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Effects of local climate, landscape structure and habitat quality on leafhopper assemblages of acidic grasslands

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ABSTRACT

Grassland biodiversity is severely threatened by recent land-use change. Agricultural intensification on the one hand, and cessation of traditional land use on the other, have caused habitat loss, fragmentation and often a deterioration in habitat quality of the remaining habitat fragments. However, knowledge about the different environmental effects on species richness is still limited, in particular for under-sampled groups like leafhoppers (Auchenorrhyncha). Our study therefore aims to analyse the impact of local climate, landscape structure and habitat quality on leafhopper assemblages.

Several environmental factors were assessed and species richness of leafhoppers was sampled on 30 acidic grassland patches in Central Germany. We used generalised linear models (GLM) to determine the variables that influence species richness.

Both landscape structure and habitat quality had a strong influence on the number of leafhopper species. At the landscape scale, a high diversity of open land cover types positively affected species richness. Furthermore, species richness increased with decreasing cover of arable land in the surroundings of a habitat fragment. The best predictor at the habitat scale was the structural diversity, which had a positive impact on the numbers of leafhoppers. Local climatic conditions and patch area played a minor role and had an effect only on threatened species.

We recommend establishing a great variety of different structural types within a patch in order to promote species-rich leafhopper assemblages. In addition, conservationists should focus their efforts on the maintenance of different types of grasslands in the surroundings of habitat fragments.

1. Introduction

The recent decline of biodiversity is of global concern and primarily driven by land-use change (Sala et al., 2000; Stoate et al., 2009; Foley et al., 2005). Intensification of agricultural production has dramatically changed landscape composition, leading to homogenisation, loss and fragmentation of natural and semi-natural habitats (Benton et al., 2003; Fahrig, 2003; Marini et al., 2012). Additionally, habitat fragments have frequently suffered from degradation, i.e., from deterioration in habitat quality (Fischer and Lindenmayer, 2007). On the one hand, this can be caused by the intensification of land use, and on the other hand, by the abandonment of traditional land use (MacDonald et al., 2000; Duprè et al., 2010).

Particularly affected by land-use change are grasslands (Bakker and Berendse, 1999; Hodgson et al., 2005; Krause et al., 2011). Over the last few decades, the area and biodiversity of European grasslands have decreased considerably (Stoate et al., 2009). The majority of former nutrient-poor grasslands have been fertilised or transformed into arable land, forest or settlements (Hodgson et al., 2005; Walz, 2008; Krause et al., 2011). However, semi-natural grasslands are very rich in plant and animal species and, thus, are of vital importance for biodiversity conservation in Europe (Baur et al., 2006; Veen et al., 2009; Wilson et al., 2012).

In order to develop suitable conservation strategies, it is essential to gain detailed knowledge of the importance of landscape composition, habitat fragmentation and habitat quality on plant and animal communities. When analysing the effects of habitat fragmentation on species richness, the landscape is often divided into habitat fragments and the landscape matrix (Krämer et al., 2012). However, the composition of the matrix should also be considered because different elements may act either as a barrier or corridor for dispersal (Krämer et al., 2012; Poniatowski et al., 2016). Moreover, habitat quality is rarely taken into account in fragmentation studies or studies fail to detect an influence (Mortelliti et al., 2010; Krämer et al., 2012). According to Mortelliti

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Table 1

Comparison (mean values ± SE) of the six studied structural types. The measurement of structural parameters was conducted on every botanical plot before plants were recorded. The cover of different layers and vegetation density were estimated in steps of 5%. If values were above 95% or below 5%, steps of 2.5% were applied (cf. Helbing et al., 2014).

