Species richness in dry grassland patches of eastern Austria: A multi-taxon study on the role of local, landscape and habitat quality variables

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ABSTRACT

According to island biogeography theory, the species richness of patches is determined by their size and spatial isolation, while in conservation practice, it is patch quality that determines protection and guides management. We analysed whether size, isolation or habitat quality are most important for the species richness in a set of 50 dry grassland fragments in agricultural landscapes of eastern Austria. We studied two plant taxa (vascular plants, bryophytes) and 11 invertebrate taxa (gastropods, spiders, springtails, grasshoppers, true bugs, leafhoppers and planthoppers, ground beetles, rove beetles, butterflies and burnets, ants and wild bees). The species richness of three categories was analysed: (1) dry grassland specialist species, (2) all grassland species and (3) all species. We used regression and hierarchical partitioning techniques to determine the relationship between species richness and environmental variables describing patch size and shape, patch quality, landscape configuration and landscape quality. The area-isolation paradigm was only applicable for dry grassland specialists, which comprised 12% of all species. Richness of all grassland species was determined mostly by landscape heterogeneity parameters. Total species richness was highly influenced by spillover from adjacent biotopes, and was significantly determined by the percentage of arable land bordering the patches. When analysing all taxa together, species richness of dry grassland specialists was significantly related to historical patch size but not to current patch size, indicating an extinction debt. At the landscape scale, the variable 'short-grass area' was a better predictor than the less specific variable 'area of extensively used landscape elements'. 'Distance to mainland' was a good predictor for specialists of mobile animal taxa. Plant specialists showed a pronounced dependence on quality measures at the patch scale and at the landscape scale, whereas animal specialists were influenced by patch size, patch quality, landscape quality and isolation measures. None

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of the taxa benefited from linear structures in the surroundings. In conclusion, high patch quality and a network of high-quality areas in the surrounding landscape should be the best conservation strategy to ensure conservation of dry grassland specialists. This goal does not conflict with the specific demands of single taxa.

1. Introduction

Large grassland areas once were a prominent landscape feature in many temperate regions, particularly in central and eastern Europe. They resulted from a long history of low-intensity farming systems until the middle of the 20th century (Poschlod and WallisDeVries, 2002; WallisDeVries et al., 2002). Change in land use after the Second World War, in particular agricultural intensification and afforestation, led to large-scale fragmentation of these grasslands. In most regions, semi-natural grasslands have been reduced to small, isolated habitat patches, where soils are too poor or slopes are too steep for a more intensive land use. In such landscapes, semi-natural grassland fragments have been increasingly appreciated as important biodiversity sources (Bignal and McCracken, 1996; Hodgson et al., 2005), providing not only valuable ecosystem services for agriculture such as pollination and biological control, but also harbouring a number of highly threatened species that are dependent on high temperatures and insolation rates. Owing to their small size, grassland fragments are increasingly threatened by pesticide and fertiliser spillover from adjacent arable fields. Cessation of grazing and fertilisation may trigger shrub encroachment and eutrophication, leading to an overall deterioration of habitat quality and the loss of original open short-grass conditions. Stochastic extinction events affecting patch organisms may no longer be counterbalanced by re-immigration from other grassland sites owing to dispersal impediments imposed by an increasingly hostile and intensively farmed agricultural matrix and large distances between grassland patches.

Ecology and conservation biology have developed a comprehensive framework to predict the conditions for species persistence in small isolated habitat patches. According to the theories of island biogeography (MacArthur and Wilson, 1967) and metapopulation dynamics (Hanski, 1999), species will survive in isolated fragments if the patch area is sufficiently large to support a viable population and/or if the landscape structure allows re-immigration into patches once a population becomes extinct. Consequently, in principle, populations in small isolated grassland fragments could be managed by (1) improving the local conditions, e.g. by enlarging the patch or (2) improving the landscape connectivity, e.g. by providing stepping stones or migration corridors.

The question whether local or landscape factors are more important in determining the fate of species in habitat fragments has been studied extensively over the past decades. Nonetheless, the results have remained inconclusive even for single taxa. For example, butterfly species richness was found to increase with patch size in several studies (Brückmann et al., 2010; Krauss et al., 2003; Steffan-Dewenter and Tscharntke, 2000; Wettstein and Schmid, 1999), but showed no significant relationship in others (Pöyry et al., 2009). Landscape factors (such as patch isolation) were found to be sometimes highly important for vascular plant species richness (Piessens et al., 2004) and sometimes insignificant (Dauber et al., 2003; Herrera and Laterra, 2011). Reviewing the evidence on landscape variables and invertebrate species richness in patches, Mazerolle and Villard (1999) concluded that most studies failed to detect a significant relationship. However, more recently several studies found an important landscape effect on invertebrates (e.g. Dauber et al., 2003; Marini et al., 2008). Apparently, the constantly growing body of scientific evidence on the relevance of local and landscape factors for species in fragmented habitats has not yet produced a coherent picture, let alone led to guidelines for conservation managers on how to manage fragmented landscapes to maximise the benefits for patch-dependent species.

Apart from the dichotomy between local and landscape factors, a second dichotomy, that between size and quality measures, presents an even greater complication for an efficient conservation management of fragmented grasslands. The basic model underpinning island biogeography theory is a binary island-ocean contrast, which distinguishes only between habitat and non-habitat for a particular organism group. Consequently, fragmentation theory is couched in size measures, such as the size of the local habitat patch or the total area of stepping stones, typically without considering variation in habitat conditions (Hanski, 1998). By contrast, practical conservation usually attempts to improve local habitat conditions, e.g. by implementing grazing management, mowing or shrub removal, normally without any consideration of landscape geometry, configuration, habitat isolation patterns or patch network structure. Although evidence shows that a theory-driven network approach and local quality management could complement each other (Thomas et al., 2001), it remains to be analysed which size or quality variables are the most influential. While some studies have incorporated habitat quality measures into their set of patch-level variables (e.g. Abensperg-Traun et al., 1996; Collinge et al., 2003), landscape-level habitat quality measures have been rarely tested in fragmentation studies, despite accumulating evidence that matrix quality may significantly modulate species persistence in the patches (e.g. Bender and Fahrig, 2005; Ricketts, 2001).

Many of the problems and unsolved questions in fragmentation research appear to result from focusing on single organism groups, often butterflies or vascular plants. On the one hand, the level of a single group is too narrow to derive comprehensive landscape management guidelines, since other taxa might show quite different responses to landscape fragmentation. On the other hand, the level of single taxa is usually too broad for a detailed analysis of the relationship between fragmentation response and particular biological or ecological traits, since taxa are often comprised of species with a wide variety of life cycle and dispersal strategies. As shown for range shifts in response to global warming in fragmented habitats, within-taxon variation in habitat preference, dispersal capacity, longevity and body size is so high that generalisations at the taxon level are usually of limited value (Hickling et al., 2006). Even within the butterflies, a group superficially appearing to be homogeneous with regard to dispersal capacity and habitat use, Öckinger et al. (2009) detected disparate responses towards habitat fragmentation between sedentary and mobile species. Studies addressing taxon species richness will thus combine species with different response patterns in unknown proportions, and are thus likely to lead to inconsistent results (Debinski and Holt, 2000).

