - *Mocydia crocea*, Neoalb - *Neophilaenus albipennis*, Psacep - *Psammotettix cepalotes*, Ribpun - *Ribautodelphax pungens*, Tursoc - *Turrutus socialis*.

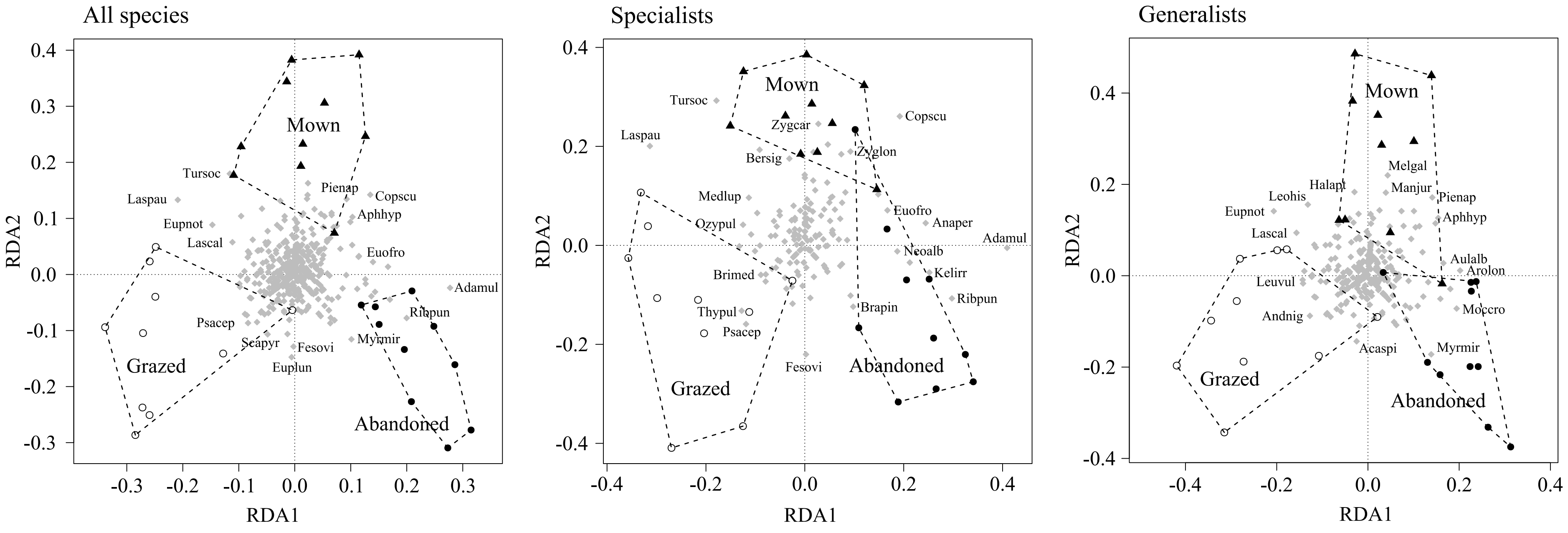


Table 2. Results of RDA analyses: influence of landscape composition (% arable land), connectivity and management type on the community composition of all species, specialists, generalists, bees, butterflies, grasshoppers, true bugs, plants, spiders, rove beetles, syrphid flies and leafhoppers. *P*-values < 0.05 are in bold characters.

		partial RDA % of variation	F	*P*			partial RDA % of variation	F	*P*
All taxa	% Arable land	3.2	0.98	0.500	True bugs	% Arable land	3.1	0.95	0.537
	Connectivity	3.2	0.98	0.517		Connectivity	2.3	0.66	0.706
	Management	11.6	1.77	**0.001**		Management	11.5	1.76	**0.001**
	Total	18.4	1.41	**0.001**		Total	14.4	1.05	0.374
Generalists	% Arable land	3.4	1.02	0.430	Plants	% Arable land	3.1	0.93	0.560
	Connectivity	3.1	0.93	0.609		Connectivity	4.0	1.21	0.215
	Management	11.1	1.67	**0.001**		Management	9.0	1.34	**0.048**
	Total	17.4	1.32	**0.003**		Total	16.6	1.25	**0.050**
Specialists	% Arable land	2.6	0.81	0.792	Spiders	% Arable land	2.3	0.67	0.937
	Connectivity	3.5	1.09	0.307		Connectivity	2.5	0.75	0.870
	Management	13.5	2.12	**0.001**		Management	11.9	1.77	**0.001**
	Total	20.8	1.64	**0.001**		Total	16.4	1.23	**0.049**
Bees	% Arable land	3.6	1.11	0.292	Rove beetles	% Arable land	1.8	0.53	0.882
	Connectivity	2.7	0.83	0.723		Connectivity	3.8	1.11	0.326
	Management	11.4	1.74	**0.007**		Management	9.3	1.36	0.151
	Total	17.7	1.34	**0.019**		Total	14.1	1.02	0.401
Butterflies	% Arable land	3.4	1.05	0.362	Hoverflies	% Arable land	6.0	1.79	**0.012**
	Connectivity	3.8	1.19	0.234		Connectivity	2.6	0.78	0.786
	Management	12.4	1.93	**0.006**		Management	7.7	1.15	0.236
	Total	19.8	1.54	**0.008**		Total	16.6	1.24	0.089
Grasshoppers	% Arable land	4.6	1.35	0.208	Leafhoppers	% Arable land	2.6	0.85	0.637
	Connectivity	2.3	0.66	0.746		Connectivity	3.0	0.95	0.540
	Management	7.2	1.06	0.431		Management	15.5	2.49	**0.001**
	Total	14.4	1.05	0.406		Total	22.5	1.81	**0.002**

Fig. 3. Overall response of standardized species richness per taxon in relation to a) the significant interaction of management and taxon (sta = rove beetles, but = butterflies, spi = spiders, het = true bugs, zik = leafhoppers, gra = grasshoppers, syr = hoverflies, pla = plants, bee = bees), b) the proportion of arable land and c) the significant interaction of connectivity and taxon. Shown is the predicted standardized species richness per taxon (y-axis) and 95 % CIs, based on the best linear mixed model. Standardized species richness is calculated as species richness divided by the mean species richness of that taxon across the study. For improved visualisation, average species richness per taxon (= 1) is indicated by a horizontal dashed line.

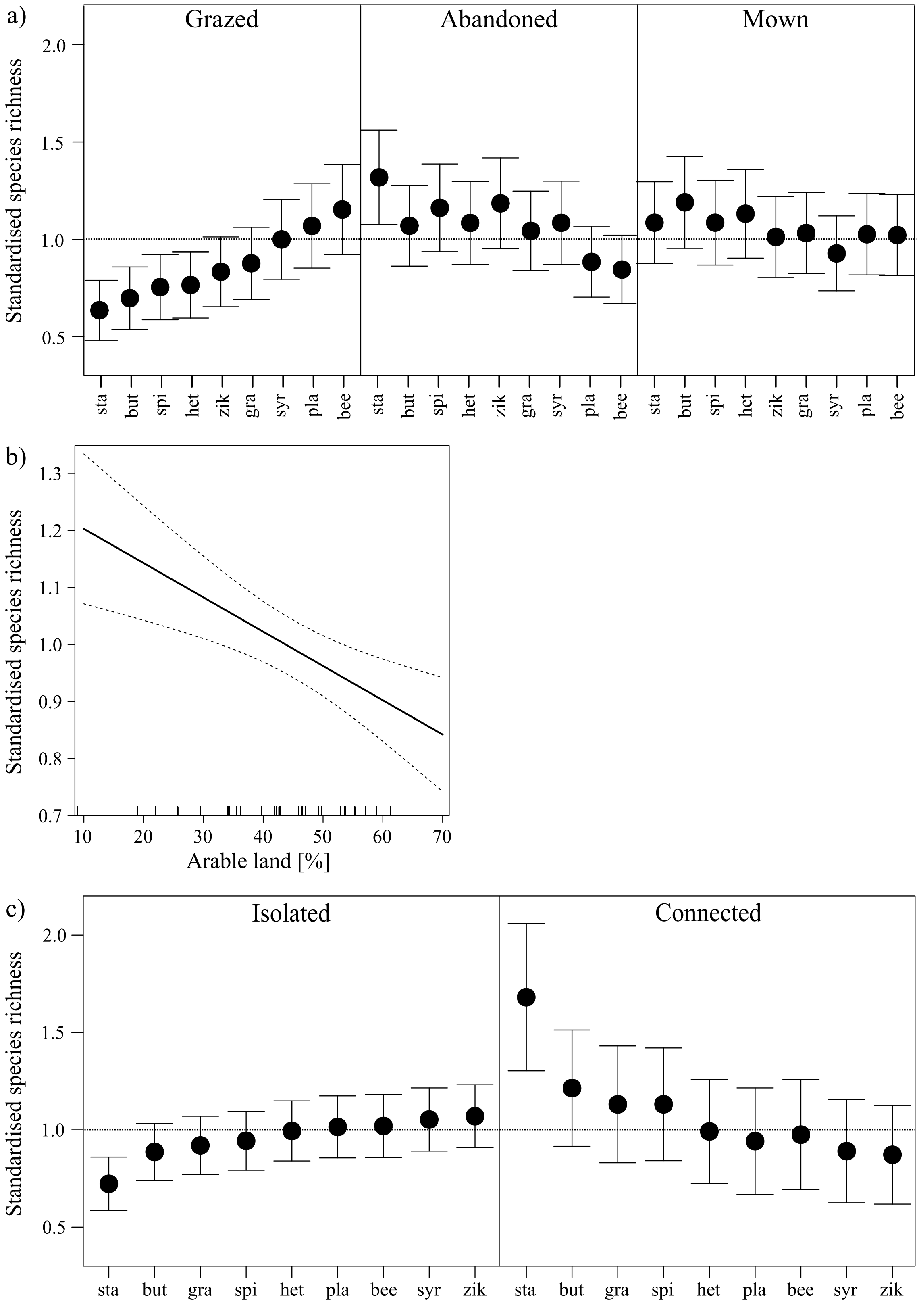


Fig. 4. Response of trait-specific species richness per taxon predicted by the best linear mixed model including all species. a) Response of large and small species to habitat connectivity, b) response of red-listed and unthreatened species to local management. Shown is the standardized species richness per taxon (y-axis). Standardized species richness is calculated as species richness divided by the mean species richness of that taxon for large or small species respectively in a), and divided by the mean species richness of that taxon for unthreatened and red-listed species respectively in b). For improved visualisation, average species richness per taxon (= 1) is indicated by a horizontal dashed line in b).