Sampled parameter	Structural type						P
	STONE ($N = 17$)	BARE ($N = 27$)	SHORT ($N = 30$)	MEDIUM ($N = 24$)	HIGH ($N = 24$)	SHRUB ($N = 18$)	
Cover (%)							
Total vegetation	56.2 ± 3.4^{a}	84.6 ± 2.2^{a}	97.5 ± 0.7^{b}	99.8 ± 0.1^{b}	100.0 ± 0.0^{b}	99.4 ± 0.6^{b}	***
Shrub layer	0.4 ± 0.3^{a}	0.5 ± 0.4^{a}	0.6 ± 0.3^{a}	1.1 ± 0.9^{a}	1.9 ± 1.2^{a}	83.1 ± 2.3^{b}	***
Field layer	46.5 ± 3.8^{a}	80.6 ± 2.4^{a}	96.5 ± 0.9^{b}	99.8 ± 0.1^{b}	99.6 ± 0.4^{b}	73.9 ± 4.1^{a}	***
Cryptogam layer	$14.0 \pm 2.5^{a,b}$	8.8 ± 1.2^{a}	44.4 ± 6.0^{b}	$33.3 \pm 6.3^{a,b}$	12.9 ± 3.1^{a}	$31.0 \pm 7.9^{a,b}$	***
Litter layer	4.0 ± 1.7^{a}	$8.6 \pm 0.9^{a,b}$	$17.1 \pm 3.0^{b,c}$	28.3 ± 4.6^{c}	66.9 ± 4.2^{d}	$38.6 \pm 4.9^{c,d}$	***
Bare ground	$7.2 \pm 1.5^{a,b}$	14.6 ± 2.0^{a}	$2.3 \pm 0.6^{b,c}$	0.2 ± 0.1^{c}	0.0 ± 0.0^{c}	0.6 ± 0.6^{c}	***
Stony surface	37.9 ± 3.6^{a}	0.3 ± 0.2^{b}	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	***
Vegetation height (cm)	7.1 ± 0.6^{a}	$13.1 \pm 0.5^{a,b}$	$22.0 \pm 0.7^{b,c}$	$38.0 \pm 1.6^{c,d}$	$50.9 \pm 2.8^{d,e}$	95.8 ± 7.0^{e}	***
Horizontal vegetation density (%)	9.8 ± 1.3^{a}	22.0 ± 1.4^{a}	48.4 ± 1.8^{b}	$60.9 \pm 2.2^{b,c}$	78.4 ± 3.0^{c}	74.5 ± 3.2^{c}	***
Plant species number	21.4 ± 1.4^{a}	22.2 ± 0.9^{a}	25.4 ± 0.9^{a}	24.6 ± 1.0^{a}	22.8 ± 1.1^{a}	15.1 ± 1.2^{b}	***

Differences between structural types were tested using a Kruskal–Wallis H test (ANOVA for 'Plant species number'). Different letters indicate significant differences (Holm–Sidak test for 'Plant species number', otherwise Dunn's test, $P < 0.05$).

*** $P < 0.001$.

et al. (2010), habitat quality should be described not only by structural parameters, such as vegetation height, but also by resource abundances in order to detect the most appropriate parameters for certain taxa. However, besides landscape and habitat quality parameters, the composition of animal communities within a certain area may also be influenced by the local climate (Nieto-Sánchez et al., 2015).

Leafhoppers are very rich in species and often have specific life strategies (Nickel, 2003). Moreover, they respond rapidly to environmental changes (Biedermann et al., 2005). The plant sucking insects constitute a major component of the phytophagous fauna as they are abundant consumers, prey for predators such as birds or invertebrates and hosts for parasitoids (Biedermann et al., 2005). In grassland habitats, densities may exceed 1000 individuals/m^2 (Biedermann et al., 2005). Thus, leafhoppers are well suited as indicators of habitat change or as model organisms for the study of effects at the landscape and habitat scale (Biedermann et al., 2005). In this study, the term leafhopper is used for all Auchenorrhyncha, including planthoppers, froghoppers and treehoppers.

Grasslands are important habitats for leafhoppers. A total of 120 species are known to prefer managed grasslands of Central Europe (Nickel, 2003; Nickel and Achtziger, 2005). Hitherto, there have been only a few studies, which have analysed the impact of climate (Masters et al., 1998), landscape complexity together with vegetation structure (Kőrösi et al., 2012; Zulka et al., 2014) or habitat connectivity together with fragment size (Rösch et al., 2013) on leafhopper assemblages. However, a study, which considers all of these parameters and tests for their effects on grassland leafhoppers, has not been previously conducted. In this study, we analysed the effects of local climate, landscape structure and habitat quality on leafhopper assemblages of 30 Central European acidic grassland patches. In particular, we have addressed the following hypotheses:

(i) Plant species richness and structural diversity on a habitat fragment positively influence leafhopper species richness.
(ii) Smaller and more isolated patches have a lower species richness.
(iii) The landscape composition in the surroundings of a habitat fragment mainly affects habitat generalists, because many species of this group are able to use a matrix dominated by open land cover types as stepping stone or even as permanent habitat.
(iv) Local climate affects thermophilous leafhopper species rather than eurythermous habitat generalists.

2. Materials and methods

2.1. Study area

The study area, Medebacher Bucht, is located in Central Germany along the border between the federal states of North Rhine-Westphalia and Hesse (51°11′ N/8°41′ E). It is a mountain basin 171 km^2 in size, with an elevation reaching from 300 m a.s.l. in the east to 680 m a.s.l. at its western edge. The Medebacher Bucht is situated on the leeward side of the Rothaar Mountains. Mean annual temperature decreases with increasing elevation from 7.6 to 6.4 °C, whilst the mean annual precipitation increases from 700 to 1100 mm (MURL NRW, 1989).

