

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

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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 ‘single large or several small’ 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

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 [single large or several small (SLOSS) (e.g. Maiorano et al. 2008; Tjørve and Tjørve 2008; Tjørve 2010; Tschardtke 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 β -diversity (community dissimilarity) and thereby supporting more species in total (Tschardtke 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

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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 an 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). Central European calcareous grasslands have declined at an alarming rate due to their conversion to arable land or the abandonment of historic land-use practices like extensive grazing (Poschlod and WallisDeVries 2002). For example, in Southwestern Germany, more than 70 % of the calcareous grasslands that were present in 1900 have disappeared (Mattern et al. 1992). As a result, the connectivity of the remaining fragments has been reduced dramatically.

Within the study area (districts of Göttingen and North-eim, Lower Saxony, Germany; 2391.5 km²) 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 the 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: (a) plants; (b) leafhoppers, planthoppers and frog-hoppers (Auchenorrhyncha, hereafter referred to as ‘leafhoppers’); (c) true bugs (Heteroptera); and (d) 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 sizes and therefore restricted mobility like leafhoppers, true bugs and snails is far less common (but see Boschi and Baur 2007; Körösi et al. 2012; Kormann et al. 2015). 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.

Materials and methods

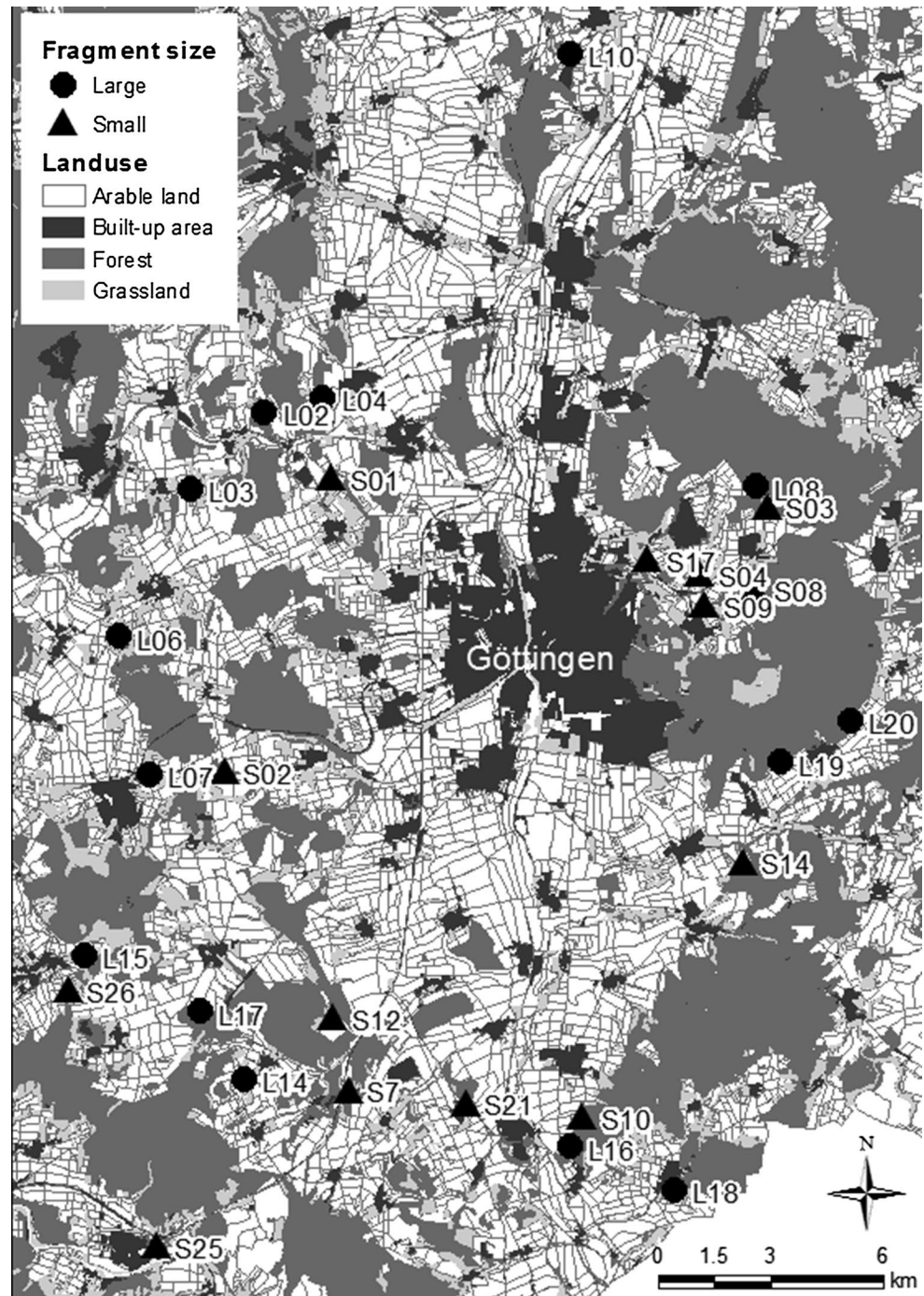
Study area

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

Fig. 1 Location of the 28 grasslands, and their site number (see Table S2), with the city of Göttingen in the centre of the map. *L* large grasslands, *S* small grasslands



Landesvermessung und Geobasisinformationen Niedersachsen 1991–1996, Hannover) with the geographical information system ArcGIS 10.0 (ESRI Geoinformatik, Hannover) 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 the fragments in the study area are smaller than 1 ha and only a few larger fragments exist (Fig. S1; Krauss et al.

2003). The fragments were chosen along two orthogonal gradients (Fig. S2): (a) 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 to them; and (2) a habitat connectivity gradient, measured by a connectivity index (CI) described by Hanski et al. (2000):

$$CI_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^\beta$$