To address these problems, we based our study not on a single selected taxon, but on a large set of plant and animal taxa with pronounced differences in dispersal power, habitat requirements, life cycles and food chain positions. This means that responses to fragmentation are potentially quite diverse. While it is impossible to investigate all taxa living in a landscape, this broad selection should provide a more balanced and representative picture on fragmentation responses. Any conservation measures altering the landscape configuration or the ecological conditions in grassland patches will affect all species living there, not just a single taxon addressed in a particular study. Therefore, the first step was to analyse the net response of wholesale biodiversity. In a second step,

we sought to determine whether the general pattern obtained for all taxa analysed together would also apply for animal and plants analysed separately and for individual taxa.

We tested a number of variables that were not only related to patch and landscape element size and configuration, but also to habitat quality. In addition to patch quality characteristics, we explored quality attributes of landscape elements that could potentially function as corridors or stepping stones. The aim of the study was thus to relate the species richness of patches to a 2×2 predictor matrix reflecting the local-landscape dichotomy and the size-quality dichotomy. As the concepts of island biogeography and metapopulation ecology are only applicable to species with habitat preferences that are consistent with the island-ocean paradigm, we classified species according to their dependence on dry grassland patches into categories; in particular, we distinguished between species completely restricted to those patches and species preferring dry grassland patches but occurring also in other non-arable landscape elements. Our main questions were: (1) Which percentage of species conforms to the island-ocean paradigm? (2) How important are local, landscape and quality variables for the species richness of dry grassland specialist species, all grassland species, all species and individual taxa? (3) To what extent does the pattern observed for specialist species richness of all taxa agree with the pattern observed for single taxa?

2. Materials and methods

2.1. Study area

The study was conducted in the Pannonian part of eastern Austria, i.e. in the lowlands that extend from the eastern Alps to the Carpathians (Fig. 1). Until the Second World War, these landscapes were characterised by large, extensively used grassland areas (Bieringer and Grinschgl, 2001; Kohler et al., 1994). With the exception of some nature reserves (Paar et al., 1993) and military training areas (Bieringer et al., 2001), most of the large grassland areas have disappeared. However, within the landscape now largely dominated by intensive agriculture, a number of small grassland patches have persisted (Holzner et al., 1986; Paar et al., 1994). Agricultural use of these patches gradually ceased during the 1960s and 1970s, but has partly been re-established during the last decades, encouraged by agri-environmental schemes. Fifty dry semi-natural grassland patches were selected in the study area between the outskirts of Vienna, the eastern slopes of the Alps, the 'Seewinkel' region east of Lake Neusiedl, and the river Danube in the north. The climate is subcontinental with 610–660 mm annual precipitation, average temperatures between 9.4 °C and 9.8 °C and an annual temperature amplitude of about 20 °C between the temperature average of the coldest and the warmest month (Walter and Lieth, 1967). Altitudes range from 117 to 290 m a.s.l.

2.2. Site selection

From a set of about 90 known dry grassland fragments (Holzner et al., 1986; Paar et al., 1994, unpubl. data), we selected 50 study patches. Selection criteria were (1) the dominant plant community belonging to the class *Festuco-Brometea* Braun-Blanquet et Tüxen ex Soó 1947 (Mucina and Kolbek, 1993; Willner et al., 2013), (2) a patch size between 0.05 and 10 ha and (3) Tertiary or Quaternary geology (rock grasslands along the periphery of the region were excluded). To avoid pseudoreplication due to spatial proximity, only one patch of a group of patches within a distance of patch centroids less than 1000 m was retained in the set of study sites. Preliminary correlation analyses were calculated to identify groups of patches that showed a high degree of autocorrelation. To ensure

homogenous coverage of the variable space, only one patch of such groups was retained in the final set of studied patches. We standardised the sampling effort across all 50 habitat patches. Within each patch, we established two nested permanent sampling plots of 5 m × 5 m and 20 m × 20 m around the patch centroid, henceforth referred to as 25-m^2 plot and 400-m^2 plot.

2.3. Sampling of organism groups

We sampled vascular plants within the 25-m^2 plot. All species were recorded, and their cover and abundance was estimated using a modified Braun-Blanquet scale (Rabotnov, 1984). Additionally, to determine the variable patch heterogeneity (*PHET*; see Section 2.4), plant species richness within the 400-m^2 plot was estimated by recording all additional species occurring in four rectangles of 5 m × 7.5 m adjacent to the central quadrat. The plots were visited three times during the year (early spring, early and late summer). A comprehensive account on the plant communities recorded in the patches was provided in Willner et al. (2004).

Bryophytes were collected once in April 2001, a time of the year known to be optimal for bryophyte growth in the investigated area (Zechmeister, 1998). Thirty minutes were spent recording all bryophytes within the 25-m^2 plot. Specimens were collected and identified in the laboratory.

We sampled gastropods (Gastropoda), spiders (Araneae), surface-active springtails (Collembola), grasshoppers (Orthoptera), ground beetles (Carabidae), rove beetles (subfamily Staphylininae) and ants (Formicidae) by pitfall trapping. Three pitfalls (glass jars of 4.5 cm opening diameter, converging on top, half-filled with ethylene glycol as preservative and some droplets of a detergent) were placed in a triangle around the patch centroid, with two pitfalls in the corners of the 25-m^2 plot and one in the middle of the opposite side. Pitfalls were continuously exposed from 12 April to 9 November 2001 and emptied every three weeks. No roof was used to avoid microclimate modification. Trap loss was negligible. In the laboratory, we pooled the contents of the three traps per site, sorted them by organism groups and stored the material in ethanol for identification. Owing to the large numbers, surface-active springtails were only used from the first trapping period (12 April to 4 May 2001). Grasshoppers were additionally assessed by two field surveys. The period of the first field survey was from 30 June to 10 July 2001. From the centre of each grassland patch, all singing species were recorded for 5 min with an ultrasound detector (Mini-3-Bat, Ultra Sound Advice). All patches were visited between 12:00 and 18:00. The second field survey was conducted from 24 to 27 August between 08:30 and 16:00. Circles of 20 m diameter around the centre of each patch were observed for 10 min. Species were identified by acoustic or morphological characters, as appropriate.

True bugs, planthoppers and leafhoppers (Heteroptera, Fulgoromorpha and Cicadomorpha) were sampled with a sweeping net (20 strokes along each length in the periphery of the 25-m^2 plot). Additional specimens were obtained by visually collecting specimens on food plants within the 400-m^2 plot for half an hour per site and from pitfall trapping. Field work was done during two-week periods in May, July and September between 9:00 and 18:00 on clear days without precipitation.

