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Extinction debt across three taxa in well-connected calcareous grasslands

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ABSTRACT

The biodiversity in calcareous grasslands suffered from severe habitat loss due to land-use intensification and abandonment across Europe. Although these grasslands are now protected under the EU Habitats Directive, many species in the remaining habitat patches are still declining. Recent studies suggest that species across different taxa may become extinct with a substantial time delay, even without further habitat loss. Consequently, there might be an extinction debt, which poses a major challenge for conservation. Here, we analysed the response of plant, grasshopper and butterfly species richness in calcareous grasslands to habitat fragmentation over the last five decades. In this study, habitat area and connectivity have undergone a marked decline between 1970 and 1990 but have only slightly declined during the last three decades. Despite this, the current richness of specialist and generalist species among plants and butterflies was equally or better explained by past than present landscape conditions. This finding indicates the existence of an extinction debt in both taxa in the still well-connected grasslands of the study area. We conclude that increased conservation measures since the 1990s have favoured species persistence, despite severe habitat loss in the more distant past. By contrast, grasshopper diversity weakly responded to habitat area and connectivity; rather it is likely to depend mainly on habitat quality. To inhibit future extinctions, it is crucial to maintain large-scale patches by traditional land-use practices (i.e. rough grazing or mowing once a year), as well as restore former habitat to facilitate species dispersal in fragmented landscapes.

1. Introduction

Habitat loss driven by land-use change is the major threat to biodiversity across ecosystems all over the globe (Hanski, 2011; Sala et al., 2000). In Europe, semi-natural habitats such as calcareous grasslands have especially suffered from severe declines due to land-use intensification and abandonment (Gustavsson et al., 2007; Poschlod and WallisDeVries, 2002; WallisDeVries et al., 2002). Calcareous grasslands are among the most species-rich habitats and thus have an outstanding value for biodiversity conservation (van Swaay, 2002; Wilson et al., 2012). Although they are currently protected by the European Habitats Directive (EC, 1992), many species associated with calcareous grasslands are still declining (WallisDeVries et al., 2002; Wenzel et al., 2006).

Recent studies suggest that many species persisting in fragmented habitats may become extinct with a substantial time delay, even without further habitat destruction (e.g. Krauss et al., 2010; Lindborg and Eriksson, 2004; Sang et al., 2010). The number of species for which habitat conditions are no longer met but which have not yet gone extinct contributes to an extinction debt (Hylander and Ehrlén, 2013; Kuussaari et al., 2009). Most studies considering extinction debt were undertaken within a metapopulation context (e.g. Kuussaari et al., 2009). However, mechanisms at the individual or population level can also result in time-delayed extinctions. For instance, if species are characterized by one or several resistant life-cycle stages, they might be able to persist detrimental environmental conditions for a long time (Hylander and Ehrlén, 2013). Recently, it has been emphasised that an extinction debt poses a major challenge for biodiversity conservation (Cousins and Vanhoenacker, 2011; Kuussaari et al., 2009). The probability of an extinction debt is generally higher in long-lived and less mobile organisms, such as most vascular plants (Krauss et al., 2010; Kuussaari et al., 2009). Furthermore, its occurrence is more likely in landscapes where large and well-connected habitat patches have remained despite severe habitat loss (Cousins, 2009). Hence, it may also occur in short-lived and mobile taxa, including butterflies, in only slightly fragmented landscapes (Bommarco et al., 2014; Sang et al., 2010). During the last decades, an increasing number of studies have reported evidence for an extinction debt in calcareous grasslands (e.g. Gustavsson et al., 2007; Helm et al., 2006; Krauss et al., 2010; Piqueray et al., 2011). However, most of them focused on vascular plants,

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whereas extinction debt has rarely been examined in short-lived taxa such as insects (e.g. Sang et al., 2010). The few studies that have investigated extinction debt across multiple taxonomic groups suggest that it may cause cascading effects across species of different trophic levels (e.g. Bommarco et al., 2014; Krauss et al., 2010). However, the determinants and mechanisms behind extinction debt are still not fully understood (Hylander and Ehrlén, 2013).

In this study, we aimed to investigate the existence of extinction debt across three indicator groups in calcareous grasslands situated in a Central European biodiversity hotspot. Species richness (generalists and specialists) of vascular plants (hereafter referred to as plants), Orthoptera (hereafter referred to as grasshoppers) and butterflies, including burnet moths (hereafter referred to as butterflies), was related to past (1970 and 1990) and present (2015) habitat area and connectivity, respectively. Given that these taxa have shown a differential response to habitat fragmentation in previous research (Brückmann et al., 2010; Maes and Bonte, 2006; Poniatowski et al., 2016, 2018), they are well-suited indicators to unravel the role of extinction debt for biodiversity conservation in calcareous grasslands.