A_j is the area of the neighbouring fragment j (in square metres) and d_{ij} is the edge to edge distance (in metres) 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 m² within a radius of 2000 m around each study site were taken into account. Roadsides and field margins with plant species typical of 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 "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 fragments were grazed or mown, while for 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, diameter 38 cm; BioQuip) 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 in size and were approximately 10-m long. The specimens of leafhoppers and true bugs caught were transferred into ethanol (70 % volume) 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 (*Ribautodelphax*, *Anaceratagallia*, *Psammotettix*, *Rhopalopyx*) was not possible (Biedermann and Niedringhaus 2004). Thus, if male specimens were present, female specimens were assumed to belong to the same species (we used this criterion in the case of 84 specimens, which represented around 1 % of the total abundance). If male specimens were not present, females 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: (1) their specific habitat requirements typical for calcareous grassland (i.e. warm and dry habitat conditions, short, grazed swards, open soil); and (2) their dietary 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 (1) and/or (2) were fulfilled; it was classified as a generalist if neither (1), nor (2) 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 Groh (Hackenheim), personal communication]. The soil samples were washed through sieves of four different mesh sizes (4, 2, 1, 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 died by 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 1–3 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).

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 calculated from summed species abundances for all statistical analyses. In an analogous way, 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 (Tables S2, S3; Fig. S2).

Species-area accumulation curves were established by starting with the smallest fragment and continuing 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 and continuing 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 Estimate S [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 a random effect for the $n = 20$ sites. Starting values for the parameters were estimated using the SSmicmen function in the 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 the 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 the R package vegan (Oksanen et al. 2013) was used to assess the 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 the R package vegan (Oksanen et al. 2013) with distance matrices using Bray-Curtis indices created with function vegdist from the R package vegan (Oksanen et al. 2013).