The Medebacher Bucht is an old cultural landscape, characterised by nutrient-poor and permeable acidic soils, small fields, low agricultural yields and a high proportion of species-rich semi-natural habitat fragments (e.g., mesic grasslands, heathlands and acidic grasslands) (Schmitt and Fartmann, 2006; LWL and LVR, 2008). Grassland and arable land are the dominant land cover types, accounting for 55–60% of the total area. Forests cover 30–35% of the landscape (Hölker, 2002). The heterogenous landscapes harbour a large number of endangered plant and animal species (e.g., plants: Schmitt and Fartmann, 2006; birds: Hölker, 2002; Orthoptera: Behrens and Fartmann, 2004). Three quarters of the study area are strictly protected sites designated under the EU Birds Directive or Habitats Directive (BfN, 2016).

2.2. Study patches

Semi-dry acidic grasslands are classified as vulnerable in Germany (Riecken et al., 2006) and host many stenotopic leafhopper species (Nickel et al., 2002). Therefore, they are a very suitable model systems for analysing the effects of environmental change on leafhopper assemblages. Sampling was conducted on all available patches of acidic grasslands ($N = 30$). Patch area varied between 0.1 and 6.4 ha. Patches were considered discrete when the distance to the nearest neighbouring patch exceeded 50 m (cf. Krämer et al., 2012). The majority of patches were grazed by cattle (43%) or sheep (30%). Only three patches (10%) were mown once a year, whereas five (17%) did not have any land use. Since type of land use had no effect on leafhopper species richness (Kruskal–Wallis H test, $P > 0.05$), it was not considered in further analyses.

Based on structural parameters (Table 1), we subdivided the patches into a maximum of six different types of vegetation structure according to Behrens and Fartmann (2004) and Poniatowski and Fartmann (2008). The structural types were characterised by increasing

Table 2
Overview of the environmental parameters recorded on the study patches ($N = 30$) and their statistical analysis. If two variables were strongly intercorrelated (Spearman's rank correlation, $r_S > 0.6$), only one was used in the subsequent analysis.

Sampled parameter	Correlation			Mean (± SE)	Min.–Max.
	r_S		Used variable[a]		
Response variable					
Species number[b]	–		✓	36.5 ± 1.4	18–51
Predictor variables					
Local climate					
Average annual temperature (C°)	−0.76	▶	Annual precipitation (mm)	7.2 ± 0.1	6.4–7.6
Annual precipitation (mm)	1.00			866.2 ± 15.0	713–1093
Landscape					
Patch area (ha)	–		✓	1.7 ± 0.3	0.1–6.4
Patch connectivity (Index)[c]	–		✓	73.7 ± 14.4	0–256.6
Diversity of all land cover types (Index)[d]	–		✓	1.6 ± 0.0	0.9–1.9
Diversity of open land cover types (Index)[d]	–		✓	0.8 ± 0.1	0.1–1.3
Cover (%)[d]					
Arable land	–	▶	✓	11.2 ± 2.8	0–74
Forest	−0.68		Mesic grassland	25.3 ± 3.1	1–67
Mesic grassland	1.00			55.7 ± 3.5	4–86
Habitat quality					
Host plant species number			✓	21.4 ± 0.7	14–30
Number of structural types	0.69	▶	Diversity of structural types (Index)	4.7 ± 0.2	2–6
Diversity of structural types (Index)[e]	1.00			1.2 ± 0.1	0.5–1.5

[a] Used for GLM analyses. See Table 5.
[b] Values for all species, threatened species, habitat generalists, habitat specialists, long-winged and short-winged species were tested separately.
[c] Hanski's connectivity index (Hanski, 1999). See Section 2.5.1.
[d] Calculated within a radius of 200 m around each patch. See Section 2.5.2.
[e] See Section 2.6.

vegetation height and density representing a productivity and biomass gradient:

(1) Stony surface (STONE): STONE is characterised by a high percentage of stony surfaces and sparse vegetation.
(2) Bare ground (BARE): BARE has a higher percentage of bare ground and a greater cover of the field layer than STONE. In contrast, the cover of stony surfaces is lower. Turf height is low.
(3) Short-growing vegetation (SHORT): SHORT differs from STONE and BARE primarily in an almost complete cover of the field layer and denser vegetation. Furthermore, it has the highest cover of cryptogams.
(4) Medium-growing vegetation (MEDIUM): MEDIUM is characterised by a complete cover of medium-growing vegetation and a pronounced cryptogam layer.
(5) High-growing vegetation (HIGH): High-growing plants dominate in HIGH. The ground is completely covered by vegetation and the cover of litter is also high.
(6) Shrub-dominated (SHRUB): SHRUB has an exceptional position. The cover of the field layer is lower than in the types 2–5. Nevertheless, the ground is completely covered by vegetation due to the high cover of shrubs (mainly *Cytisus scoparius*).