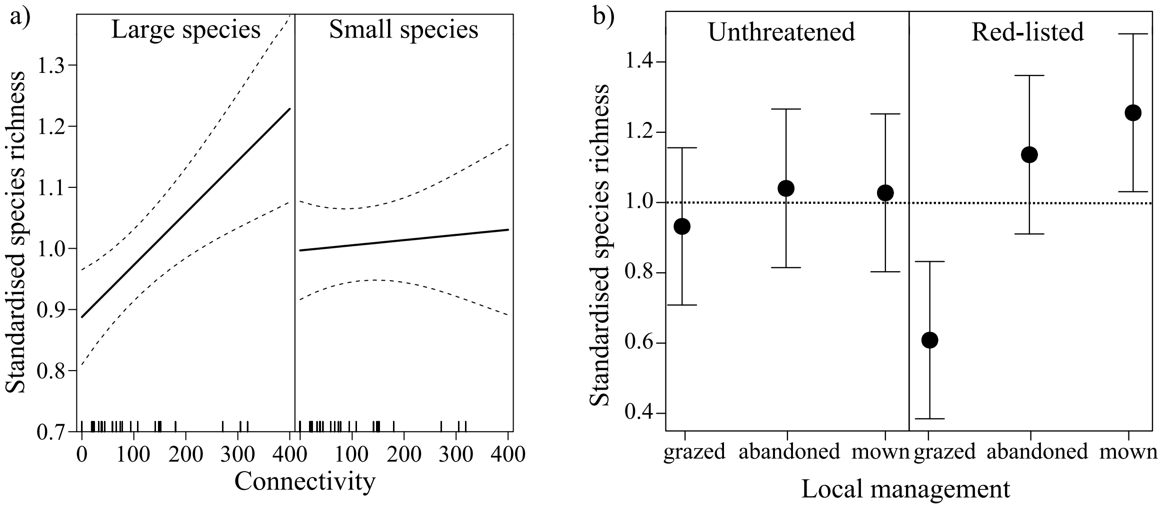


Table 3. Effects of landscape context (% arable land), connectivity and local management on overall standardized species richness per taxon. Shown is a sequential analysis of variance table for terms retained in the minimal adequate linear mixed-effects model. Only variables included in the final model are shown. Variables significant at P ≤ 0.05 are printed bold. numDF, denDF: numerator and denominator degrees of freedom.

	numDF	denDF	F	*P*
Intercept	1	208	1467.64	**<0.001**
Connectivity	1	25	0.07	0.7917
Taxon	8	208	1.00	0.3679
Management	2	25	8.95	**0.0012**
Connectivity : Taxon	8	208	2.41	**0.0163**
Management : Taxon	16	208	2.96	**0.0002**

Table 4. Effects of landscape context (% arable land), connectivity and local management on overall standardized species richness for large and small species per taxon. Sequential analysis of variance table (as in Table 3) for the terms in the minimal adequate linear mixed-effects model for the overall trend in species richness across taxa in large and small species. Only variables included in the final models are shown. Variables significant at P < 0.05 are shown in bold.

	numDF	denDF	F	*P*
Intercept	1	434	1.52	**<0.001**
% Arable land	1	25	11.00	**0.003**
Connectivity	1	25	2.00	0.217
Size	1	434	0.00	1.000
Taxon	7	434	0.00	1.000
Management	2	25	6.00	**0.008**
Connectivity : Size	1	434	6.00	**0.014**
Connectivity : Taxon	7	434	2.00	**0.016**

Table 5. Effects of landscape context (% arable land), connectivity and local management on overall standardized species richness for red-listed and unthreatened species per taxon. Sequential analysis of variance table (as Table 3) for the terms in the minimal adequate linear mixed-effects model for the overall trend in species richness across taxa in red-listed and unthreatened species. Only variables included in the final models are shown. Variables significant at P < 0.05 are shown in bold.

	numDF	denDF	F	*P*
Intercept	1	447	348.39	< 0.001
% Arable land	1	26	2.29	0.142
Connectivity	1	447	0.00	1.000
Management	2	26	4.67	**0.019**
RL status : Management	2	447	4.24	**0.015**

Discussion

Our sampling approach combined with our joint analysis allowed us to disentangle the effects of local management, habitat connectivity and landscape complexity on a broad array of taxa. As hypothesized, high proportions of arable land reduced species richness for all taxa combined, whereas habitat connectivity increased overall species richness. Similar patterns were found at the taxon level. Local management strongly influenced community composition in most taxa. Grazing generally reduced species richness and abundance more than mowing or abandonment and affected red-listed species in particular. As expected, the effect of habitat connectivity was modified by body size. Within each taxon, increasing habitat connectivity increased species richness more in large than in small-bodied species.

Landscape complexity

Landscape simplification had a surprisingly consistent, negative influence on species richness across taxa. Simple landscapes dominated by agriculture are often characterized by low matrix quality, offering less alternative habitat, since many species require resources outside fragment borders (Öckinger et al., 2012). In addition, dispersing individuals may experience a lack of resources (Rösch et al., 2013) and an inhospitable matrix (e.g. Nowicki et al., 2014, Baum et al., 2004). Similar to our study, Prugh et al. (2008) emphasized the central importance of matrix effects for patch occupancy in a broad variety of species.

Local communities are subsets of the landscape wide species pool (Tscharntke et al., 2012). Since agriculturally dominated landscapes often show depauperate species pools (Steffan-Dewenter et al., 2002; Tscharntke et al., 2005; Ekroos et al., 2010), habitat fragments embedded in such landscapes will only gain few additional species through disperal. In contrast, complex landscapes harbour a more diverse species pool and can therefore be assumed to subsidize local species richness to a greater extent. Small fragments as studied by us may also experience greater edge effects and higher spillover from adjacent arable land (Rand et al., 2006).

Bee and butterfly abundance both decreased by approximately two thirds in highly simplified landscapes (Fig. S1). Effects of reduced pollinator availability in simple landscapes could include reduced pollination efficiency in insect-pollinated plants, threatening their persistence on grassland fragments (Meyer et al., 2007; Clough et al., 2014). In contrast to all other taxa, hoverfly abundance (but not species richness) increased in agriculturally dominated landscapes. This likely resulted from increased densities of the hyperabundant species *Syrphus vitripennis* (869 vs, 400 specimens on fragments in simple vs. complex landscapes), whose aphidophagous larvae feed on cereal aphids (Speight et al., 2008).

Habitat connectivity

Despite variation between taxa, increasing habitat connectivity generally boosted species richness, and this effect was most accentuated for butterflies, grasshoppers and rove beetles. This is in line with a previous meta-analysis (Öckinger et al., 2010), which showed a positive effect of connectivity on insect species richness across studies. As predicted by metapopulation theory, connected fragments can be reached by dispersing individuals more easily than isolated ones, recolonising them after extinction events (Hanski, 1998). Interestingly, we found that relative body size consistently modified the positive connectivity effect: The species richness of large species within each taxon increased with increasing connectivity, while species richness of small species did not. Large-bodied species tend to have stronger dispersal capacities and can thereby benefit from connectivity (Sekar, 2012), whereas smaller-bodied species appeared unable to bridge the given connectivity level in our landscapes. Apparently, the isolated small fragments of calcareous grassland were already too distant from each other for the majority of the small species, which can be assumed to be less dispersive. However, body size may not always be directly linked with dispersal ability: For example, several species of grasshoppers, leafhoppers and true bugs display a wing dimorphism or are short-winged, which impairs their flight ability and thereby their capability of bridging gaps between habitats (Biedermann & Niedringhaus, 2004; Wachmann et al., 2004, 2006, 2007, 2008; Baur et al., 2006). Further, large spiders disperse better by walking, but some small spiders can disperse aerially by ballooning (Crawford et al., 1995). This dichotomy explains well why connected patches were more easily reached by larger spiders, while small spiders were unaffected by connectivity (Oberg et al., 2008), as these could equally well transverse the matrix by ballooning (Weyman, 1993).

Effects of management

Our results suggest that local management strongly modifies species richness, abundance and community composition. While vertebrate herbivory is often selective and long-term, mowing is a rather sudden event that unselectively removes a large part of the food resources available (Humbert et al., 2009). For most taxa, we found high species richness and abundances in mown patches. This supports previous research that showed that calcareous grasslands require management for long-term persistence (Poschlod & WallisDeVries, 2002). In contrast, the positive effect of short term abandonment was unexpected (but see Pöyry et al., 2006). Short-term abandonment (5-15 years) can be beneficial for species richness since it increases local habitat heterogeneity and leads to the development of different successional plant communities with associated arthropod communities (WallisDeVries et al., 2002). In contrast, long-term abandonment (>15 years) may lead to a gradual decrease in species richness due to increasing dominance of grass species (e.g. *Brachypodium*, *Bromus*), gradually replacing other plant species. The next stage is shrub encroachment by woody species like *Prunus spinosa* and *Crataegus monogyna*, ultimately leading to a loss of the characteristic open structure favouring thermophilic organisms (Butaye et al., 2005; Piqueray & Mahy, 2010).

The traditional management paradigm of yearly grazing has been shown to efficiently keep calcareous grasslands open and support typical plant species, which in turn host specialist arthropod species (Pöyry et al., 2009; Westrich et al., 2011; Littlewood et al., 2012). Grazing also generates and maintains areas of open soil that are important e.g. as nesting sites for bees (Westrich, 1989) and for the establishment of plant seedlings (Kahmen et al., 2002). These areas of open soil help to increase the temperatures near the ground level, generating microclimatic conditions preferred by thermophilic species (e.g. Krämer et al., 2012). Furthermore, sheep-mediated propagule dispersal guarantees genetic connectivity of plant populations, important for long-term persistence of isolated populations (Wagner et al., 2013; Rico et al., 2014).

Surprisingly, our results starkly contrast with this paradigm: Grazing the way it is conducted at present seems to be the least appropriate management strategy for small fragments of calcareous grassland. Intensive and prolonged grazing by heavy livestock such as cattle or horses causes a drastic and continuous removal of food resources for herbivorous insects through consumption of plants and trampling. This either directly affects herbivores like leafhoppers or butterflies, or indirectly affects predatory arthropods like spiders, which suffer from decreases in prey abundance and a loss of structural heterogeneity of the vegetation (e.g. Szinetár & Samu, 2012). Our results are particularly alarming, since we found that red-listed species, the focus of conservation management, were affected most strongly. These species can be assumed to be most vulnerable due to very specific habitat requirements (Davies et al., 2004). They are thus likely to be the first to be negatively affected by unsuitable management like grazing over a too long time period or with to high stocking rates. Some previous studies have reported negative effects of grazing intensity, in particular on herbivorous insects (e.g. Kruess & Tscharntke, 2002; Pöyry et al., 2006; Kőrösi et al., 2012). In line with our results, these studies suggested that insect herbivores benefit from local breaks of one or a few years in grazing management, or from landscape-scale variation in grazing intensity (Öckinger et al., 2006; Pöyry et al., 2006; Konvicka et al., 2007).