Species richness was analysed using generalized linear models with negative binomial errors [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 the 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 corrected Akaike information criterion

(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://www.wuser.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 the R package `vegan` (Oksanen et al. 2013). With the resulting distance matrices we then performed Mantel tests with the function `mantel` from the 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 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 seven and 29 species per fragment. In the first three shell age classes we recorded 28 snail species (ten specialists and 18 generalists) with 7199 specimens. Species richness ranged from five to 16 species per fragment (see Tables S2, 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 km²) than the few large fragments of similar area (on average, three large fragments taken together only covered 56 km²; 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 that of 12 plots from two large fragments. On average, the attained species

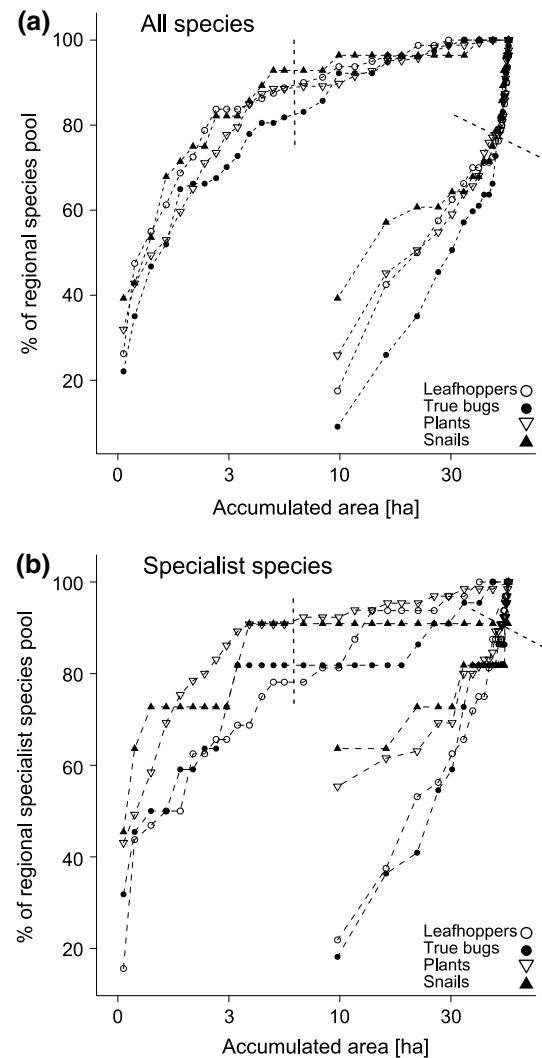


Fig. 2 Species-area accumulation curves of **a** overall and **b** specialist species richness of plants, leafhoppers, true bugs and snails: the cumulative number of species of the regional species pool (in percent, y-axis) in relation to cumulative grassland area (in ha) (x-axis) of the 14 small and 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

richness was 30 % higher in the small fragments (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 in small fragments selected in this way).