2.3. Leafhopper sampling

A G-Vac suction sampler (Stihl SH 56) with a fine gauze collection bag (300 µm) on the inside of the inlet nozzle was used to sample leafhoppers (diameter of the suction tube: 12.5 cm). Suction samplers enable the collection of quantitative data and capture epigeal species better than sweep nets (Stewart, 2002). Sampling was conducted on three occasions per patch in May, June and September 2014. On each study patch, we took 100 suction samples, evenly distributed over the available number of structural types (see Section 2.2). This means that if there were five structural types, there were 20 samples taken from each. The samples were taken randomly and only under dry, warm and sunny weather conditions by holding the nozzle onto the ground for 10 s. In order to separate leafhoppers from plant and soil debris and to spare other invertebrates, the collected catches were transferred into a bucket and all leafhoppers were collected using a suction exhauster.

Leafhoppers were identified at the species level in the laboratory using a digital microscope (Keyence VHX-500F) and identification literature by Holzinger et al. (2003), Biedermann and Niedringhaus (2004) and Kunz et al. (2011). Scientific nomenclature follows Nickel et al. (2016). Females of some genera cannot be identified at the species level (e.g. *Macrosteles*, *Psammotettix*, *Ribautodelphax*). If present, we assigned them to the appropriate males; otherwise we identified them at the genus level. In cases of more than one species of a genus, we assumed the number of females to correspond to the number of males.

Thermophilous leafhopper species, which are at least regionally restricted to dry habitats with short vegetation and open soil, were classified as habitat specialists. Those species with different or variable preferences were defined as habitat generalists. This classification was based on Nickel et al. (2002), Nickel (2003) and Helbing and Poniatowski (2015). Wing length served as an indicator for the mobility of the species. Species were classified as short-winged and long-winged according to Biedermann and Niedringhaus (2004). Wing-dimorphic species were assigned to the predominant type of wing length. Another category we analysed was threatened species (threat categories CR, EN, VU and NT; see Table A.1). The threat status of leafhopper species in Germany was derived from Nickel et al. (2016).

2.4. Climate parameters

We obtained climate data from 1 km^2 grid datasets from Germany's National Meteorological Service using the geographical information system ArcGIS 10.1. From these data, we used average annual temperature (°C) and annual precipitation (mm) (mean values 1961–1990) for our analyses. If patches were situated on more than one grid cell, we calculated mean values.

Table 3
Resistance values of the land cover types used for the cost-distance model. The percentages of land cover types are shown in brackets (calculated within a radius of 2 km around each patch).

Land cover type	Resistance value
Habitat	
Acidic grassland (< 1%)	1
Landscape matrix	
Mesic grassland (22%)	4
Park, cemetery (1%)	
Arable land (20%)	8
Road, lane, railway, river (6%)	
Forest, shrubbery (47%)	16
Settlement (3%)	

Table 4
Land cover types, which were used to calculate a diversity index of the surrounding landscape matrix (within a radius of 200 m around each patch). Check marks indicate those land cover types, which were used to calculate an 'open land cover types index' (see Section 2.5.2). The percentage cover of the various land types are shown in brackets.

Land cover type	Used for the 'open land cover types index'
Meadow (improved) (28%)	.
Meadow (semi-natural) (2%)	✓
Pasture (22%)	✓
Arable land (11%)	.
Fallow land (3%)	✓
Heathland (< 1%)	✓
Park, cemetery (1%)	✓
Forest clearing (3%)	✓
Christmas tree plantation, afforestation (2%)	.
Shrubbery (5%)	.
Forest (18%)	.
Quarry (< 1%)	.
Settlement (< 1%)	.
Road (2%)	.
Lane (2%)	.
Water body (< 1%)	.
River (< 1%)	.

2.5. Landscape scale parameters

To evaluate the role of the landscape in which the patches were located, we calculated landscape parameters (Table 2) using digital maps (ALKIS-data © Hochsauerlandkreis, 16-G-093; geodata © Hessische Verwaltung für Bodenmanagement und Geoinformation) with ArcGIS 10.1. In addition, we mapped land cover types in the field within a radius of 200 m around each patch to achieve a more detailed classification in the immediate surroundings.

2.5.1. Patch connectivity

We calculated functional edge-to-edge distances (least-cost paths) from each patch to all other patches within a radius of 2 km (cf. Rösch et al., 2013) around the patch using the cost-distance tool in ArcGIS 10.1 (Adriaensen et al., 2003; Chardon et al., 2003; Poniatowski et al., 2016). To consider the structure and the different levels of permeability of the landscape matrix, resistance values were entered into the calculation (Villalba et al., 1998; Adriaensen et al., 2003). As a simple assignment of resistance values provides good results in metapopulation analyses (Poniatowski et al., 2016), we differentiated land cover types into one habitat and three landscape matrix groups (Table 3). Mesic grassland may serve as a corridor for some leafhoppers and obtained a resistance value only four times higher than acidic grassland (Poniatowski et al., 2016). Forest, shrubbery and settlement can act as physical barriers for migrating grassland leafhoppers and thus received the highest values. Other land cover types held an intermediate position (Krämer et al., 2012).