The decreasing number of sheep flocks combined with the necessity of keeping calcareous grasslands open, leads to increasing reliance on unsuitable livestock. However, our study shows that this management alternative entails a high uncertainty concerning the persistence of endangered communities.

Conclusions

Taxa as different as the ones studied here strongly differ in their ecological requirements and life history traits. Given this striking plurality, it is remarkable that our joint analysis revealed generalisable responses across taxa. Cross-taxon biodiversity was strongly affected both by landscape simplification and by connectivity. Large-bodied and more dispersive species benefited from connectivity. Intensive grazing led to reduced species richness, with a particularly severe reduction in red-listed species. Given these results, grazing in the way it is currently practised, seems to be the least favourable management option.

An intermediate management strategy, alternating between mowing or lenient grazing (preferably late in the season) and short-term abandonment, combined with complex landscapes surrounding each fragment and low levels of habitat isolation, would benefit plant and arthropod species richness on small fragments of calcareous grassland most. We conclude that appropriate local management is essential, but must be complemented by a landscape perspective.

Acknowledgements

We thank Filipe Nogueira Madeira, Nora German, Felix Weiß and Cecilia Cantor for help with field data collection, Zsolt Józan for bee identification, Sándor Tóth for hoverfly identification, László Ádám for rove beetle identification and Susanne Grube for true bug identification. We thank Laura Sutcliffe for language editing and comments. Ingolf Kühn and four anonymous referees provided valuable comments. Financial support to VR by the MWK graduate school “Biodiversität und Gesellschaft”, to UK by the DFG Research Training Group 1644 (Scaling Problems in Statistics), to FS by OTKA (K81971) and to PB by the German Research Foundation (DFG BA4438/1-1) is acknowledged.

References

Baum, K.A., Haynes, K.J., Dillemuth, F.P., & Cronin, J.T. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**, 2671–2676.

Baur, B., Baur, H., Roesti, C., & Roesti, D. (2006) *Die Heuschrecken der Schweiz.* Haupt, Bern.

Biedermann, R. & Niedringhaus, R. (2004) *Die Zikaden Deutschlands - Bestimmungstafeln für alle Arten.* WABV Fründ, Scheeßel.

Binot-Hafke, M., Balzer, S., Becker, N., Gruttke, H., Haupt, H., Hofbauer, N., Ludwig, G., Matzke-Hajek, G., & Strauch, M. (2011) *Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 3: Wirbellose Tiere (Teil 1),* Bundesamt für Naturschutz, Bonn-Bad Godesberg.

Brückmann, S.V., Krauss, J., & Steffan-Dewenter, I. (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology*, **47**, 799–809.

Butaye, J., Adriaens, D., & Honnay, O. (2005) Conservation and restoration of calcareous grasslands: a concise review of the effects of fragmentation and management on plant species. *Biotechnology, Agronomy, Society and Environment*, **9**, 111–118.

Clough, Y., Ekroos, J., Báldi, A., Batáry, P., Bommarco, R., Gross, N., Holzschuh, A., Hopfenmüller, S., Knop, E., Kuussaari, M., Lindborg, R., Marini, L., Ockinger, E., Potts, S.G., Pöyry, J., Roberts, S.P., Steffan-Dewenter, I., & Smith, H.G. (2014) Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology Letters*, **17**, 1168–1177.

Crawford, R.L., Sugg, P.M., & Edwards, J.S. (1995) Spider Arrival and Primary Establishment on Terrain Depopulated by Volcanic Eruption at Mount St-Helens, Washington. *American Midland Naturalist*, **133**, 60–75.

Dancey, C., & Reidy, J. (2004) *Statistics without Maths for Psychology: using SPSS for Windows*, Prentice Hall, London.

Davies, K.F., Margules, C.R., & Lawrence, J.F. (2004) A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology*, **85**, 265–271.

Ekroos, J., Heliölä, J., & Kuussaari, M. (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, **47**, 459–467.

Ellenberg, H. & Leuschner, C. (2010) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht.* Ulmer, Stuttgart.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., & Pullin, A.S. (2012) A meta-analysis on the impact of different matrix structures on species movement rates. *Landscape Ecology*, **27**, 1263–1278.

Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.

Gardiner, T. & Hill, J. (2006) A comparison of three sampling techniques used to estimate the population density and assemblage diversity of Orthoptera. *Journal of Orthoptera Research*, **15**, 45–51.

Gardiner, T., Hill, J., & Chesmore, D. (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. *Journal of Insect Conservation*, **9**, 151–173.

Garve, E. (2004) Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen - 5. Fassung, Stand 1.3. 2004. *Informationsdienst Naturschutz Niedersachsen*, **1**, 1–76.

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

Hanski, I., Alho, J., & Moilanen, A. (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239–251.

Holzschuh, A., Dormann, C.F., Tscharntke, T., & Steffan-Dewenter, I. (2013) Mass-flowering crops enhance wild bee abundance. *Oecologia*, **172**, 477–484.

Hothorn, T., Bretz, F., & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Humbert, J.-Y., Ghazoul, J., & Walter, T. (2009) Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems & Environment*, **130**, 1–8.

Jenkins, D.G., Brescacin, C.R., Duxbury, C. V., Elliott, J.A., Evans, J.A., Grablow, K.R., Hillegass, M., Lyon, B.N., Metzger, G.A., Olandese, M.L., Pepe, D., Silvers, G.A., Suresch, H.N., Thompson, T.N., Trexler, C.M., Williams, G.E., Williams, N.C., & Williams, S.E. (2007) Does size matter for dispersal distance? *Global Ecology and Biogeography*, **16**, 415–425.

Kahmen, S., Poschlod, P., & Schreiber, K.-F. (2002) Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation*, **104**, 319–328.

Konvicka, M., Benes, J., Cizek, O., Kopecek, F., Konvicka, O., & Vitaz, L. (2007) How too much care kills species: Grassland reserves, agri-environmental schemes and extinction of *Colias myrmidone* (Lepidoptera: Pieridae) from its former stronghold. *Journal of Insect Conservation*, **12**, 519–525.

Kőrösi, Á., Batáry, P., Orosz, A., Rédei, D., & Báldi, A. (2012) Effects of grazing, vegetation structure and landscape complexity on grassland leafhoppers (Hemiptera: Auchenorrhyncha) and true bugs (Hemiptera: Heteroptera) in Hungary. *Insect Conservation and Diversity*, **5**, 57–66.

Krämer, B., Kämpf, I., Enderle, J., Poniatowski, D., & Fartmann, T. (2012) Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. *Journal of Insect Conservation*, **16**, 857–865.

Krauss, J., Steffan-Dewenter, I., & Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, **30**, 889–900.

Kruess, A. & Tscharntke, T. (2002) Grazing Intensity and the Diversity of Grasshoppers, Butterflies, and Trap-Nesting Bees and Wasps. *Conservation Biology*, **16**, 1570–1580.

Legendre, P. & Gallagher, E. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Littlewood, N.A., Stewart, A.J.A., & Woodcock, B.A. (2012) Science into practice - how can fundamental science contribute to better management of grasslands for invertebrates? *Insect Conservation and Diversity*, **5**, 1–8.

Losos, J.B. & Ricklefs, R.E. (2010) *The Theory of Island Biogeography Revisited.* Princeton University Press, Princeton, New Jersey.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography.* Princeton University Press, Princeton, New Jersey.

Melber, A. (1999) Rote Liste der in Niedersachsen und Bremen gefährdeten Wanzen mit Gesamtartenverzeichnis, 1. Fassung, Stand 31.12.1998. *Informationsdienst Naturschutz Niedersachsen*, **5**, 1–44.

Meyer, B., Gaebele, V., & Steffan-Dewenter, I.D. (2007) Patch Size and Landscape Effects on Pollinators an Seed Set of the Horseshoe Vetch, Hippocrepis comosa, in an Agricultural Landscape of Central Europe. *Entomologia Generalis*, **30**, 173–185.

Nowicki, P., Vrabec, V., Binzenhöfer, B., Feil, J., Zakšek, B., Hovestadt, T., & Settele, J. (2014) Butterfly dispersal in inhospitable matrix: rare, risky, but long-distance. *Landscape Ecology*, **29**, 401–412.

Oberg, S., Mayr, S., & Dauber, J. (2008) Landscape effects on recolonisation patterns of spiders in arable fields. *Agriculture, Ecosystems & Environment*, **123**, 211–218.

Öckinger, E., Eriksson, A.K., & Smith, H.G. (2006) Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biological Conservation*, **133**, 291–300.

Öckinger, E., Lindborg, R., Sjödin, N.E., & Bommarco, R. (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, **35**, 259–267.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S., & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology letters*, **13**, 969–979.

Oksanen, J., Blanchet, F.G., Kindt, R., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Sólymos, P., Stevens, M.H.H., & Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.0-9, http://cran.r-project.org/package=vegan, accessed 09 March 2015.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R-Core-Team (2014) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-116, http://CRAN.R-project.org/package=nlme, accessed 09 March 2015.

Piqueray, J. & Mahy, G. (2010) Revue bibliographique sur la restauration des pelouses calcicoles en Europe: contraintes rencontrées et solutions proposées. *Biotechnologie, Agronomie, Société et Environnement*, **14**, 471–484.

Poschlod, P. & WallisDeVries, M.F. (2002) The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. *Biological Conservation*, **104**, 361–376.

Pöyry, J., Luoto, M., Paukkunen, J., Pyka, J., Raatikainen, K., & Kuussaari, M. (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. *Oikos*, **3**, 401–412.

Pöyry, J., Paukkunen, J., Heliölä, J., & Kuussaari, M. (2009) Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. *Oecologia*, **160**, 577–87.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., & Brashares, J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 20770–20775.

Rand, T.A., Tylianakis, J.M., & Tscharntke, T. (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology letters*, **9**, 603–14.

Remane, R., Achtziger, R., Fröhlich, W., Nickel, H., & Witsack, W. (1997) Rote Liste der Zikaden in der Bundesrepublik Deutschland (Homoptera, Auchenorrhyncha). *Cicadina*, **1**, 243–249.