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

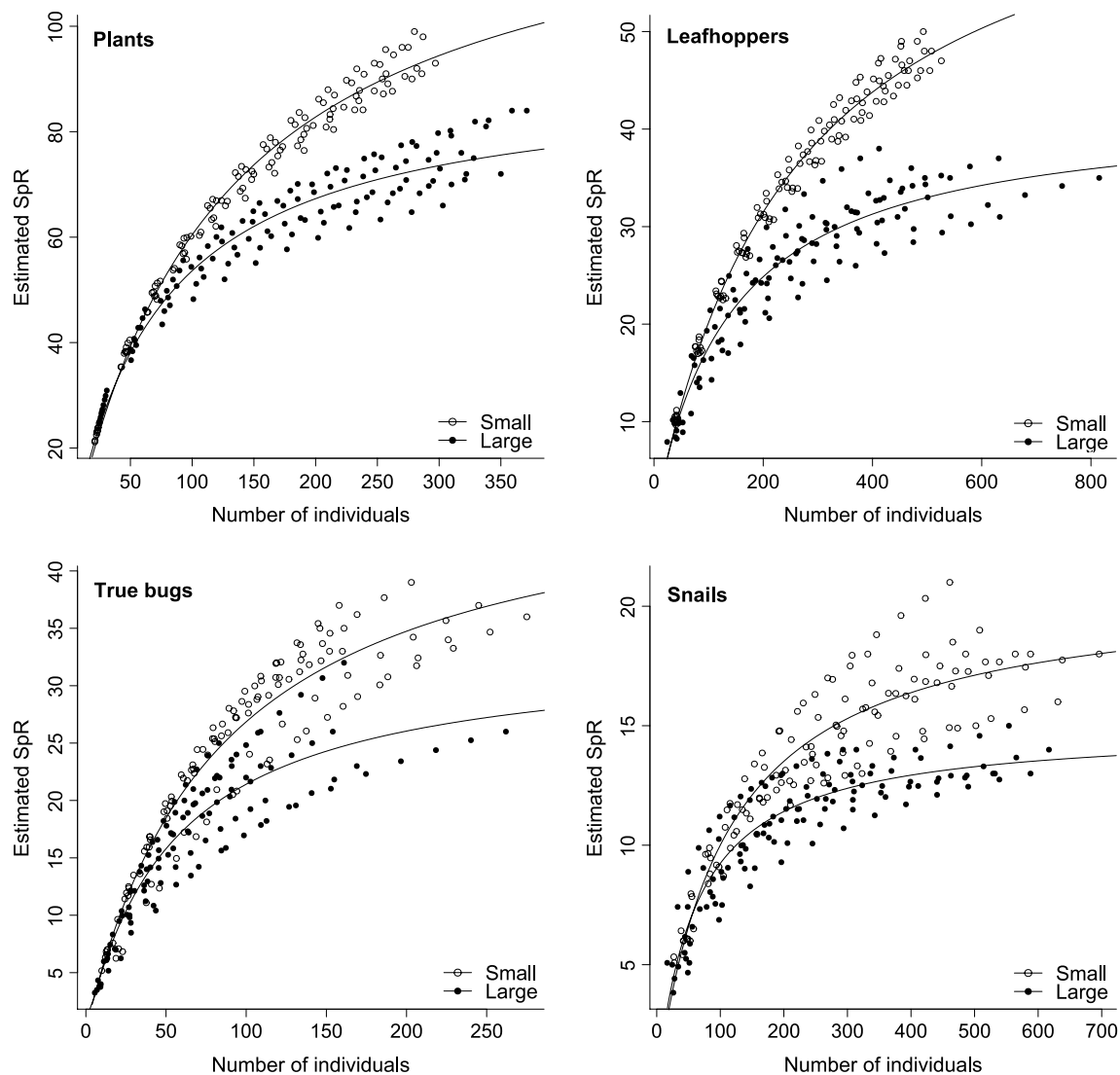


Fig. 3 Sample-based rarefaction curves showing the estimated species richness (*SpR*) against the number of individuals per sampling plot of 12 plots originating from either 12 different small fragments (ten curves of randomly selected fragments and plots; *open symbols*) vs. 12 plots originating from each two randomly selected large frag-

ments (*filled symbols*). For plants, the analysis was based on presence-absence data. Note that this sampling was replicated ten times at random (ten curves of randomly selected fragments). *Lines* represent the average curve for the ten randomly selected curves per fragment size category

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 List specialist species occurred on large fragments exclusively (Table 1). In the case of plants and snails, Red List 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