We calculated Hanski's connectivity index I_i (Hanski, 1999), modified according to Moilanen and Nieminen (2002), for each patch i using the following equation:

$$I_i = \sum_{i \neq j} \exp(-\alpha \cdot d_{ij}) \cdot A_j^b$$

where d_{ij} is the distance (in km; here: the functional distance) between the patch i and the neighbouring acidic grassland patch j and A_j is the area size (in m^2) of the neighbouring patch j. The parameter α is the reciprocal of the average migration distance of a species. In light of the fact that we studied a whole community and no empirical data for migration distances of the species were available, we had to apply one general, appropriate value for α. In respect of the low migration distances of some species, $1/\alpha$ was conservatively determined to be 0.1 km (Poniatowski et al., 2016). To ensure that the ratio of patch edge to patch area decreases when the patch area increases, b was set at 0.5 (Moilanen and Nieminen, 2002; Poniatowski et al., 2016). Higher values of the functional connectivity index I_i stand for better connected patches than lower values.

Table 5
Influence of several environmental parameters (predictor variables) on the number of (a) all species, (b) threatened species, (c) habitat generalists, (d) habitat specialists, (e) long-winged species and (f) short-winged species (Error structures: Habitat specialists: Gaussian, long-winged species: negative binomial, otherwise: Poisson) (Table 2). The best-fitting models were selected using stepwise backward selection by AIC values ($P > 0.05$). Only significant predictors are shown. R^2_{MF} = Pseudo R^2 [McFadden].

	Estimate	SE	Z	P		Estimate	SE	Z	P
(a) All species ($R^2_{MF} = 0.59$)					**(b) Threatened species ($R^2_{MF} = 0.29$)**				
(Intercept)	2.841	0.16	17.62	***	(Intercept)	3.824	0.73	5.22	***
Diversity of structural types	0.488	0.11	4.46	***	Patch area	0.084	0.04	2.22	*
Diversity of open land cover types	0.219	0.11	1.99	*	Annual precipitation	−0.002	0.00	−2.55	*
(c) Habitat generalists ($R^2_{MF} = 0.58$)					**(d) Habitat specialists**				
(Intercept)	2.369	0.20	12.09	***	n.s.				
Diversity of structural types	0.586	0.13	4.38	***					
Diversity of open land cover types	0.300	0.13	2.36	*					
Arable land	−0.692	0.27	−2.56	*					
(e) Long-winged species ($R^2_{MF} = 0.58$)					**(f) Short-winged species ($R^2_{MF} = 0.30$)**				
(Intercept)	2.474	0.19	12.84	***	(Intercept)	1.765	0.25	7.15	***
Diversity of structural types	0.497	0.13	3.78	***	Diversity of structural types	0.434	0.19	2.24	*
Diversity of open land cover types	0.296	0.13	2.34	*					
Arable land	−0.582	0.27	−2.19	*					

n.s., not significant.
* $P < 0.05$.
*** $P < 0.001$.