Rico, Y., Holderegger, R., Boehmer, H.J., & Wagner, H.H. (2014) Directed dispersal by rotational shepherding supports landscape genetic connectivity in a calcareous grassland plant. *Molecular Ecology*, **23**, 832–842.

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2013) Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology*, **50**, 387–394.

Roschewitz, I., Hücker, M., Tscharntke, T., & Thies, C. (2005) The influence of landscape context and farming practices on parasitism of cereal aphids. *Agriculture, Ecosystems & Environment*, **108**, 218–227.

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

Saura, S., Bodin, Ö., & Fortin, M.-J. (2014) Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, **51**, 171–182.

Sekar, S. (2012) A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? *Journal of Animal Ecology*, **81**, 174–184.

Sjödin, N.E., Bengtsson, J., & Ekbom, B. (2007) The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology*, **45**, 763–772.

Speight, M.C.D., Castella, E., Sarthou, J.-P., & Monteil, C. (2008) *Species accounts of European Syrphidae (Diptera).* Syrph the Net publications, Dublin.

Standen, V. (2000) The adequacy of collecting techniques for estimating species richness of grassland invertebrates. *Journal of Applied Ecology*, **37**, 884–893.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421–1432.

Stephen, W.P. & Rao, S. (2005) Unscented Color Traps for Non-Apis Bees (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society*, **78**, 373–380.

Van Swaay, C.A.M. (2002) The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, **104**, 315–318.

Szinetár, C. & Samu, F. (2012) Intensive grazing opens spider assemblage to invasion by disturbance-tolerant species. *Journal of Arachnology*, **40**, 59–70.

Thies, C., Steffan-Dewenter, I., & Tscharntke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, **101**, 18–25.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, **8**, 857–874.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., & Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, **12**, 354–363.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S.* Springer, New York.

Wachmann, E., Melber, A., & Deckert, J. (2004) *Wanzen 2 - Tierw. Deutschlds., 75: 1-294.* Goecke & Evers, Keltern.

Wachmann, E., Melber, A., & Deckert, J. (2006) *Wanzen 1 - Tierw. Deutschlds., 77: 1-263.* Goecke & Evers, Keltern.

Wachmann, E., Melber, A., & Deckert, J. (2007) *Wanzen 3 - Tierw. Deutschlds., 78: 1-272.* Goecke & Evers, Keltern.

Wachmann, E., Melber, A., & Deckert, J. (2008) *Wanzen 4 - Tierw. Deutschlds., 81: 1-230.* Goecke & Evers, Keltern.

Wagner, H.H., Rico, Y., Lehnert, H., & Boehmer, H.J. (2013) Process-based long-term evaluation of an ecological network of calcareous grasslands connected by sheep herding. *Ecography*, **36**, 374–382.

WallisDeVries, M.F., Poschlod, P., & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, **104**, 265–273.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-dewenter, I., Monographs, E., Biesmeijer, C., & Kunin, E. (2008) Measuring Bee Diversity in Different European Habitats and Biogeographical Regions. *Ecological Monographs*, **78**, 653–671.

Westrich, P. (1989) *Die Wildbienen Baden-Württembergs. Allgemeiner Teil: Lebensräume, Verhalten, Ökologie und Schutz.* Ulmer, Stuttgart.

Westrich, P., Frommer, U., Mandery, K., Riemann, H., Ruhnke, H., Saure, C., & Voith, J. (2011) Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. 5. Fassung, Stand Februar 2011. Bundesamt für Naturschutz. *Naturschutz und Biologische Vielfalt*, **70**, 373–416.

Weyman, G.S. (1993) A review of the possible causative factors and significance of ballooning in spiders. *Ethology, Ecology & Evolution*, **5**, 279–291.

Wilmanns, O. (1993) *Ökologische Pflanzensoziologie, Eine Einführung in die Vegetation Mitteleuropas.* Quelle und Meyer, Heidelberg & Wiesbaden.

Zulka, K.P., Abensperg-Traun, M., Milasowszky, N., Bieringer, G., Gereben-Krenn, B.-A., Holzinger, W., Hölzler, G., Rabitsch, W., Reischütz, A., Querner, P., Sauberer, N., Schmitzberger, I., Willner, W., Wrbka, T., & Zechmeister, H. (2013) Species richness in dry grassland patches of eastern Austria: A multi-taxon study on the role of local, landscape and habitat quality variables. *Agriculture, Ecosystems & Environment*, **182**, 25–36.

Supporting information

Fig. S1. Fragment size distribution in the study area.

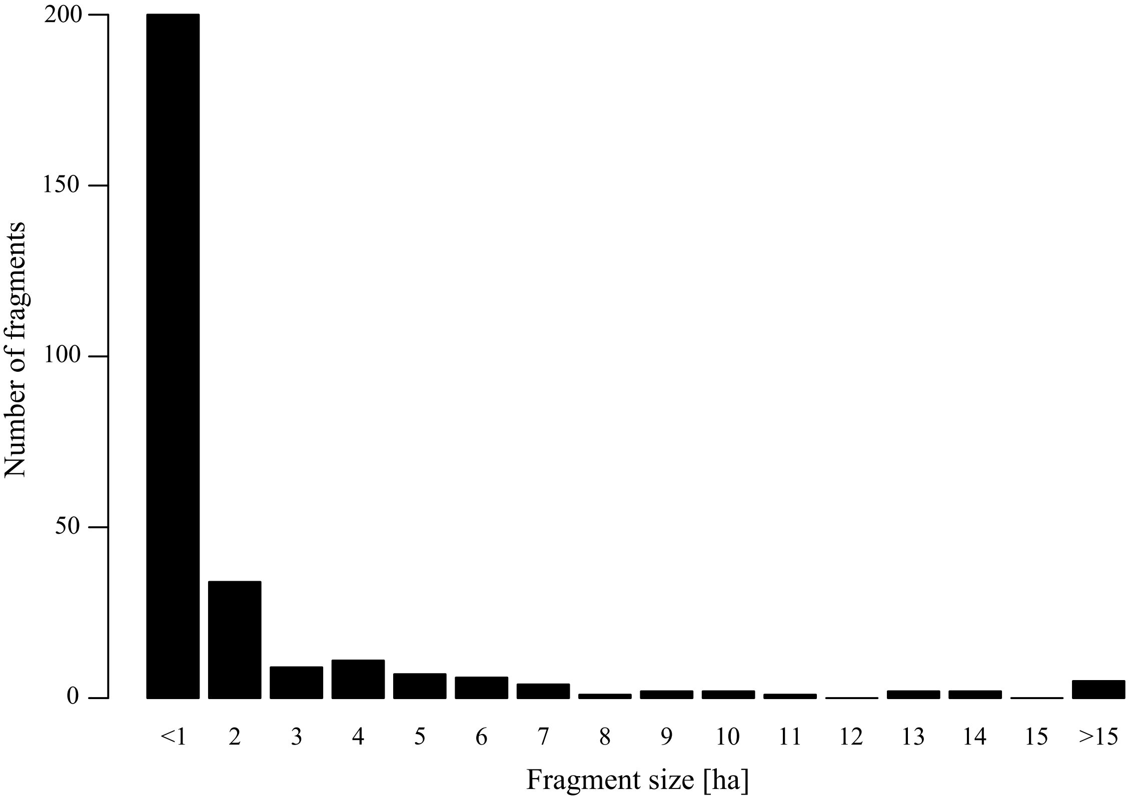
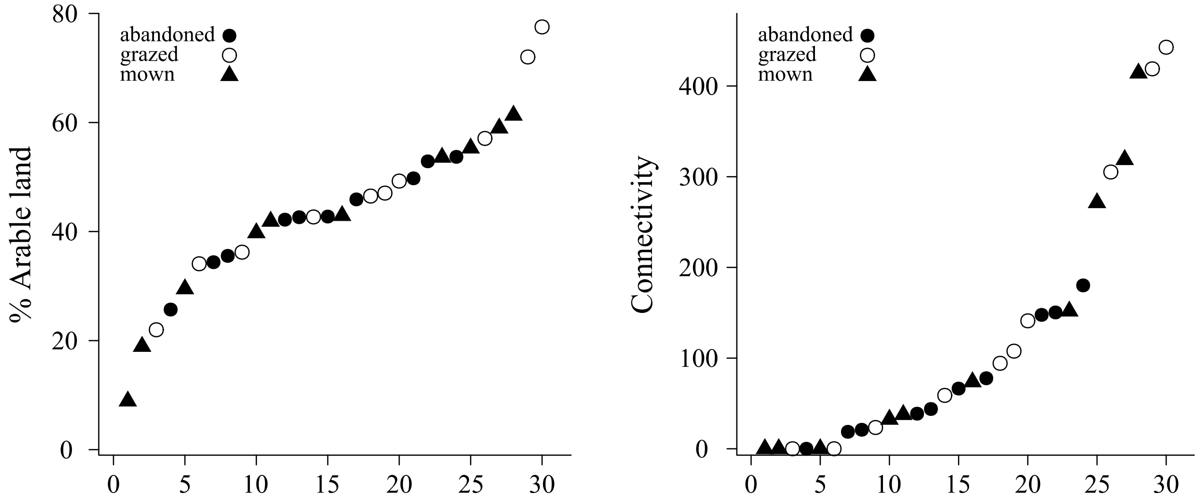


Fig. S2. Gradients of landscape complexity and connectivity of the 30 fragments of calcareous grassland.



Map S1. Location of the 30 small fragments of calcareous grassland. Grazed grasslands are marked in green, mown grasslands in yellow and abandoned ones in pink, each of them with a subsequent site number (see Table S3).