True butterflies (Papilionoidea), skippers (Hesperiidae) and burnets (Zygaenidae), were surveyed three times between May and August. The 400-m^2 plot was paced in loops lasting 15 min per sampling period. Surveys were conducted between 10:00 and 17:00 during weather conditions suitable for butterfly recording (Pollard, 1977), which was controlled by air-temperature (Testotherm testo) and wind-velocity measurements (ATP Messtechnik) as well as cloudiness estimation. Individuals were caught with a sweep net (38 cm in diameter), identified to species level and released. Species requiring genital identification were killed and transferred to the
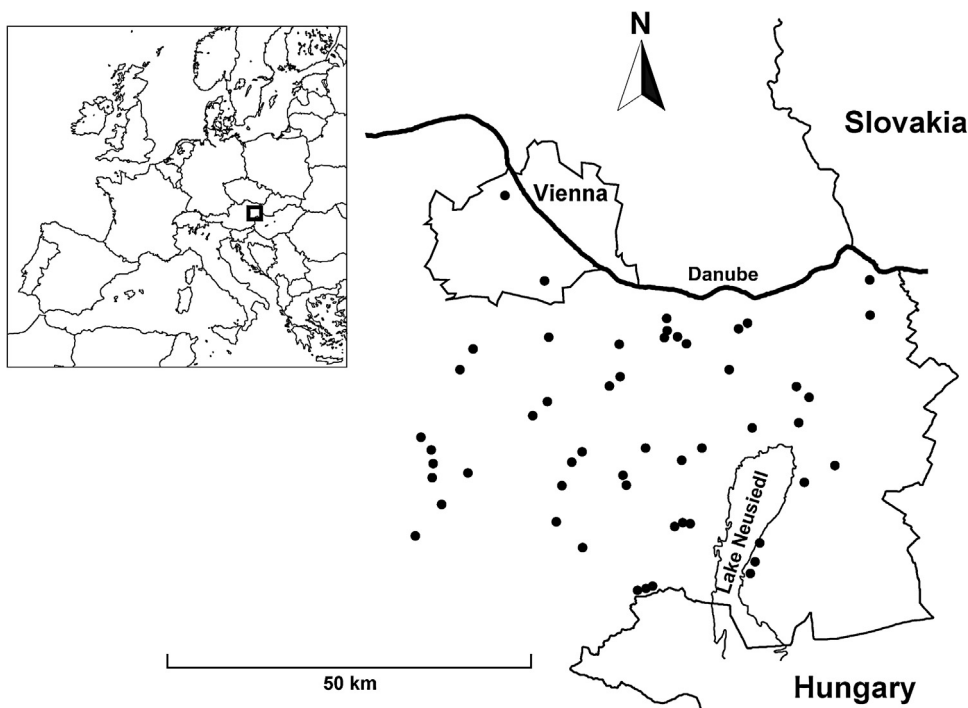
Fig. 1. Study area in eastern Austria and spatial arrangement of the dry grassland patches in the region.

laboratory. The species pairs *Zygaena purpuralis* and *Z. minos*, *Colias hyale* and *C. alfacariensis*, *Plebeius idas* and *P. argyrognomon*, as well as *Melitaea aurelia* and *M. britomartis* were not separated, referred to as species complexes, and counted as one species each.

Wild bees (Hymenoptera: Apoidea) were collected by sweep-netting, using a sweep-net of 30 cm diameter. Every patch was visited between 14 April and 14 June and between 14 July and 14 September. In every 25-m² plot, three 1 m × 1 m squares were haphazardly positioned. Within these squares, all flowers were sampled for 5 min. About 40% of the individuals were identified in the field, the remainder collected for later laboratory identification.

Elutriation and subsequent dry sieving of soil samples complemented pitfall trapping results for gastropods. Between 8 and 10 August, three soil samples of 10 cm² area and 7 cm depth were taken in each patch along the sides of the 25-m² plot. Samples were pooled, homogenised and elutriated. The remaining soil was dried and sifted through five sieves of different mesh width. Sieve remainders were inspected under a stereomicroscope for live and fresh dead gastropods.

2.4. Environmental variables

We recorded a series of variables classified into local vs. landscape, and quantity vs. quality variables (Table 1). Current patch area *(AR00)* was obtained by GIS analysis of aerial photographs taken near the year 2000. On these photographs, a 1 km × 1 km quadrat around each patch centroid (henceforth referred to a 1-km² quadrat) was delineated and digitised, using the program ArcInfo (ESRI Inc.). The variables *AR00*, patch fractal dimension *PFD* (the ruggedness of the patch border) and shape index *SHAPE* (the deviation of the patch shape from a quadrat) were obtained from this digitisation using the program ArcView Patch Analyst (Elkie et al., 1999) and Fragstats (McGarigal and Marks, 1995). Historical patch area *(AR50)* was delineated on aerial photographs taken in 1950. We used SigmaScanPro 5.0 (Systat Software Inc.) for the area calculation.

To quantify the habitat quality of the patch, we measured aboveground standing phytomass in the patches in April and August *(PHYT4* and *PHYT8)* using a disc pasture meter (Bransby and Tainton, 1977; Dörgeloh, 2002). A 20 cm × 20 cm disc of 100 g weight was released from 1 m height and its final position above the ground was measured. An average of fifteen measures, made within the 400-m² plot, was used in the analyses. The proportion of these measures below 10 cm was used to calculate short-grass area 2000 *(SH00)* by multiplying area with this fraction (Table 1) and thus to enable a direct comparison between geometrical patch measures and quality-weighted patch measures. To account for a possible extinction debt, a historical version of this variable was similarly calculated by multiplying the current proportion of short-grass area with historical patch area *(SH50)*. The variable shrub encroachment *(SHRUB)*, quantifying the proportion of the patch dominated by shrubs, was obtained from the GIS analysis of aerial photographs and ground truthing.

We determined soil temperature sums *(TEMP)* during a 25-day period in August and September using the polarimetric sugar inversion method of Pallmann et al. (1940). The velocity of sucrose hydrolysis into glucose and fructose is temperature-dependent; all of the sugars are optically active in solution, from the rotation angle ratio before and after exposition, the sugar concentration ratio and the temperature sums during exposition can be determined. In each plot, two plastic tubes containing 20 ml of sugar solution were buried in 5 cm depth. During transport, the samples were kept in a cold box. Rotation angles were measured immediately before the start and shortly after the end of the exposition period with a circular polarimeter (Atago Polax-D). We used rotation angles instead of mean temperatures in the analyses.