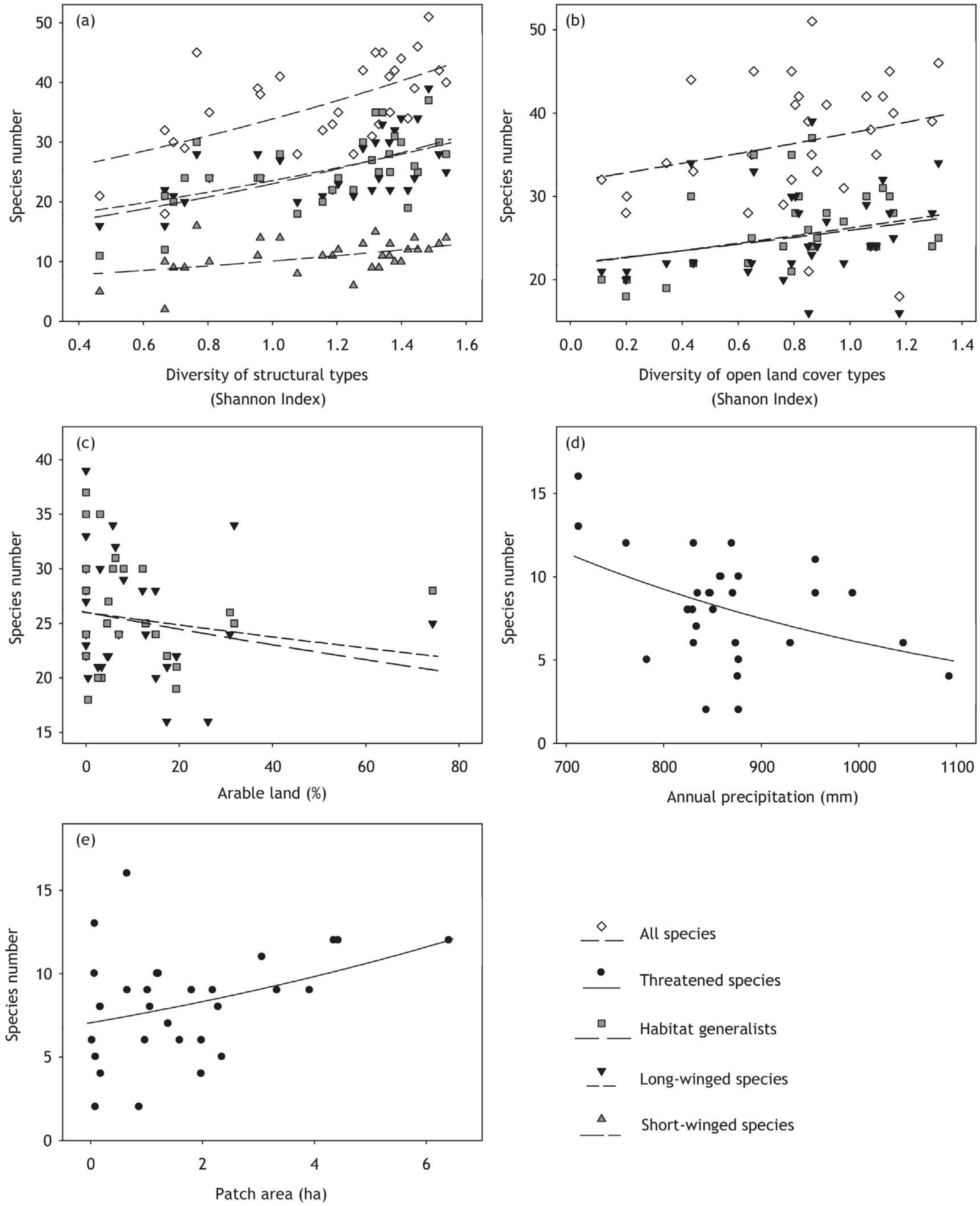

Fig. 1. Results of the GLM analyses: relationship between number of all species, threatened species, habitat generalists, long-winged and short-winged species and the significant environmental parameters (a) diversity of structural types, (b) diversity of open land cover types, (c) arable land, (d) annual precipitation and (e) patch area (see Table 5). The regression slopes were fitted using single predictor GLM.

2.5.2. Habitat surroundings

We calculated the percentages of the three dominating land cover types, arable land (mean = 11%), mesic grassland (meadows, pastures, fallow grassland; mean = 56%) and forest (mean = 25%) within a radius of 200 m around each patch (Table 2). The percentage cover of mesic grassland and forest were highly intercorrelated ($r_s = -0.68$, $P < 0.001$, $N = 30$). Thus, only mesic grassland and arable land were used for further statistical analyses.

Land cover types within a radius of 200 m around each patch were used to calculate a Shannon-Index H' (Shannon and Weaver, 1949) of the surrounding diversity of land cover types (cf. Jonsen and Fahrig, 1997; Krauss et al., 2003).

As leafhoppers of acidic grassland possibly benefit from adjacent open habitat types, we also calculated a Shannon-Index of the diversity of open land cover types (Table 4). We did not include intensively used meadows and arable land in this index as leafhoppers hardly survive on these types of land cover (Nickel et al., 2002).

2.6. Habitat scale parameters

Between mid-July and the beginning of August 2014 we recorded vascular plants on one 4 × 4 m botanical plot per structural type of each patch ($N_{\text{total}} = 140$) using identification literature by Seybold (2009). For each plant, its status as a leafhopper host plant was evaluated (Nickel and Remane, 2002; Kunz et al., 2011) and the number of host plants served as a habitat quality parameter. Furthermore, the proportional coverage of the structural types on each patch (cf. Section 2.2) was used to calculate a Shannon-Index of the structural diversity.

2.7. Statistical analyses

To determine which climate, landscape structure and habitat quality parameters explain the species number of leafhoppers (all species, threatened species, habitat generalists, habitat specialists, long-winged and short-winged species), we conducted generalised linear models (GLM). Prior to analyses, we tested all groups of leafhoppers for spatial autocorrelation by calculating Global Moran's I with ArcGIS 10.1. Since there were no significant results ($P > 0.05$), spatial autocorrelation was rejected. Furthermore, we tested all predictor variables for intercorrelation and excluded strongly intercorrelated variables (Spearman's rank correlation, $r_s > 0.6$) (cf. Krämer et al., 2012; Helbing et al., 2014). Species numbers were summed up over the whole sampling period (leafhoppers) and over all structural types of each patch (leafhoppers and plants). The best fitting models were selected using stepwise backward selection by AIC values ($P > 0.05$).