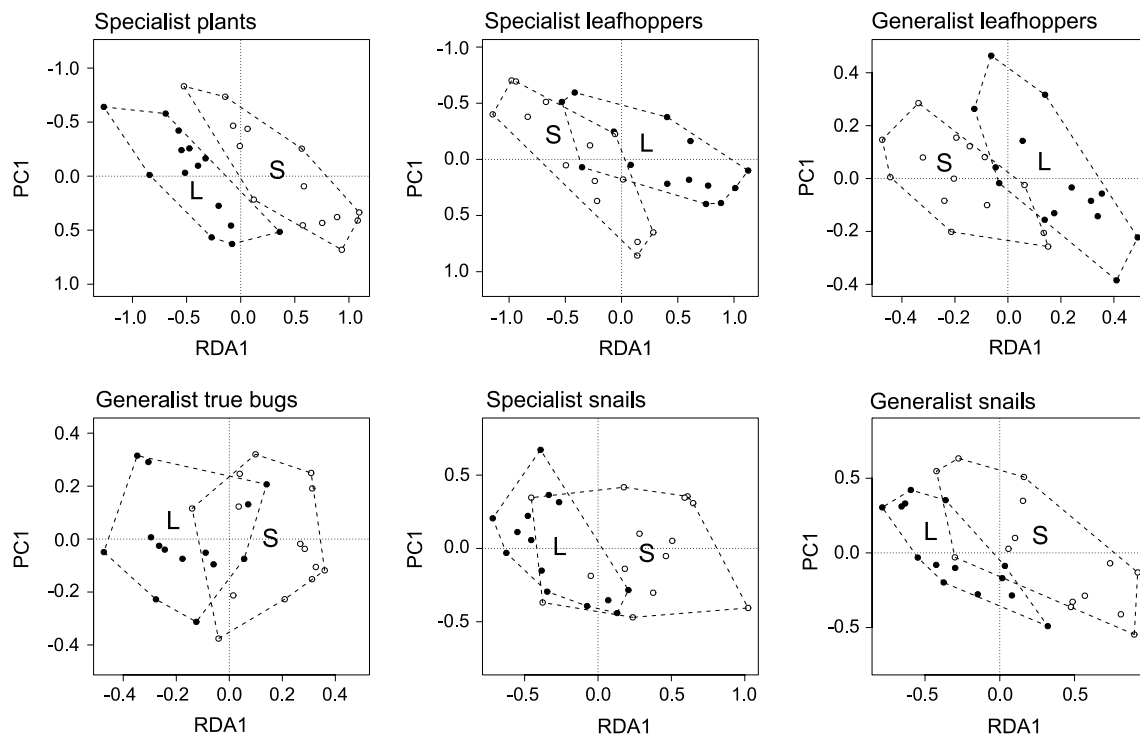


Fig. 4 Redundancy analysis (RDA) plots for species composition of specialist plants, generalist true bugs, specialist and generalist leafhoppers and specialist and generalist snails showing the effect of

fragment size with minimum convex polygons. *Closed circles* Large fragments (L), *open circles* small fragments (S)

crops), whereas it decreased with increasing connectivity in complex landscapes (Table 3; Fig. 5a). We found an increase in species richness for overall and generalist true bug species 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).

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 fragments (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 when comparing 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 for 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 km²) than few large fragments of similar area (on average, three large fragments taken together only covered 56 km²; 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

Table 1 Specialist species of plants, leafhoppers, true bugs and snails that exclusively occurred on either large (L) or small (S) fragments

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

^a Red list status derived from Remane et al. (1997), Melber (1999), Garve (2004) and Teichler and Wimmer (2007); categories: critical (1), endangered (2), vulnerable (3), near-threatened (4)

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 List specialist species were mostly restricted to large fragments. It was only in the case of plants and snails that some Red List specialists occurred on small fragments as well. This could at least partly be due to an unpaid extinction debt on small

Table 2 Results of redundancy analysis (RDA): the 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 (*SpR*) (for leafhoppers and true bugs) on the community composition of plants, leafhoppers, true bugs and snails

	All species			Specialists			Generalists		
	Partial RDA % of variation	<i>F</i>	<i>P</i>	Partial RDA % of variation	<i>F</i>	<i>P</i>	Partial RDA % of variation	<i>F</i>	<i>P</i>
Plants									
Type	5.7	1.58	<i>0.017</i>	6.5	1.85	<i>0.025</i>	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	<i>0.024</i>	15.5	1.47	<i>0.024</i>	12.5	1.14	0.170
Leafhoppers									
Type	6.2	1.82	<i>0.008</i>	6.3	1.79	<i>0.047</i>	6.2	1.84	<i>0.024</i>
% Arable	5.8	1.68	<i>0.019</i>	5.0	1.44	0.119	6.4	1.90	<i>0.009</i>
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	<i>0.001</i>	19.1	1.36	<i>0.042</i>	22.6	1.68	<i>0.001</i>
True bugs									
Type	7.1	2.06	<i>0.003</i>	5.0	1.33	0.182	7.8	2.32	<i>0.003</i>
% 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	<i>0.016</i>	4.3	1.15	0.315	6.6	1.95	<i>0.004</i>
Total	20.4	1.48	<i>0.003</i>	14.1	0.95	0.584	22.7	1.68	<i>0.001</i>
Snails									
Type	8.6	2.47	<i>0.001</i>	9.0	2.51	<i>0.022</i>	8.3	2.44	<i>0.013</i>
% 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	<i>0.015</i>	14.3	1.34	0.146	18.4	1.80	<i>0.014</i>