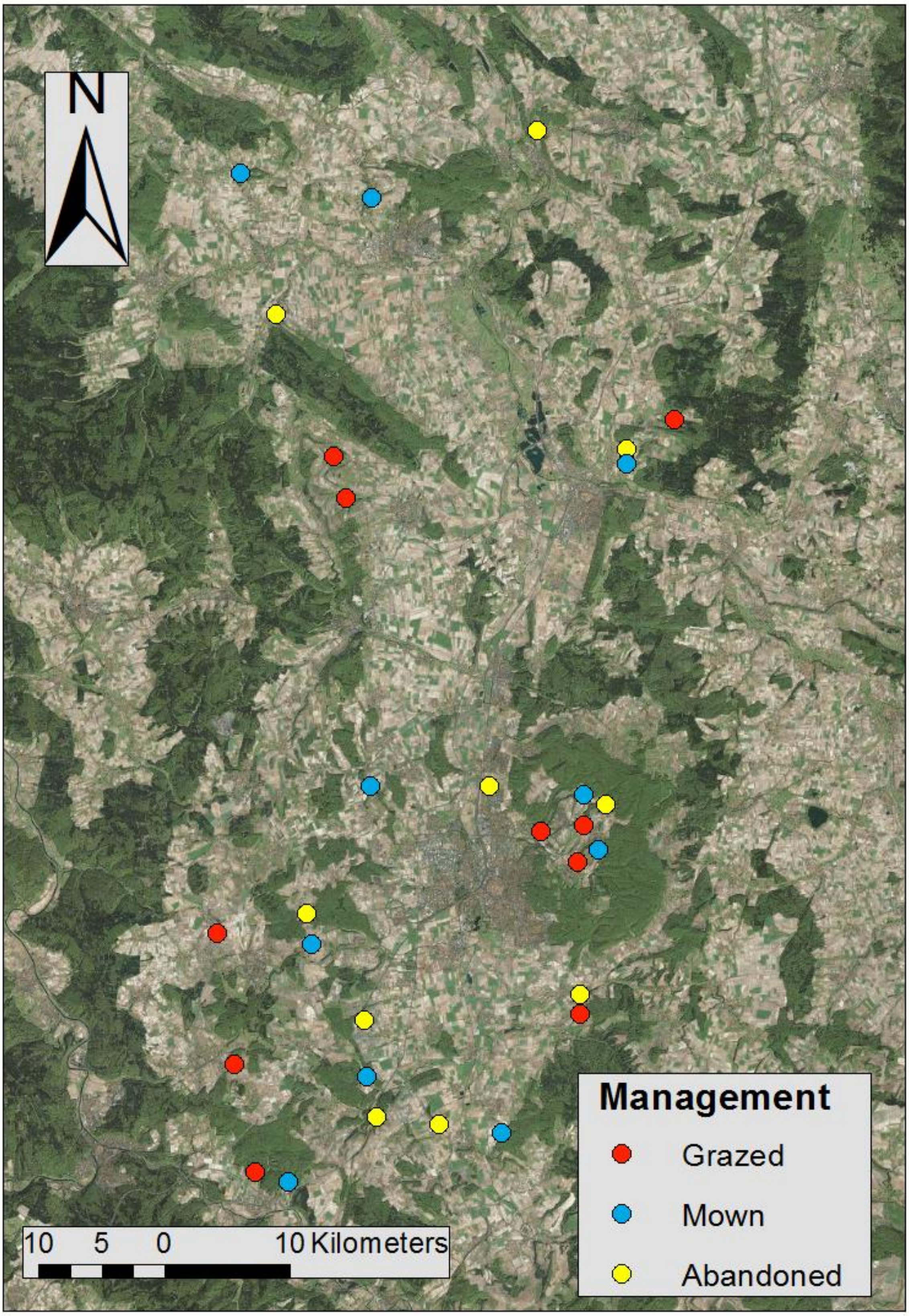


Table S1. Models used for the analysis of abundance and species richness (SpR) of the nine taxa (glm.nb: generalized linear model with negative binomial errors, glm (Poisson): generalized linear model with Poisson errors, lm: linear model).

	Abundance	SpR
All taxa	glm.nb	glm.nb
Specialists	glm.nb	glm.nb
Generalists	glm.nb	glm.nb
Plants	—	glm.nb
Bees	glm.nb	glm (Poisson)
Butterflies	glm.nb	lm
Grasshoppers	glm.nb	lm
True bugs	glm.nb	glm (Poisson)
Spiders	glm.nb	glm (Poisson)
Hoverflies	glm.nb	lm
Rove beetles	glm.nb	glm.nb
Leafhoppers	glm.nb	glm (Poisson)

Table S2. Overall species richness (SpR), overall abundances and mean ± SEM of abundances and species richness of all nine taxa on the 30 fragments of calcareous grassland.

	Overall SpR	SpR per fragment	Overall abundance	Abundance per fragment
Plants	148	41.9 ± 2.1	-	-
Specialists	61	22.5 ± 1.2	-	-
Generalists	87	19.4 ± 1.2	-	-
Bees	82	17.5 ± 0.9	4318	143.9 ± 27.2
Specialists	12	2.1 ± 0.2	2342	78.1 ± 25.4
Generalists	69	15.4 ± 0.8	1975	65.8 ± 4.8
Butterflies	47	14.2 ± 1.0	2553	85.1 ± 9.5
Specialists	16	3.4 ± 0.5	960	32.0 ± 6.7
Generalists	31	10.7 ± 0.7	1593	53.1 ± 5.3
Grasshoppers	10	3.8 ± 0.2	891	29.7 ± 4.5
Specialists	3	0.9 ± 0.2	136	4.5 ± 1.6
Generalists	7	2.9 ± 0.2	755	25.2 ± 3.8
True bugs	80	11.8 ± 0.7	1167	38.9 ± 4.4
Specialists	20	3.4 ± 0.3	397	13.2 ± 2.6
Generalists	60	8.4 ± 0.5	770	25.7 ± 3.2
Spiders	83	15.7 ± 0.7	1030	34.3 ± 2.2
Specialists	16	3.0 ± 0.2	147	4.9 ± 0.5
Generalists	67	12.7 ± 0.6	883	29.4 ± 2.1
Hoverflies	46	12.2 ± 0.5	2528	84.3 ± 9.9
Rove beetles	43	4.4 ± 0.5	1008	33.6 ± 7.8
Leafhoppers	65	16.4 ± 0.8	6202	206.7 ± 31.8
Specialists	26	7.8 ± 0.5	4034	134.5 ± 20.5
Generalists	39	8.6 ± 0.7	2168	72.3 ± 16.2

Table S3. Code number, site name, management, percentage of arable land in a 1000 m radius around each site, fragment area [m^2] and values of a connectivity index (Hanski et al., 2000) of the 30 fragments of calcareous grassland.

Code	Site name	Management	% Arable land	Connectivity	Area [m²]
7	Volkerode	abandoned	53.6	107.7	1306
21	Bratental 8	abandoned	34.4	442.7	5143
46	Diemarden 1	abandoned	57.1	150.3	1269
88	Weende	abandoned	45.9	0.0	4520
90	Dahlenrode 1	abandoned	42.8	77.8	2548
116	Orxhausen	abandoned	34.1	21.0	1000
138	Wellersen 1	abandoned	55.3	23.5	2527
151	Langenholtensen 1	abandoned	46.5	66.4	5560
170	Elkershausen1	abandoned	72.0	0.0	2499
177	Ossenfeld ost	abandoned	42.2	37.7	2707
3	Nikolausberg 1	grazed (goats)	22.0	318.8	4444
20	Bratenta l 4	grazed (horses)	41.9	418.9	2324
58	Dransfeld 4	grazed (highland cattle)	77.5	38.7	1325
111	Bratental 1	grazed (highland cattle)	39.8	271.2	1556
139	Denkershausen	grazed (cows)	36.2	0.0	1645
143	Oldenrode 1	grazed (sheep)	49.3	32.5	6875
146	Nienhagen 5	grazed (sheep)	53.7	147.7	2236
187	Scheden 2	grazed (ponies)	42.7	414.2	6843
202	Herberhausen	grazed (highland cattle)	35.5	73.8	4790
203	Hedemünden 10	grazed (ponies)	29.5	58.9	5613
1	Tiefetal	mown	25.7	43.9	3372
2	Emmenhausen 1	mown	42.9	18.7	4017
11	Roringen 1	mown	18.9	0.0	2114
63	Varmissen 1	mown	61.3	0.0	4385
71	Friedland 1	mown	47.1	305.2	835
125	Andershausen 2	mown	52.9	0.0	1663
172	Hedemünden 1	mown	8.9	151.8	2324
178	Reinhausen 3	mown	49.8	141.1	3138
192	Langenholtensen 2	mown	42.6	94.2	2476
193	Portenhagen 1	mown	59.0	180.1	3016

Fig. S3. Response of species richness and abundance in the nine taxa (y-axis) to the landscape parameters and local management (x-axis). Shown are the effects of the taxon specific full models.

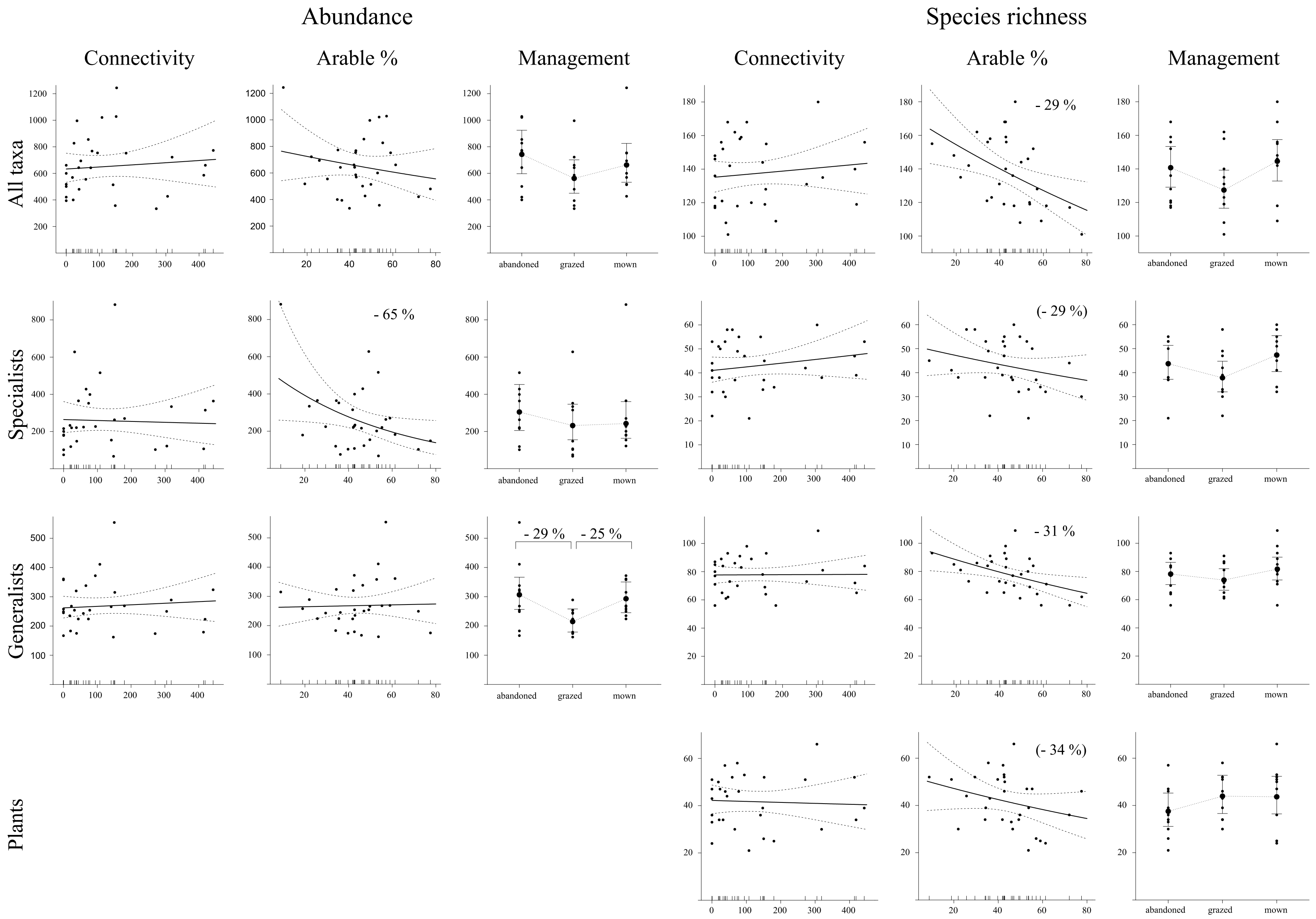


Fig. S3. Continued.