We analysed species richness of habitat specialists using Gaussian error structure due to normally distributed residuals and long-winged species using negative binomial error structure to control for overdispersion. All other GLM were conducted using Poisson error structure.

For statistical analyses, we used R 3.0.2 (R Development Core Team, 2016), SigmaPlot 12.5 and SPSS 23.0. Graphics were drawn with SigmaPlot 12.5.

3. Results

3.1. Differences between structural types

All structural parameters and the number of plant species significantly differed between the six structural types (Table 1), confirming that we subdivided the patches appropriately. The cover of total vegetation, the field layer and litter layer as well as vegetation height and density increased along the productivity and biomass gradient from STONE to HIGH. The cover of the stony surface reached the highest values at STONE, significantly differing from all other structural types. The cryptogam layer peaked at SHORT and differed significantly from BARE and HIGH. As mentioned above (cf. Section 2.2), SHRUB differed strongly from all other structural types. The field layer cover was significantly lower than at SHORT, MEDIUM and HIGH. Additionally, the cover of shrubs was highest and the mean plant species number lowest, being significantly different from all other structural types.

3.2. Leafhopper community composition

We recorded a total of 102 leafhopper species comprising 10,226 individuals on the 30 patches (Table A.1). Among these species 16 were considered threatened and 15 near threatened. Thirty species were categorised as habitat specialists and 76 as long-winged. The species recorded in this study account for approximately 16% of the German leafhopper fauna (Nickel et al., 2016). The most abundant species were *Psammotettix confinis* ($N = 1211$; 12%), *Psammotettix helvolus* ($N = 816$; 8%), *Delphacodes venosus* ($N = 567$; 6%) and *Streptanus marginatus* ($N = 511$; 5%). With regard to the frequency on patches, *Doratura stylata*, *Megophthalmus scanicus*, *P. confinis* and *P. helvolus* were the dominant species, all occurring on 97% of the patches.

3.3. Effects of local climate, landscape structure and habitat quality

The GLM revealed that both the diversity of open land cover types in the surrounding of a patch and the diversity of structural types on a patch had a positive effect on total species richness and the number of both habitat generalists and long-winged species (Table 5a, c, e, Fig. 1a, b). Species number of habitat generalists and long-winged species additionally increased with decreasing cover of arable land in the surrounding landscape (Fig. 1c). The only predictor of species richness of short-winged species was the diversity of structural types per patch (Table 5f, Fig. 1a). Their number increased with increasing structural diversity. In contrast, the variable host plant species number was excluded from the final GLM (Table 5a–f). However, it was positively correlated with the predictor structural diversity (Spearman's rank correlation, $r_s = 0.47$, $P < 0.001$, $N = 30$).

The number of threatened species increased with increasing patch area and decreased with increasing annual precipitation (Table 5b, Fig. 1d, e). The explanatory power of the five models with significant predictors was generally high (McFadden Pseudo R^2: 0.29–0.59). For the richness of habitat specialist species, there was no relationship with any of the analysed parameters (Table 5d). Patch connectivity, the diversity of all land cover types, the cover of mesic grassland and the number of host plant species had no influence on species richness in any of the models.

4. Discussion

In this study, both landscape structure and habitat quality had a strong influence on the number of leafhopper species in Central European acidic grasslands. At the landscape scale, the diversity of open land cover types and the cover of arable land in the surrounding of a patch were the most important parameters explaining species richness. The best predictor of species richness at the habitat scale was the diversity of structural types within a patch. Local climatic conditions and patch size played a minor role and had an effect only on threatened species.

Threatened species were negatively associated with annual precipitation and, hence, also positively with annual temperature (cf. Table 2). The majority of threatened species sampled in this study are at least regionally xerothermophilous (Nickel, 2003). Accordingly, threatened species were concentrated on patches characterised by favourable climatic conditions with low precipitation and high temperatures.

Patch area was another predictor for the number of threatened species, however, not for the other analysed groups. Leafhopper species have different requirements for the minimum habitat size. There are many species that are able to persist on small habitat fragments (Rösch et al., 2013; this study) as long as they offer a sufficient amount of host plants and appropriate microclimatic conditions (Nickel et al., 2002; Nickel, 2003). Some species even feed and oviposit on the same plant individual for their whole life (Nickel et al., 2002). In contrast, some specialised species depend on large habitat fragments (e.g., Biedermann, 2000, 2002), since small fragments exhibit an increased risk of extinction due to environmental stochasticity (Lande, 1993). This appeared to be true for most of the threatened species sampled in this study.