Another modifier of the patch quality is soil composition, both directly by influencing the habitat of soil-inhabiting and surface-active organisms, and indirectly by modifying microclimate. To analyse soil composition, we took three soil samples from the 25-m² plot boundary in August. Soil cylinders of 10 cm² surface area and 10 cm depth were homogenised and dried at 105 °C. Dry sieving separated gravel content (*GRAV*, >2 mm) from the remaining

Table 1
Independent environmental variables, their abbreviations, variable transformations used in the analyses and gradient lengths. Further explanations of the variables can be found in the text.

Variable	Abbreviation	Unit	Transformation	Min	Mean	Max
Local size and shape measures						
Patch area 2000	AR00	ha	ln	0.04	1.29	9.73
Patch area 1950	AR50	ha	ln	0.05	6.69	60.41
Patch fractal dimension	PFD			1.28	1.41	1.60
Shape index	SHAPE			1.15	1.57	2.61
Local quality measures						
Above-ground standing phytomass April	PHYT4	cm		5.3	9.8	15.8
Above-ground standing phytomass August	PHYT8	cm		5.9	12.3	26.7
Short-grass area 2000	SH00	ha	ln	0.01	0.82	9.73
Short-grass area 1950	SH50	ha	ln	0.01	4.32	60.02
Shrub encroachment	SHRUB	%	angular	0%	7%	30%
Temperature	TEMP	°		11.3	19.3	32.6
Clay content	CLAY	%	angular	1%	17%	44%
Silt content	SILT	%	angular	0%	28%	73%
Sand content	SAND	%	angular	10%	55%	99%
Gravel content	GRAV	%	angular	0%	21%	72%
Organic material content	ORGM	%	angular	1%	8%	24%
Agricultural edge	AGRIC	%	angular	0%	19%	95%
Shading edge	SHADE	%	angular	0%	21%	100%
Patch heterogeneity	PHET			5	17.14	40
Landscape scale: size and distance measures						
Area of extensively used elements	EXTEN	ha	ln	1.64	10.22	35.54
Area of linear elements	LINEA	ha	ln	0.24	1.03	2.67
Distance to mainland	MAINL	m	ln	250	4610	12,250
Landscape scale: quality measures						
Area of extensive grassland	EXTGR	ha	ln	0.00	1.39	27.18
Area of fallow land	FALLO	ha	ln	0.97	10.61	31.02
Area of short-grass dry grassland	SHGRA	ha	ln	0.00	0.51	6.49
Area of short-grass linear elements	SHLIN	ha	ln	0.00	0.10	0.99
Landscape heterogeneity	LHET			13	22.34	37

fine soil (<2 mm). The fine soil components were further separated by sedimentation analysis. Percentages of sand fractions *(SAND)*, silt *(SILT)* and clay *(CLAY)* fractions refer to fine soil; the percentage of gravel content *(GRAV)* refers to total soil weight. The content of organic material *(ORGM)* was determined by burning fine soil at 500 °C and assessing the weight loss (Austrian Federal Agency for Soil Analysis). Patch heterogeneity *PHET* was measured as the increase in vascular plant species richness between the 25-m^2 quadrat and the 20 m × 20 m cross (cf. Section 2.3).

To determine edge and landscape effects on patch species richness, spatial elements (Forman, 1995, p. 39) were delineated within the 1-km^2 quadrat around the patch on the aerial photograph. By ground-truthing, one of 62 pre-defined land use types out of 10 pre-defined land cover classes was assigned to each landscape element. Disturbance effects of an agricultural matrix (variable 'agricultural edge', *AGRIC*) were determined by calculating the percentage of the edge bordering intensively farmed agricultural land use types (agricultural fields, vineyards, intensively used meadows). Shading effects *(SHADE)* were quantified by calculating the percentage of woodland types (forests, single trees, shrubs and hedges) bordering the patch.

To define a quantitative isolation measure, the distance between patch centroid and the nearest large dry grassland area (>15 ha, termed as 'mainland') was measured on a topographical map (scale 1:50,000; *MAINL*). Additionally, a series of landscape composition variables was determined. Within the 1-km^2 quadrat around the patch, a subset of land use types that were assumed to facilitate re-colonisation and to enhance landscape connectivity of dry grassland patches were classified in closer detail. Spatial elements containing grassland of various kind, verges, margins and other semi-natural biotope types dominated by herbaceous vegetation were considered, provided that they were only slightly affected by human influence (β-hemerobic or less intensive, cf. Zechmeister and Moser, 2001). Attributes describing vegetation height,

vegetation density, substrate conditions, shape (in particular linearity), resource availability (dryness, nutrients), richness in structural elements (flowers, stones), and shrub density were assigned to each spatial element or sub-element. Landscape elements along with their attribute vector were entered into a database. Queries against this database provided land use type selections of increasing quality. The variable 'area of extensively used elements' *EXTEN* provided a landscape measure without any quality considerations; in this variable, essentially all landscape elements with no or extensive agricultural use were combined (i.e. set-asides, verges, extensively used grasslands, vineyards). The variables 'area of fallow land' *FALLO* and 'area of extensive grassland' *EXTGR* reduced this selection to fallows and extensively used grasslands, respectively. The variable 'area of short-grass dry grassland' *SHGRA* restricted the selection of landscape elements to natural high-quality grasslands with a short sward. Similarly, we distinguished between linear landscape elements without quality restriction (*LINEA*, typically field margins) and high-quality linear elements with short-grass vegetation *(SHLIN)*. Finally, to obtain a measure for landscape heterogeneity, the number of land use types in the 1-km^2 quadrat around the patch was counted *(LHET)*.

2.5. Species richness variables

We used the species richness values obtained by the various trapping methods as dependent variables. Since only the centre of the patch was sampled, the numbers should not be regarded as indicative of the whole-patch species richness, but rather as species density values. We classified the species into the following categories of patch dependence: (1) Highly patch-dependent dry grassland specialist species. Owing to their habitat requirements, persistence of these species in the agricultural matrix is not possible. Species in this category usually require dry and warm conditions. (2) Species with a preference for grassland habitats.

Table 2
Cumulative species richness of all 50 dry grassland patches. Species were classified according to their patch dependence: 1 = dry grassland specialists; 2 = other grassland species; 3 = other species.

Organism group	1	2	3	Total
Mosses and Liverworts (Bryophyta)	8	21	43	72
Vascular plants (Trachaeophyta)	60	119	164	343
Gastropods (Gastropoda)	2	11	17	30
Spiders (Araneae)	24	60	102	186
Springtails (Collembola)	9	12	65	86
Grasshoppers (Orthoptera)	5	18	15	38
True bugs (Heteroptera)	16	96	151	263
Leafhoppers and planthoppers (Fulgoromorpha and Cicadomorpha)	14	41	63	118
Ground beetles (Carabidae)	24	42	47	113
Rove beetles (Staphylininae)	7	16	30	53
Butterflies and burnets (Rhopalocera and Zygaenidae)	10	45	8	63
Ants (Formicidae)	3	23	20	46
Wild bees (Apoidea)	1	96	35	132
Total	183	600	760	1543

These species prefer the patches over the agricultural matrix, yet are not restricted to the patch habitats; they may live and reproduce in other elements of the agricultural landscape as well, e.g. in road verges or set-asides. (3) Other species. In the analyses, we tested species richness of the category 1 species (dry grassland specialists), numbers of group 1 and 2 species combined (all grassland species) and all categories together (all species). Species were assigned using habitat preference data obtained from an earlier project (Sauberer et al., 2004), literature data, own collection data and personal experience.