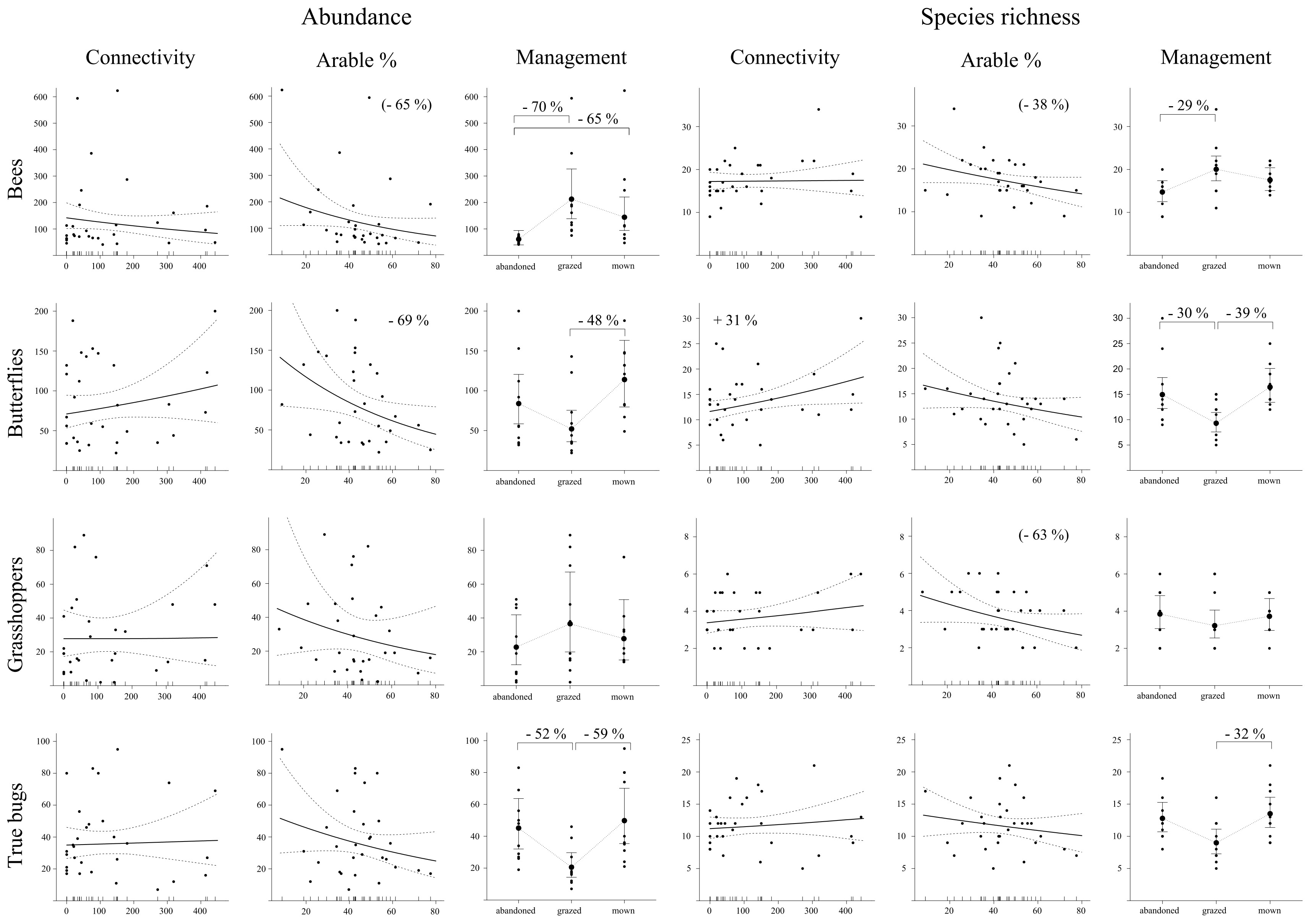


Fig. S3. Continued.

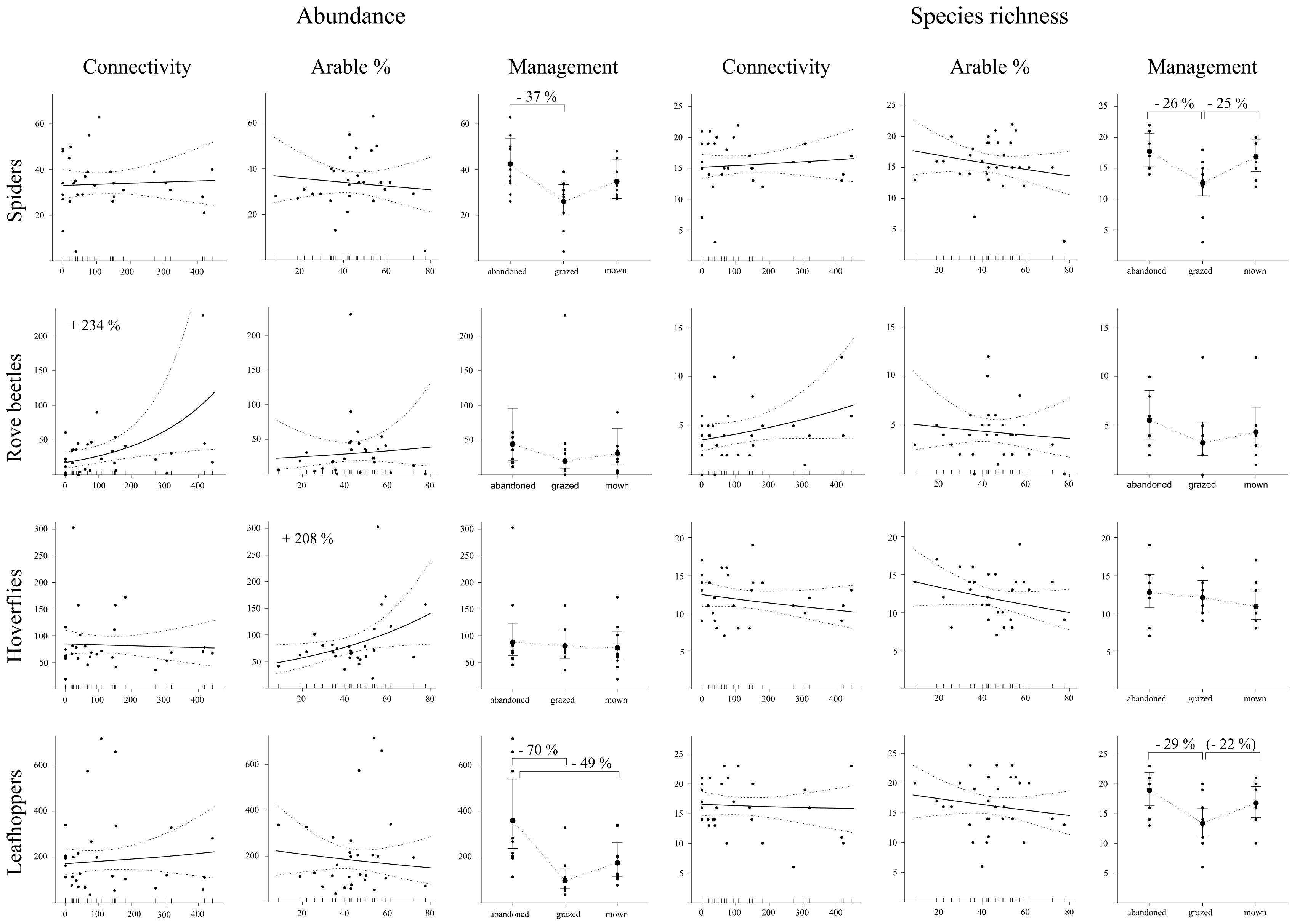


Table S4. Generalized linear models and linear models on the effects of landscape context (% arable land), connectivity (a connectivity index described by Hanski et al. (2000)) and management on the abundance and species richness of all nine taxa. For management, successive differences between treatment levels are shown (g: grazed, m: mown, a: abandoned). The table shows parameter estimates on the scale of the linear predictor. Note that differences between management types are Tukey’s pairwise comparisons (ignoring covariates) calculated using the *glht* function (R package multcomp (Hothorn et al., 2008)). Only variables included in the final models are shown. *P*-values < 0.05 are depicted in bold characters.