P values <0.05 are depicted in *italic*

fragments resulting from the 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, plants, leafhoppers, true bugs and snails, 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, and explained 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

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 SpR (for true bugs) on the SpR of plants, true bugs and snails

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

Only variables included in the final models are shown

P values <0.05 are depicted in *italics*

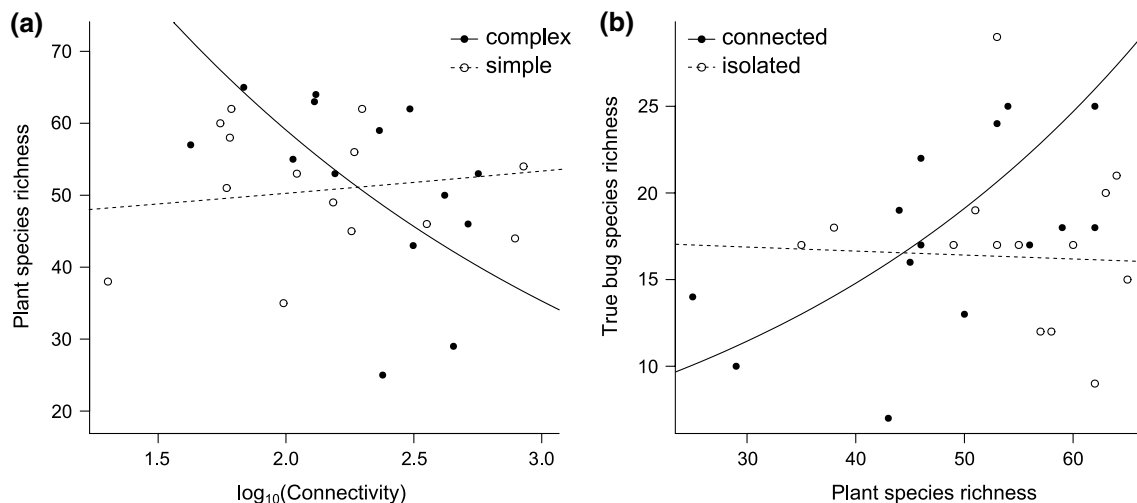


Fig. 5 Interaction plots showing the relationship between plant or true bug species richness (y-axis) and landscape parameters. **a** Effects of landscape composition and habitat isolation [measured by a connectivity index (Hanski et al. 2000), \log_{10} transformed] on plant species richness (complex landscape, 27–46 % of arable land in 500-m

buffer; simple landscape, 47–77 % of arable land). **b** Effects of increasing plant species richness on true bug species richness in conjunction with habitat isolation (connected habitat, values of the connectivity index from 180 to 849; isolated habitat, values from 19 to 155)

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 (1) the probability that an appropriate host plant per species is present (sampling effect), and (2) 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 set-up 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 much less area is needed to accumulate a large number of species, including habitat specialists, when combining several small habitat fragments across landscapes, and shows 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 List 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 many small fragments as well as a few large fragments are needed for successful biodiversity conservation, especially in situations where the majority of fragments have already been lost. Such a diversified habitat fragmentation strategy should be considered when setting priorities for conservation management in fragmented landscapes worldwide.

Author contribution statement T. T., P. B. and V. R. conceived and designed the study. V. R. collected the data (supported by P. B.), performed the data analysis and wrote the first draft of the manuscript. C. S. and P. B. contributed to the data analysis and all authors contributed substantially to the revisions.

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