2.6. Statistical analysis

In the first step, we calculated a Pearson correlation matrix between the 26 independent variables (Table 1, ESM 1). In the second step, we performed single regressions between the independent variable and the three species richness measures (category 1, categories 1 + 2, all species). In test runs, we modelled species richness using generalised linear modelling (McCullagh and Nelder, 1983) with log link and Poisson errors, but owing to overdispersion, quasi-Poisson error structures had to be assumed (software R 3.0.1, package glm, R Core Team, 2013). However, GLM with quasi-Poisson errors led to error probabilities that were numerically very similar to error probabilities obtained with ordinary least squares regression. Consequently, for sake of simplicity and better interpretability, the latter regression modelling approach was applied for single regression analyses (Table 3). Variables were transformed as necessary (Tables 1 and 3). Owing to the large number of tests on the same data body, we calculated the positive false discovery rate using the R package qvalue 1.36.0 (Dabney et al., 2013) and set the probability threshold to $q = 0.05$ (Table 3, ESM 2). The positive false discovery rate approach developed by Storey et al. (2004) is a far more powerful approach to significance correction in multiple testing compared to Bonferroni-type adjustments and allows for the initial screening of a large number of variables (Roback and Askins, 2005).

Based on the correlation and single regression results, we subjected species richness values of category-1 species (dry grassland specialists) to multiple regression analyses. We selected nine variables representing the local vs. landscape and quantity vs. quality categories with high explanatory power in single regressions and a low degree of mutual correlation. Since the main goal was to identify variables with a high direct influence on species richness (cf. Mac Nally, 2000), we used hierarchical partitioning for the analysis (Chevan and Sutherland, 1991). Hierarchical partitioning calculates all possible regression subsets, averages model improvements across all hierarchies and thus permits a ranking of variables by their independent effects. We calculated models for all taxa combined, for animals and plants and for individual taxa with at least 10 category-1 species (cf. Table 2) using the R package 'hier.part' (Walsh and Mac Nally, 2013). To identify non-redundant variables in the set of the nine variables, we additionally performed multiple regression analyses with backward elimination (P_F to remove > 0.1), starting with the full set of all nine variables. Pearson correlations, single regressions and multiple regressions with backward elimination were calculated with the software SPSS 10.0.5 (SPSS Inc., now IBM Corp.).

3. Results

3.1. Catch results and species richness

We recorded a total of 1543 species in the 13 organism groups, with vascular plants and true bugs being the most species-rich groups. On average, only 12% of the species in the small grassland fragments were dry grassland specialists (category 1), with proportions ranging from 1% in wild bees to 21% in ground beetles (Table 2). About 51% of the species could be classified as grassland species in a broader sense (categories 1 and 2 combined).

3.2. Correlations among environmental variables and single regressions

Pearson correlation analysis of the independent variable data set showed a generally low degree of correlation (ESM 1). However, some patch shape indices and measures of linear landscape elements were substantially correlated.

In single regressions, AR00 was a poor predictor of the species richness of dry grassland specialists; it performed even worse for all grassland species (categories 1 and 2 combined) and the richness of all species (Table 3). Using the historical patch size (AR50) instead of the current patch size improved the explanatory power considerably, especially for dry grassland specialists (category 1). The sign of the shape variables PFD and SHAPE was negative, but variance explanation was limited and the models were insignificant.

By contrast, several variables describing the patch conditions qualitatively were highly significant predictors for dry grassland specialist species, in particular PHYT4, PHYT8 and GRAV. The highest species richness of dry grassland specialists was found in open patches on gravel with a short sward. The quality-weighted area measures SH00 and SH50 had much higher explanatory power than the geometrical area measures AR00 and AR50. None of the patch quality measures was a significant predictor for total grassland species richness, but species richness of all species responded positively to the percentage of agricultural matrix around the patch AGRIC and patch heterogeneity PHET (Table 3).

Species richness of specialists and grassland species increased significantly with the amount of extensively used landscape elements (EXTEN) in the 1-km² quadrat around the patches. All three measures of species richness decreased significantly with increasing distance to the next large grassland area in the region (MAINL; Table 3).

Among the qualitative landscape-scale variables, SHGRA was a significant predictor of all three species richness measures, though variance explanation was about twice as high for specialist species and grassland species richness than for the species richness of all species. Specialist richness and grassland species richness were also significantly higher in complex landscapes with many biotope types (LHET, Table 3). The explanatory power of other qualitative

Table 3
Single regressions of the three species richness measures against patch and landscape variables (b = sign of the regression coefficient, r^2 = goodness of fit, P = error probability).

Variable	Category 1 (dry grassland specialists)			Categories 1 and 2 (all grassland species)			All categories (all species)		
	b	r^2	P	b	r^2	P	b	r^2	P
Local quantity (size and shape) measures									
AR00	+	0.020	0.331	+	0.013	0.431	+	0.000	0.895
AR50	+	0.122	0.013*	+	0.037	0.181	+	0.019	0.341
PFD	−	0.057	0.094	−	0.024	0.282	−	0.024	0.285
SHAPE	−	0.074	0.056	−	0.033	0.208	+	0.001	0.815
Local quality measures									
PHYT4	−	0.218	0.001*	−	0.017	0.360	+	0.100	0.026
PHYT8	−	0.182	0.002*	−	0.052	0.111	+	0.016	0.376
SH00	+	0.072	0.060	+	0.028	0.245	−	0.004	0.647
SH50	+	0.189	0.002*	+	0.052	0.113	+	0.004	0.651
SHRUB	−	0.001	0.870	+	0.027	0.254	+	0.064	0.077
TEMP	+	0.069	0.066	+	0.033	0.210	−	0.006	0.592
CLAY	−	0.024	0.284	−	0.004	0.670	+	0.006	0.601
SILT	−	0.036	0.184	+	0.000	0.986	+	0.029	0.234
SAND	+	0.063	0.080	+	0.004	0.646	+	0.018	0.354
GRAV	+	0.204	0.001*	+	0.067	0.069	−	0.000	0.937
ORGM	+	0.056	0.098	+	0.052	0.111	+	0.040	0.165
AGRIC	+	0.005	0.623	+	0.057	0.094	+	0.100	0.026*
SHADE	+	0.005	0.620	+	0.001	0.834	+	0.004	0.655
PHET	+	0.007	0.576	+	0.085	0.039	+	0.216	0.001*
Landscape scale: quantity measures									
EXTEN	+	0.109	0.019*	+	0.098	0.027*	+	0.040	0.165
LINEA	−	0.029	0.234	−	0.031	0.220	−	0.058	0.092
MAINL	−	0.121	0.013*	−	0.147	0.006*	−	0.108	0.020*
Landscape scale: quality measures									
FALLO	+	0.056	0.097	+	0.019	0.336	+	0.005	0.614
EXTGR	+	0.000	0.945	−	0.017	0.367	−	0.031	0.224
SHGRA	+	0.193	0.001*	+	0.199	0.001*	+	0.104	0.023*
SHLIN	+	0.008	0.527	+	0.003	0.721	+	0.022	0.308
LHET	+	0.120	0.014*	+	0.146	0.006*	+	0.033	0.207