Abundance

	Plants				Bees				Butterflies			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept					4.74	0.41	11.49	**<0.001**	5.23	0.35	14.81	**<0.001**
% Arable land					-0.01	0.01	-1.78	0.075	-0.02	0.01	-2.76	**0.006**
Connectivity												
Management g-a					1.18	0.27	4.42	**<0.001**	-0.42	0.23	-1.83	0.159
Management m-a					0.84	0.27	3.11	**0.005**	0.26	0.23	1.12	0.504
Management m-g					-0.34	0.26	-1.29	0.399	0.68	0.23	3.00	**0.008**

	Grasshoppers				True bugs				Spiders			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	3.39	0.1537	22.06	**<0.001**	3.79	0.15	24.51	**<0.001**	3.7329	0.09657	38.656	**<0.001**
% Arable land												
Connectivity												
Management g-a					-0.74	0.22	-3.31	**0.003**	-0.46	0.14	-3.25	**0.003**
Management m-a					0.16	0.22	0.72	0.751	-0.18	0.14	-1.33	0.381
Management m-g					0.90	0.22	4.03	**<0.001**	0.28	0.14	1.93	0.131

	Rove beetles				Hoverflies				Leafhoppers			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	3.10	0.25	12.27	**<0.001**	3.68	0.27	13.42	**<0.001**	5.84	0.18	32.75	**<0.001**
% Arable land					0.02	0.01	2.78	**0.005**				
Connectivity	0.003	0.001	1.96	**0.050**								
Management g-a									-1.19	0.25	-4.70	**<0.001**
Management m-a									-0.68	0.25	-2.70	**0.019**
Management m-g									0.51	0.25	2.00	0.112

Species richness

	Plants				Bees				Butterflies			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	4.00	0.15	26.8	**<0.001**	2.94	0.17	17.50	**<0.001**	2.54	0.11	23.58	**<0.001**
% Arable land	-0.01	0.003	-1.871	0.061	-0.01	0.003	-1.84	0.066				
Connectivity									0.001	<0.001	2.59	**0.016**
Management g-a					0.31	0.11	2.81	**0.014**	-0.45	0.15	-3.08	**0.013**
Management m-a					0.17	0.11	1.51	0.287	0.14	0.14	1.02	0.570
Management m-g					-0.14	0.10	-1.34	0.373	0.59	0.15	4.07	**0.001**

	Grasshoppers				True bugs				Spiders			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	1.65	0.20	8.43	**<0.001**	2.53	0.09	28.24	**<0.001**	2.86	0.08	37.68	**<0.001**
% Arable land	-0.01	0.004	-2.02	**0.053**								
Connectivity												
Management g-a					-0.31	0.14	-2.23	0.066	-0.31	0.12	-2.64	**0.023**
Management m-a					0.08	0.12	0.68	0.774	-0.02	0.11	-0.22	0.975
Management m-g					0.39	0.13	2.90	**0.011**	0.28	0.12	2.43	**0.041**

	Rove beetles				Hoverflies				Leafhoppers			
	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*	Estimate	SEM	z	*P*
Intercept	1.49	0.12	12.54	**<0.001**	2.47	0.05	53.15	**<0.001**	2.93	0.07	40.23	**<0.001**
% Arable land												
Connectivity												
Management g-a									-0.35	0.11	-3.06	**0.006**
Management m-a									-0.10	0.11	-0.95	0.608
Management m-g									0.25	0.12	2.12	0.086

References S1. Experts who provided information on habitat specialisation and literature used for classification of species into specialists and generalists.

1) H. Nickel (Göttingen, Germany), leafhoppers
2) M. Goßner (Fronreute, Germany), true bugs
3) R. Theunert (Hohenhameln, Germany), bees

Biedermann, R. & Niedringhaus, R. (2004) *Die Zikaden Deutschlands - Bestimmungstafeln für alle Arten.* WABV Fründ, Scheeßel.

Hanski, I., Alho, J. & Moilanen, A. (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239–251.

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, **30**, 889–900.

Meyer, B. (2007) *Pollinator communities and plant-pollinator interactions in fragmented calcareous grasslands.* Georg-August Universität, Göttingen,

Wachmann, E., Melber, A. & Deckert, J. (2004) *Wanzen 2 - Tierwelt Deutschlands 75: 1-294.* Goecke & Evers, Keltern.

Wachmann, E., Melber, A. & Deckert, J. (2006) *Wanzen 1 - Tierwelt Deutschlands, 77: 1-263.* Goecke & Evers, Keltern.

Wachmann, E., Melber, A. & Deckert, J. (2007) *Wanzen 3 - Tierwelt Deutschlands, 78: 1-272.* Goecke & Evers, Keltern.

Wachmann, E., Melber, A. & Deckert, J. (2008) *Wanzen 4 - Tierwelt Deutschlands, 81: 1-230.* Goecke & Evers, Keltern.

Summary

Land-use change, habitat loss and fragmentation are among the main drivers of the decline of biodiversity worldwide. In Central Europe, calcareous grasslands belong to the most species-rich habitats. They harbour a great diversity of xero- and thermophilic plant and invertebrate species but are increasingly under threat from agricultural intensification and abandonment. They depend on grazing or mowing, but today, these traditional land use practices have become unprofitable for farmers. Therefore, increasingly smaller fragments are embedded within a matrix that is often unsuitable for most of the plant and invertebrate species specialised on calcareous grasslands.

The **first part** of this thesis analyses the effects of fragment size, connectivity, the composition of the surrounding landscape and plant species richness on leafhopper community structure. Leafhoppers are a highly diverse group of phytophagous insects with a close connection to vegetation structure and composition. We selected 14 large (>1 ha) and 14 small (<1 ha) fragments of calcareous grassland in the surroundings of Göttingen along gradients of increasing connectivity to other calcareous grasslands, increasing plant species richness and in the increasing complexity of the surrounding landscape, i.e. the percentage of arable land within a 500 m radius.

Increasing habitat isolation reduced leafhopper species richness in simple (dominated by arable crops), but not in complex landscapes. This effect was driven by generalist species. Moreover, generalist species richness increased with increasing connectivity on small fragments, whereas it remained stable on large fragments. Finally, generalist species richness increased more steeply with increasing plant species richness on connected than on isolated fragments, suggesting that more colonisers reach connected fragments and can subsequently use the available plant resources. Our results show that insect biodiversity on fragmented calcareous grasslands not only depends on habitat connectivity but that it is interactively affected by habitat connectivity, landscape composition, habitat area and plant species richness. Isolated fragments that are either small or located in simple landscapes are less likely to receive immigrants after extinction events, potentially leading to a gradual reduction in species richness over time.

In the **second part** of this thesis we aim to contribute to the resolution of the so-called SLOSS debate ("Single Large Or Several Small"), which considers whether it is better to conserve single large or several small fragments of a habitat. Small fragments are expected to cover greater habitat heterogeneity due to a larger geographical distance and thereby greater total species richness, whereas large fragments offer more stable habitat conditions and bigger

population sizes. In this study, in addition to plants and leafhoppers, we also collected data on true bugs and snails. Species richness of all four taxa as well as the richness of habitat specialists was substantially higher on several small fragments than on one or two large fragments of equal total size. However, community composition of large and small fragments differed and some of the rarest specialist species were confined to large fragments. The complexity of the landscape surrounding the fragments did not play an important role for species richness and community composition. These results question the focus on either small or large fragments and imply that both large and small habitat fragments are needed for successful biodiversity conservation.

In the **third part** of the thesis, we explore the effects of grassland management (grazing, mowing and abandonment), connectivity and landscape composition on species richness, abundance, community composition and trait-based responses (body size and Red List status) of nine taxa: plants, butterflies, bees, grasshoppers, hoverflies, spiders, true bugs, rove beetles and leafhoppers. We selected 30 small fragments (<1 ha) of calcareous grassland along orthogonal gradients of habitat connectivity and landscape complexity.

We found a negative effect of an increasing percentage of arable land in the surroundings of the fragments, which led to a 29 % loss of overall species richness. We presume that landscapes dominated by arable land offer less alternative habitat and resources for foraging or during migration, resulting in lower species richness. Habitat connectivity generally enhanced species richness across all taxa. This was more accentuated in the large species per taxon, which can be expected to be good dispersers. Finally, grazing reduced species richness and abundance much more than mowing (once a year) or short-term abandonment (for 5-15 years), in particular of red-listed species, presumably due to the greater damage caused, reducing food resources for phytophagous insects. Furthermore, each of the three management types resulted in a different community composition of all taxa. Therefore, the preferential management strategy for small fragments of calcareous grassland should be an alternation between mowing and short-term abandonment combined with a diversification of the surrounding landscape.

Overall, we conclude that the widespread concentration on large habitat fragments should be reconsidered, leading to the conservation of both large and small habitat fragments. When planning conservation measures for fragmented grassland habitats, a focus on local factors like fragment size and management is important but insufficient: landscape factors including habitat connectivity and landscape complexity need to be taken into account to ensure the long-term survival of specialised plant and invertebrate populations.

Zusammenfassung

Landnutzungsänderungen, Habitatverlust und Fragmentierung gehören zu den Hauptursachen des weltweiten Biodiversitätsrückgangs. In Mitteleuropa zählen Kalkmagerrasen zu den artenreichsten Lebensräumen. Sie weisen eine hohe Vielfalt an xero- und thermophilen Pflanzen- und Invertebratenarten auf, sind jedoch zunehmend durch landwirtschaftliche Intensivierung und Nutzungsaufgabe gefährdet. Sie sind auf Beweidung und Mahd angewiesen, was jedoch für die Landwirte heutzutage unwirtschaftlich geworden ist. Daher finden sich zunehmend kleine Fragmente innerhalb einer für die meisten der spezialisierten Magerrasenarten ungeeigneten, von intensiver Landwirtschaft geprägten Umgebung.

Der **erste Teil** dieser Arbeit untersucht den Einfluss der Fragmentgröße, der Habitatkonnektivität, der Zusammensetzung der umgebenden Landschaft und der Pflanzenartenzahl auf die Zusammensetzung der Zikadengemeinschaft. Zikaden sind eine überaus artenreiche Gruppe phytophager Insekten mit enger Bindung an die Vegetationsstruktur und -zusammensetzung. In der Umgebung von Göttingen wählten wir 14 große (>1 ha) und 14 kleine (<1 ha) Kalkmagerrasenflächen entlang von Gradienten zunehmender Konnektivität mit anderen Magerrasenflächen, zunehmender Pflanzenartenzahl und zunehmender Landschaftskomplexität, d.h. dem Prozentsatz Ackerfläche innerhalb eines 500 m-Radius, aus.

Zunehmende Isolation verringerte die Zikadenartenzahl in einfachen (von Feldern geprägten), jedoch nicht in komplexen Landschaften. Dieser Effekt wurde von den Generalisten getrieben. Die Artenzahl der Generalisten nahm auf kleinen Fragmenten mit zunehmender Konnektivität zu, wogegen sie auf großen Flächen unverändert blieb. Weiterhin nahm die Artenzahl der Generalisten mit steigender Pflanzenartenzahl auf vernetzten Magerrasen stärker zu als auf unvernetzten. Unsere Ergebnisse zeigen, dass die Insektenartenvielfalt auf Kalkmagerrasenfragmenten nicht nur durch Konnektivität allein geprägt wird, sondern vielmehr von einem Zusammenspiel aus Konnektivität, Landschaftszusammensetzung und Pflanzenartenzahl bestimmt wird.