Contrary to our expectation, functional connectivity had no effect on leafhopper species richness. The study area still exhibits large areas of high nature value grassland, which may be used as stepping stones or even as habitats, especially by generalists. Moreover, when studying assemblages, it is hard to consider the species-specific mobility within connectivity models. In our study, many leafhopper species were long-winged and consequently exhibit rather high dispersal abilities when they either actively emigrate or drift on the wind (Nickel, 2003; Nickel and Achtziger, 2005). However, we also observed a few short-winged species, which have usually a much lower dispersal activity than the long-winged species. Some of the short-winged species are even able to persist on very isolated habitat fragments over a long time without (much) exchange (Biedermann, 2002, 2004; Rösch et al., 2013; Poniatowski et al., 2016). Consequently, we explain the lack of connectivity effects in our study by the high permeability of the matrix and the different dispersal abilities of the species.

Species richness of all species, habitat generalists and long-winged species were positively correlated with the diversity of open land-use types in the surrounding of the acidic grassland patches. These findings are consistent with Jonsen and Fahrig (1997), who also identified a relationship between the diversity of the surrounding area and habitat generalists, but not for habitat specialists. However, they included forest and settlements in their landscape diversity index, whereas this study revealed a strong connection of grassland leafhoppers to open land-use types. The majority of habitat generalists recorded on the study patches prefer mesic to moist grassland (Nickel, 2003). Thus, we assume that the surrounding open land-cover types themselves may constitute suitable habitats, which can be sources for adjacent acidic grasslands. The opposite is true for the short-winged species. Given that this group is more or less sedentary, it is possible that their occurrence is independent of the surrounding area. This specifically applies to threatened species and habitat specialists. Both groups of leafhoppers are largely restricted to acidic grassland (cf. Nickel, 2003) – the driest and warmest patches in the study area. Consequently, landscape composition had no effect on the number of threatened species and habitat specialists.

The majority of species have low survival rates on arable land because of the high disturbance frequency, and the absence of host plants and of suitable microclimatic conditions (Nickel et al., 2002; Nickel, 2003; Kormann et al., 2015). Furthermore, arable land may be sink-habitats for those species, which immigrate but are not able to reproduce (Nickel, 2015). Thus, long-winged and generalist species responded negatively to high cover of arable land, whereas there was no effect on the more sedentary threatened, short-winged and specialist species. This is in line with Rösch et al. (2013), who also observed a negative effect of cover of arable land on the number of habitat generalist species. They assumed that calcareous grassland may be an important refuge for habitat generalists in landscapes dominated by arable land, which might also apply to acidic grassland in our study area.

The number of leafhoppers is often positively correlated with the spatial complexity of the vegetation, plant diversity and height (Morris, 2000; Biedermann et al., 2005; Bucher et al., 2016). Our study supports these findings. It has been shown that, at the habitat scale, the diversity of structural types positively affects species richness of four of the six studied leafhopper groups. In addition to host plant species number, which increased with increasing diversity of structural types, enhanced structural diversity implies a variety of microclimatic conditions and numerous requisites, which are used for shelter, oviposition or overwintering (Dennis et al., 2003; Kőrösi et al., 2012). This enables the coexistence of different life strategy types.

5. Conclusions

Our results show that the nutrient-poor acidic grasslands of the study area are important habitats for leafhoppers. According to Nickel and Hildebrandt (2003) the number of all leafhopper species can be used as robust parameter for the indication of the habitat conditions in grasslands. This is because leafhoppers are a highly diverse and abundant group of primary consumers, which reacts very sensitive to environmental changes. It is therefore reasonable to suggest that favourable habitat conditions for leafhoppers also promote other arthropod groups.

In particular, patches with a high structural diversity exhibited species-rich assemblages. Ungrazed grasslands are often found to promote species richness of leafhoppers because structural complexity of the vegetation is maintained (Kruess and Tscharntke, 2002; Biedermann et al., 2005; Littlewood et al., 2012). However, cessation of land use in the long term leads to shrub and tree encroachment and, thus, to the loss of grassland with its typical leafhopper assemblages (Nickel and Achtziger, 2005; Littlewood et al., 2012). We therefore recommend preserving the traditional forms of land use in the study area. If possible, an intermediate-intensity grazing should be the first choice. This kind of management creates the highest structural diversity (van Klink et al., 2015). Another important point for the conservation of grassland leafhoppers and associated arthropod groups is the location of the patches. Acidic grasslands embedded in complex landscapes with a high diversity of open land cover types and low percentages of arable land harboured the most species-rich assemblages. This is because habitats such as semi-natural meadows, pastures and fallow land (cf. Table 4) in the surroundings of the habitat fragments function as stepping stones or even as permanent habitats for several leafhoppers (Nickel and Hildebrandt, 2003; Nickel and Achtziger, 2005). In contrast, an inhospitable matrix dominated by arable land negatively affected leafhopper-species richness (Kormann et al., 2015). The efforts of conservationists should therefore focus not only on the conservation of structurally rich acidic grasslands, but also on the maintenance of different types of grasslands in the surroundings of the habitat fragments.

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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.2017.05.024.

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