*An asterisk denotes a significant test ($P < 0.05$) with a positive false discovery rate $q < 0.05$ (see ESM 2 for a full table of all q values and P values).

landscape variables, such as fallow area *(FALLO)*, extensive grassland area *(EXTGR)* or area of short-grass linear structures *(SHLIN)*, was low and insignificant (Table 3).

3.3. Hierarchical partitioning and backward elimination

For dry grassland specialists of all taxa combined, the patch variables *PHYT4* and *GRAV* showed the highest independent effects, followed by the landscape quality variable *SHGRA* (Fig. 2). Backward elimination retained the quantitative landscape variables *EXTEN* and *LINEA* as additional non-redundant variables in the final model, but their independent and joint contributions in hierarchical partitioning analysis were considerably lower. As in single regression, specialist richness decreased with increasing area of linear elements *(LINEA)*.

The pattern for specialist plant taxa was similar, but the direct effects of quality variables at the patch scale *(PHYT4, GRAV)* were more pronounced and landscape effects were lower than for all taxa combined. By contrast, dry grassland specialist richness of animal taxa was more influenced by landscape variables, in particular *SHGRA* and *MAINL*. For animals, *LINEA* was a non-redundant variable with a negative sign. For animal species richness, patch quality variables were less important and historical patch area was more important compared to the all taxa pattern.

Except for vascular plants, variance explanation levels for single taxon models were low. Historical patch size AR50 had a positive effect on spiders (though eliminated as redundant), true bugs and ground beetles, but had almost no influence on leafhoppers and planthoppers, butterflies and burnets. The quality variable *PHYT4*, which showed a negative direct effect on species richness of all taxa combined, was also negative for spiders, true bugs and ground beetles, but not for leafhoppers and planthoppers, butterflies and
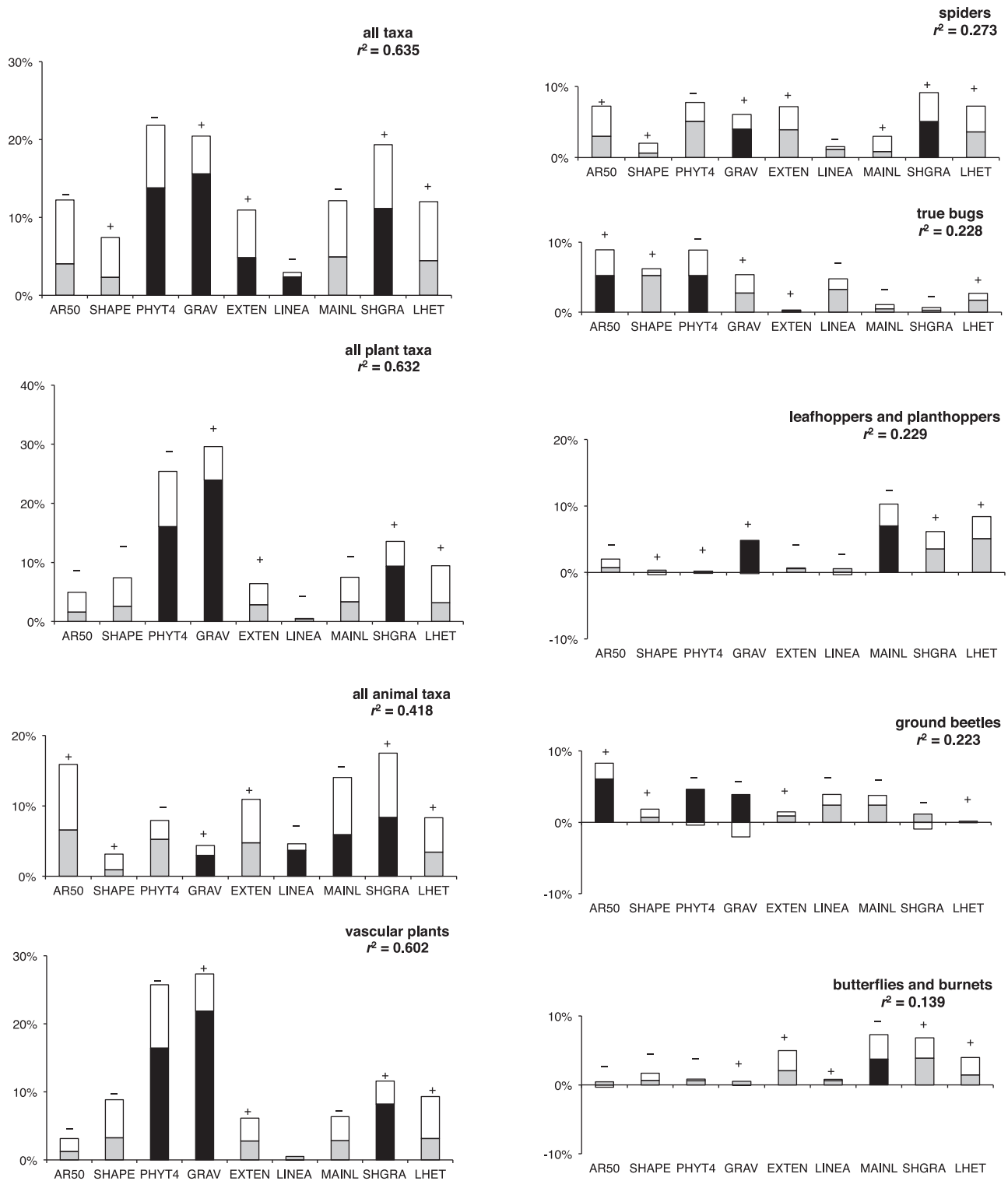
burnets. Among the landscape variables, the quality variable *SHGRA* usually had higher explanatory power than the qualitative variable *EXTEN*. *MAINL* was retained as non-redundant variable in the models for butterflies/burnets and leafhoppers/grasshoppers; for these taxa, its direct effect was amongst the highest of all variables.