Im **zweiten Teil** dieser Arbeit verfolgen wir das Ziel, zur Lösung der sogenannten SLOSS-Debatte ("Single Large Or Several Small") beizutragen, in der diskutiert wird, ob es besser ist, wenige große oder mehrere kleine Fragmente eines Habitattyps zu erhalten. Man nimmt an, dass kleine Fragmente aufgrund der größeren abgedeckten geographischen Distanzen eine größere Heterogenität und dadurch eine höhere Gesamtartenzahl aufweisen. Dagegen weisen große Fragmente stabilere Lebensraumbedingungen und größere Populationen auf. Neben Zikaden und Pflanzen wurden auch Daten zu Wanzen und

Schnecken aufgenommen. Sowohl die Gesamtartenzahl aller vier Taxa als auch die Zahl der Spezialisten war auf mehreren kleinen Fragmenten wesentlich höher als auf einem oder zwei großen Fragmenten gleicher Gesamtgröße. Jedoch war die Artenzusammensetzung auf großen und kleinen Fragmenten unterschiedlich und einige der seltensten Spezialisten waren an große Flächen gebunden. Hingegen spielte die Zusammensetzung der umgebenden Landschaft keine wichtige Rolle für Artenzahl und -zusammensetzung. Diese Ergebnisse stellen den Fokus auf entweder große oder kleine Habitatfragmente infrage. Für einen erfolgreichen Biodiversitätserhalt ist daher der Schutz sowohl großer als auch kleiner Habitatfragmente zwingend notwendig.

Im **dritten Teil** dieser Arbeit untersuchen wir den Einfluss der Bewirtschaftungsart (Beweidung, Mahd, Nutzungsaufgabe), der Landschaftszusammensetzung und Konnektivität auf die Artenzahl, Artenzusammensetzung und merkmalsbasierte Reaktionen (Körpergröße und Rote Liste-Status) von neun Taxa: Pflanzen, Schmetterlinge, Bienen, Heuschrecken, Schwebfliegen, Spinnen, Wanzen, Kurzflügler und Zikaden. Wir wählten 30 kleine Kalkmagerrasenfragmente (<1 ha) entlang von unabhängigen Konnektivitäts- und Landschaftskomplexitätsgradienten aus.

Ein zunehmender Prozentsatz an Ackerfläche in der Umgebung der Fragmente führte zu einem Verlust von 29 % der Gesamtartenzahl. Wir nehmen an, dass Landschaften, die von Ackerfläche dominiert werden, weniger Alternativhabitat und Nahrungsressourcen bieten, was zu einer verringerten Artenzahl führt. Habitatkonnektivität erhöhte im Allgemeinen die Artenzahl. Dieser Effekt war bei den großen, vermutlich ausbreitungsfähigeren Arten eines Taxons stärker ausgeprägt als bei den kleinen Arten. Beweidung hatte einen deutlich negativeren Einfluss auf die Artenzahl als Mahd (einmal jährlich) oder kurzzeitige Nutzungsaufgabe (5-15 Jahre). Der Grund dafür könnte der durch Beweidung verursachte größere Schaden und die Entnahme der Nahrungsressourcen phytophager Insekten sein. Zudem führte jeder der drei Bewirtschaftungsweisen zu einer unterschiedlichen Artenzusammensetzung aller Taxa. Daher sollte die bevorzugte Bewirtschaftungsoption kleiner Kalkmagerrasenfragmente ein Wechsel zwischen Mahd und kurzzeitiger Nutzungsaufgabe in Kombination mit einer Diversifizierung der umgebenden Landschaft sein.

Zusammenfassend lässt sich sagen, dass die allgemein verbreitete Konzentration auf große Habitatfragmente überdacht werden sollte, da der Schutz sowohl kleiner als auch großer Fragmente unerlässlich ist. Bei der Planung von Schutzmaßnahmen für fragmentierte Offenlandlebensräume sind lokale Einflüsse wie Fragmentgröße und Bewirtschaftung zwar wichtig, aber nicht ausreichend: Landschaftsfaktoren wie Habitatkonnektivität und Landschaftszusammensetzung müssen ebenfalls in die Schutzbemühungen mit einbezogen werden um das langfristige Überleben von spezialisierten Pflanzen- und Invertebratenarten zu sichern.

Acknowledgements/Danksagung

Ich möchte mich bei allen, die zum Gelingen meiner Dissertation beigetragen haben, herzlich bedanken:

- bei **Prof. Dr. Teja Tscharntke**, der mich davon abbrachte, auf Fettwiesen arbeiten zu wollen und mir dieses wundervolle Thema zur Verfügung stellte. Ihm ein besonderer Dank für fruchtbare Diskussionen und stete Hilfsbereitschaft.
- bei meinem Zweitbetreuer **Dr. Péter Batáry** für die Hilfe beim Projektdesign 2010 und 2011, beim Einstieg in Flächenauswahl und Feldarbeit, die Hilfe bei der Datenauswertung und natürlich für „Vitamin C".
- bei meinem Drittbetreuer **Dr. Christoph Scherber** für die Hilfe beim Projektdesign 2011, die Hilfe bei der Datenauswertung und für viele anregende Diskussionen und Unterhaltungen, die manchmal ins Absurde abdrifteten.
- bei **Urs Kormann** für die hervorragende Zusammenarbeit in der Feldsaison 2011, bei der Auswertung der Daten, beim Verfassen des Manuskripts und für „Chäs", „Schoki" und unzählige „Rüebli" und „Öpfl".
- bei meiner Bürokollegin **Claudia Normann** für die nette Gesellschaft im Büro und beim Mittagessen im Sozialraum und für viele fachfremde Gespräche über Gemüse und Garten.
- bei **Dr. Filipe Nogueira Madeira** für die Hilfe bei der Feldarbeit, für die schöne gemeinsame Zeit im Büro und seine Freundschaft.
- bei **allen Mitgliedern der AG Agrarökologie** für die angenehme, hilfsbereite und kollegiale Arbeitsatmosphäre, die vielen Feiern und sonstigen Freizeitaktivitäten.
- bei den **Naturschutzbehörden** der **Stadt Göttingen,** der **Landkreise Göttingen** und **Northeim** und den **Landwirten**, auf deren Kalkmagerrasenflächen ich arbeiten durfte, für die gute Zusammenarbeit.
- beim **Land Niedersachsen** für die dreijährige finanzielle Förderung durch ein Lichtenberg-Stipendium.
- bei **Dr. Sebastian Schuch** für die Einführung in die Zikadenbestimmung, ohne die ich nicht weit gekommen wäre.
- bei **Dr. Herbert Nickel** für fachliche Ratschläge zu Zikaden und ihrer Lebensweise.

- bei **Walter Wimmer** für die Bestätigung meiner Bestimmung der Schnecken der Gattung *Vallonia*.
- bei **Dr. Ira Richling** für die Genitalisierung der seltenen Zwerg-Heideschnecke *Xerocrassa geyeri*, die für die sichere Artbestimmung notwendig war.
- bei **diversen Feldassistenten** für ihre Hilfe und Begleitung bei der Feldarbeit und ihre Bereitschaft, Hitze und lange Arbeitstage zu ertragen.
- bei meinen (gelegentlich wechselnden) **Mitbewohnern** für das angenehme Zusammenleben und die rege Bereitschaft, alles zu essen, was ich kochte.
- zuletzt und ganz besonders bei **meiner Familie** für die stetige Unterstützung.

Araschnia levana (Nymphalidae)

Publications

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*, in press.

Kormann, U., **Rösch, V.**, Batáry, P., Tscharntke, T., Orci, K.M., Samu, F., & Scherber, C. (2015) Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. *Diversity and Distributions*. doi: 10.1111/ddi.12324

Rösch, V. & Schmitz, G. (2014) Phytophagous Arthropod Fauna of Chinese Mugwort *Artemisia verlotiorum*, Lamotte, 1877 (Asteraceae) in Central Europe, particularly the Lake Constance Region. *Entomologia Generalis,* **35**, 33-45.

Rösch, V. (2014) Eine Population der Mittelmeersandschnecke *Theba pisana* (O. F. MÜLLER 1774) auf Helgoland: der erste Lebendnachweis für Deutschland (Gastropoda: Stylommatophora: Helicidae). *Mitteilungen der Deutschen Malakozoologischen Gesellschaft,* **90**, 13–16.

Everwand, G., **Rösch, V.**, Tscharntke, T. & Scherber, C. (2014) Disentangling direct and indirect effects of experimental grassland management and plant functional-group manipulation on plant and leafhopper diversity. *BMC Ecology,* **14**:1.

Rösch, V., Tscharntke, T., Scherber, C. & Batáry, P. (2013) Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology*, **50**, 387–394. doi: 10.1111/1365-2664.12056

Rösch, V. (2009) Neunachweise von zwei seltenen Schneckenarten im Argental und im Eriskircher Ried in Baden-Württemberg. *Mitteilungen der Deutschen Malakozoologischen Gesellschaft,* **82**, 51–54.

Rösch, V. & Weiß, F. (2009) Ein Nachweis der Genabelten Puppenschnecke *Lauria cylindracea* (Da Costa 1778) am Isteiner Klotz: erster Lebendnachweis in Baden-Württemberg (Gastropoda: Stylommatophora: Lauriidae). *Mitteilungen der Deutschen Malakozoologischen Gesellschaft,* **81**, 29–30.

Rösch, V., Denger, K, Schleheck, D., Smits, T.H.M. & Cook, A. M. (2008) Different bacterial strategies to degrade taurocholate. *Archives of Microbiology,* **190**, 11–18.

Quillfeldt, P., Schenk, I., McGill, R.A.R., Strange I.J., Masello J.F., Gladbach, A., **Rösch, V.** & Furness, R.W. (2008) Introduced mammals coexist with seabirds at New Island, Falkland Islands: abundance, habitat preferences, and stable isotope analysis of diet. *Polar Biology,* 31, 333–349.

Lebenslauf

Verena Rösch
geboren am 29.03.1983
in Friedrichshafen am Bodensee

Promotion

04/2010 – 07/2014	Bei Prof. Dr. Tscharntke im Fachgebiet Agrarökologie der Georg-August-Universität Göttingen im Rahmen des Promotionsstudienganges „Biodiversität und Gesellschaft“

Studium

10/2002 – 02/2008	Studium der Biologie an der Universität Konstanz Titel der Diplomarbeit: Entomofauna and Growing Site Characteristics of *Artemisia verlotiorum* Lamotte (Asteraceae) in the Western Lake Constance Area.

Schulbildung

06/2002	Abitur am Montfort-Gymnasium Tettnang