In all models, the direct and indirect effects of *SHAPE* were smaller than those of most all other variables and the variable was typically flagged as redundant (Fig. 2). *LINEA* had no direct effect on plant species richness and a negative direct effect on most animal taxa (though being eliminated as redundant in single taxon analyses). The variable *LHET* was redundant in all models.

4. Discussion

4.1. Fragmentation

The habitat fragmentation paradigm emerged from island biogeography, metapopulation theory and landscape ecology. It has been the governing explanation for biodiversity patterns in highly modified agricultural landscapes over the past decades, although its generality and value as an explanatory tool have been increasingly questioned (Fahrig, 2003; Haila, 2002; Harrison and Bruna, 1999; Lindenmayer and Fischer, 2007). Conceptually, the main problem seems to be the conflation of habitat, essentially a species property, and patch, essentially a human perception of a landscape element (Lindenmayer and Fischer, 2007). In reality, species habitat requirements and patch area will never exactly match, even for typical patch-dependent species. We made considerable efforts to delineate those species across all organism groups for which the species' habitat perception and human perception of a grassland patch corresponded sufficiently, i.e. the dry grassland specialists of

Fig. 2. Combination of hierarchical partitioning and backward elimination regression analyses for species richness numbers of dry grassland specialists. Independent (light and dark grey columns) and joint variance explanation (white columns) averaged across all hierarchies of nine predictors of dry grassland species richness for all taxa combined, for animal and plant taxa and for single taxa separately. Variable abbreviations and variable categorisations as size, shape and quality variables as in Table 1. The sign indicates the direction of variable coefficients in the full nine-variable model. Variables excluded by backward elimination ($P_{F\ to\ remove} > 0.10$) are displayed in light grey, variables retained in the model are displayed in black. Negative white columns indicate suppression effects.

category 1. The proportion of species belonging to that category was remarkably low, being just 12% of the total species richness in the patches. For these species, it can be safely assumed that they are restricted to the grassland patches, experience other habitats as hostile and do not tolerate disturbances usually encountered in arable fields. Results for these category-1 specialists are generally in line with the predictions of the habitat fragmentation paradigm: We observed an increase of plot species richness with patch area, at least when measured as historical area or as current short-grass area, with landscape-level stepping stone area, again measured

preferably in area of high-quality habitat, and proximity to large grassland areas.

For the species richness of all grassland species, the patch-matrix-corridor landscape model was not applicable, as reflected in the results of Table 3. Since these species are, by definition, not restricted to the patches, it was not surprising that patch variables were not found to have high explanatory power. By contrast, several variables at the landscape scale were found to be good predictors of grassland species richness, all of which can be interpreted as enhancing landscape element diversity and complexity of agricultural landscapes. Richness of all grassland species was positively related to the area of extensively used landscape elements EXTEN, to the proximity of a large grassland MAINL, the area of short-grass dry grassland SHGRA and the number of biotope types in the surrounding 1-km quadrat LHET. Consequently, a landscape variegation model (McIntyre and Barrett, 1992; McIntyre and Hobbs, 1999) relating species richness patterns primarily to the diversity of landscape elements, describes species richness of all grassland species better than a binary island-ocean fragmentation model. The differences in the results between species richness of dry grassland specialists and richness of all grassland species is also in line with "hypothesis 8" in Tscharntke et al. (2012), which states that different management strategies are required to enhance functional diversity and ecosystem services in agricultural landscapes on the one hand and to protect endangered species on the other. However, our results suggest that these two aims can be reconciled with each other; in other words, diversification of the agricultural landscape by setting aside habitat and by providing short-grass area will benefit all grassland species, whereas additional quality-enhancing measures may be necessary at the patch scale (see Section 4.2) to protect endangered dry grassland specialists (Table 3).

Species richness of all species in the patch, however, appeared to be significantly influenced by spillover effects from arable land, not only reflected by the high proportion of non-grassland species in the patches (Table 2), but also the significant effect of the variable AGRIC representing the proportion of agricultural edge. As Blitzer et al. (2012) conclude in their review, such spillover effects have been underestimated for a long time, but as demonstrated in our study, they are highly influential on the species assemblage of grassland patches. Evidently, species richness patterns in agricultural landscapes with grassland patches appear to be a complex superposition of several responses types, requiring further concepts in addition to the island-ocean paradigm for a comprehensive description (Fahrig et al., 2011).

4.2. Local factors

Patch area is one of the central quantities of the habitat fragmentation paradigm (Debinski and Holt, 2000). Even if species richness is measured with a standardised sampling effort across patches, local species density of patch-dependent species should be higher in larger patches, since extinction is less likely and immigration is more likely than in smaller patches, all else being equal (Connor and McCoy, 1979). Our results for dry grassland specialists were in line with these predictions only after two important adjustments: (1) We found that historical patch area was a better predictor than current patch area. (2) Area measures weighted by habitat quality performed much better than patch area as calculated from aerial photography.

The result that historical patch area (AR50) was a better predictor than current area agrees with recent findings for plant species richness in several regions (e.g. Eriksson et al., 2002; Helm et al., 2006; Kuussaari et al., 2009; Lindborg and Eriksson, 2004; Piqueray et al., 2011). Species with long generation times and populations near their extinction thresholds are particularly prone to incur an extinction debt (Hanski and Ovaskainen, 2002; Kuussaari et al.,

2009). However, in our analyses, historical area had a higher independent variance explanation for animals (in particular for ground beetles and true bugs) than for vascular plants.

Regarding plants, current habitat quality measures (PHYT4, GRAV) and quality-weighted area measures (SH00, SH50) were more powerful predictors of species richness than area per se (AR00, AR50). The independent effect of phytomass on the species richness of specialists was about four times higher than the effect of historical patch area (Fig. 2). Since extinction events are typically triggered by a reduction of the patch carrying capacity plus environmental fluctuations, habitat degradation can have quick and detrimental consequences on population sizes and extinction risks (Mortelliti et al., 2010). In some earlier studies, habitat quality measures have emerged as variables that add unnecessary complexity to the description of patch occupancy (Moilanen and Hanski, 1998). Later, evidence has accumulated that habitat parameters can play a major role in determining survival in patchy landscapes (Collinge et al., 2003; Fleishman et al., 2002). Thomas et al. (2001) found that patch habitat quality variation explained patch occupancy much better than patch area for three species of British grassland butterflies. Patches with optimal habitat may have butterfly equilibrium densities more than 200 times higher than sub-optimal yet still occupied patches (Thomas, 1984). Independent effects of quality predictors for vascular plant specialist species richness eclipsed those of all other variables (Fig. 2). With respect to animals, independent effects of historical area and patch quality variables were of similar magnitude. As shown in the analyses of individual animal taxa, not all animal groups responded positively to short swards and gravel in the soil.

Among the factors affecting habitat quality in the patches, edge effects are considered important (Saunders et al., 1991). The high proportion of generalist species found in the patches (Table 2) supports this prediction. However, we found no evidence that patch shape (PFD, SHAPE) and the habitat types bordering the patch (AGRIC, SHADE) significantly affected the species richness of dry grassland specialist species in the centre of the patches (cf. Yamaura et al., 2008). By contrast, AGRIC was a significant predictor of total species richness. A sampling scheme more specifically targeted at this purpose might be necessary to further clarify possible edge effects.

4.3. Landscape factors

In our study, landscape variables were influential for all dry grassland specialist taxa combined and also for many taxa analysed individually. For vascular plant grassland specialist richness, the landscape quality measure SHGRA had the highest independent effect. For mobile animal taxa, other landscape measures, e.g. MAINL, were also important and their independent effects were often at least as high as those of local factors (Fig. 2). This contrasts with earlier studies that landscape factors are often insignificant species richness predictors for invertebrates (Mazerolle and Villard, 1999) and is in line with more recent findings that highlight the importance of the surrounding landscape for species survival in patches (e.g. Batáry et al., 2007; Janišová et al., 2013; Reitalu et al., 2012; Steffan-Dewenter and Tscharntke, 1999).

Habitat quality was important not only at the patch scale, but also at the landscape scale. The independent effect of SHGRA, a metric quantifying the area of short-grass grassland around the patch, was often more than twice as high as the independent effect of EXTEN, a metric quantifying a variety of landscape elements with low or no agricultural use (Fig. 2). Consequently, whether landscape factors are found to be significant predictors in fragmentation studies might not only depend on the selection of isolation measures, but also, and apparently to high degree, on the delineation of what counts as potentially connecting landscape element within

the surrounding landscape. This might explain the widely differing results for the importance of landscape factors in fragmentation studies.

Interestingly, measures quantifying linear elements (LINEA, SHLIN) showed no significant relationship to dry grassland richness in single regression analyses and frequently a negative effect in multiple regression analyses. What might be considered a corridor in a structural sense need not act as a corridor in a functional sense, or worse, it may even act as a habitat sink (Krewenka et al., 2011). In accord with similar findings (Liira et al., 2008), our results cast doubt on the possibilities of a cheap mitigation of fragmentation risks by field and road margins in agricultural landscapes.

4.4. Comparison of taxa

The response of dry grassland specialist plant species was characterised by a dominance of patch and landscape element quality variables (Fig. 2). This response also influenced the pattern of all taxa combined. In contrast, the response patterns of animals were more balanced between quantitative and qualitative variables, both at the patch and the landscape scale. Apparently, the wider variety of habitat requirements, life history and dispersal strategies in the many animal taxa involved in this study led to a more even response pattern with independent effects of the main predictor variables explaining a similar level of variance (Fig. 2). Overall, animal taxa conformed better to the island-ocean paradigm, whereas plant species richness was better described by habitat quality parameters. Vascular plants may resist extinction even in small isolated populations for some time as long as habitat conditions are preserved (Eriksson, 1996).

The hypothesis that sedentary taxa should be more influenced by local factors than mobile taxa (Öckinger et al., 2009) is broadly supported by our findings. Local factors were most important for vascular plants, moderately important also for animal taxa with mixed dispersal capacities, such as ground beetles, and the least important for butterflies, burnets, leafhoppers and planthoppers. By contrast, the long-distance landscape variable MAINL was among the best predictors for mobile animal taxa. Given the often widely diverging species richness patterns across taxa (cf. Turtureanu et al., 2013), it might have been reasonable to expect some conflicting differences in the responses at least for some of the taxa. However, for most variables, the signs were identical across taxa, only their relevance, measured as independent effects, varied considerably.

4.5. Conclusions and application

The results of this study indicate that a network of high quality patches, not too far apart from each other, may be the best conservation strategy in fragmented landscapes. Linear elements in the surroundings were either unimportant or even counterproductive. By contrast, size mattered, if measured as area of short-grass quality habitat. This overall outcome is in remarkable agreement with the results of a microcosm study on microarthropod metacommunities (Chisholm et al., 2011). Unfettered by the restrictions of mensurative experiments at the landscape scale, Chisholm et al. (2011) highlighted the overall importance of habitat quality and the limitations of linear elements, acting mostly as a sink habitat.

The goal of a high quality grassland network reconciles traditional management concepts with modern theoretical approaches: The first and foremost conservation goal should be the protection of short-grass dry grassland where it still exists, since these patches not only harbour the most patch-dependent specialist plant species, but also a number of very demanding animal species.

Second, the high importance of phytomass as a significant predictor of species richness at the patch scale and the similar importance of short-grass area at the landscape scale make the reduction of grass biomass a primary candidate for management intervention. This could be done by grazing or mowing, and is probably the fastest and most straightforward way to improve the habitat conditions for many dry grassland specialists. Third, landscapes with dense networks of short-grass patches should be protected or restored. Fourth, indications of an extinction debt call for the restoration of the patches to their historical size. In many cases, this might be implemented by the clearing of shrubs and subsequent grazing.

By contrast, general enhancement measures in the agricultural landscape might increase heterogeneity at the landscape scale and thus favour some generalist grassland species. This might be a complementary strategy to increase overall species richness in agricultural landscapes and to foster ecosystem services such as pollination and pest control. Extensification of grassland use alone would be insufficient to protect dry grassland specialists and generalist grassland species alike.

None of our conclusions on management strategies could have been derived from the analysis of single animal taxa alone, and biased conclusions would have been obtained by focusing only on vascular plants. We thus underline the recommendation by Söderstrom et al. (2001), who strongly advised against basing conservation strategies and the design of management actions in grassland patches on single-taxon studies. However, it might have been expected that conservation strategies derived from the responses of all taxa analysed together might have led to unfavourable consequences for single taxa within this pool; for example, vegetation-dwelling taxa such as true bugs or flower-visiting taxa such as butterflies might not benefit from reduction of sward height as suggested by the responses of vascular plant specialists and total specialist richness. Yet, we detected no such conservation strategy conflicts. This finding is in accord with Watling and Donnelly (2006), who concluded from their review of fragmentation studies that differences in response patterns between taxa were limited.

Considering further research on habitat fragmentation, the results of the present investigation indicate that habitat quality variables need particular emphasis, both at the patch and the landscape scale. Analysing species with similar traits (e.g. Öckinger et al., 2009, 2010) appears to be more informative than analysing particular taxa with a mixture of habitat requirements and dispersal strategies. However, an even better way to disentangle the complex responses of communities to habitat fragmentation would be to analyse the responses of individual species with finely tuned habitat and matrix variables and then to aggregate the results to obtain a general picture.

Issue gave valuable feedback on an earlier draft that helped to improve the analyses and the manuscript substantially.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.11.016.

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