Based on the findings of the aforementioned research, we assumed that the existence of an extinction debt in calcareous grasslands is mainly affected by the following factors: (i) the generation time and mobility of the investigated taxa; (ii) habitat specificity of the studied organisms; and (iii) the degree of habitat fragmentation in the investigated area. Accordingly, we hypothesised that the evidence for an extinction debt is stronger for plants compared to butterflies and grasshoppers in the well-connected calcareous grasslands of the study area. Furthermore, we predicted that the species richness of habitat specialists will be more strongly related to past landscape conditions, while we expected only weak signs for an extinction debt among habitat generalists.

2. Material and methods

2.1. Study area

The study was performed in the Upper Ahr Valley, which is situated in the Eifel low mountain range, approximately 40 km southwest of the city of Bonn (North Rhine-Westphalia, Germany; 50°20′ N 6°37′ E and 50°28′ N 6°46′ E). In total, the study area comprises an area of 125 km^2. The landscape in the study area is largely dominated by woodlands (~40%) and semi-natural grasslands (~34%). By contrast, arable land (~10%), settlements and other land-cover types (6%) only cover a small portion of the study area (Cologne District Government, 2018). The elevation ranges from 330 to 50860 m above sea level (a.s.l.), the mean annual temperature is 8.0 °C and average annual precipitation is 857 mm (according to the meteorological station at Kall-Sistig, which is 505 m a.s.l.; reference period 1981–2010; DWD, 2018). From the beginning of human settlement, the landscape in the study area has been shaped by traditional land-use practices. With the rise in transhumance since the sixteenth century, extensive grazing has contributed to the large-scale emergence of calcareous grasslands on low-productive soils that were not suitable for arable farming (Trein, 2011). Although > 50% of these grasslands have been lost by afforestation and abandonment since the beginning of the twentieth century (Trein, 2011), the study area still holds one of the most important strongholds of calcareous grasslands in Germany (Beinlich and Plachter, 1995) (for details, see Section 3.1). Due to their outstanding importance for biodiversity conservation, calcareous grasslands are now protected under the EU Habitats Directive (EC, 1992). As their long-term maintenance requires regular management, most of the remaining calcareous grasslands in the study area are now managed by traditional land-use practices, including rough grazing or mowing once a year (Brenner et al., 2003).

2.2. Species sampling

To analyse the relationship between species richness and past and present landscape conditions (habitat area and connectivity), respectively, we sampled data on species richness of plants, butterflies and grasshoppers in 20 calcareous grassland patches. The species sampling was conducted during the growing season in 2015, 2016 and 2017 for grasshoppers, butterflies and plants, respectively. Each species group was sampled over multiple survey dates during one season. Due to phenological differences, the period and frequency of the surveys varied among species groups (for details, see Sections 2.2.1–2.2.3).

During our surveys, all patches were checked for the occurrence of any species that potentially occur in the study area. Prior to species sampling, each patch was divided into structurally homogeneous sections that were drawn in aerial-image-based field maps (1:1000 scale). Following Helbing et al. (2017), we distinguished between a maximum of six structural types in each patch. The structural types were characterized by increasing vegetation height and density, i.e. they represented a successional gradient from sparse to shrub-dominated vegetation (for details, see Helbing et al., 2017). Species were systematically sampled in the same intensity across all structural types. Searching was stopped if no new species was detected within 0.5 h in a structural type during each survey date.

2.2.1. Plant sampling

Plant sampling was performed in 2017. Each patch was sampled three times. Two surveys were conducted during May/June and one survey in August. Due to the regionally high plant diversity, searching for species was done using a comprehensive checklist of all plant species that occur in the study area. The checklist was derived from Haeupler et al. (2003). All plant species were identified in the field using Oberdorfer (2001). The plant nomenclature follows Haeupler et al. (2003). Alien species, regionally non-resident species and species strongly associated with woodlands were excluded from the analyses (see Table A1) (cf. Ellenberg et al., 1992; Haeupler et al., 2003).

2.2.2. Grasshopper sampling

In 2015, grasshoppers were sampled twice between mid-July and the end of August, with a time lag of at least three weeks between the two surveys. The species were only sampled under favourable weather conditions (i.e. temperature > 15 °C, cloud cover < 50%) using acoustic and visual detection as well as sweep netting, all of which are among the most frequently used methods to survey the occurrence of grasshoppers (Samways et al., 2010). Species identification was performed in the field by sound and morphological characteristics using Bellmann (2006). The grasshopper nomenclature follows Fischer et al. (2016).

2.2.3. Butterfly sampling

Butterflies were sampled in 2016, specifically between the beginning of May and mid-September. In total, each patch was surveyed six times, with an interval of at least three weeks between two consecutive surveys. Butterflies were sampled with the help of a sweep net or by visual observations using a binocular. In order to avoid the results being biased by weather, butterfly sampling was only performed under dry, calm and sunny conditions (i.e. temperature > 15 °C, cloud cover < 50%, wind [Beaufort] ≤3). All butterfly species were identified in the field using Settele et al. (2015). The butterfly nomenclature follows Reinhard and Bolz (2011) and Rennwald et al. (2011). According to Ebert and Rennwald (1991), migratory species (including both true migrants and highly mobile species which frequently occur outside their breeding range) and species strongly associated with woodlands were excluded from the analyses (see Table A3).

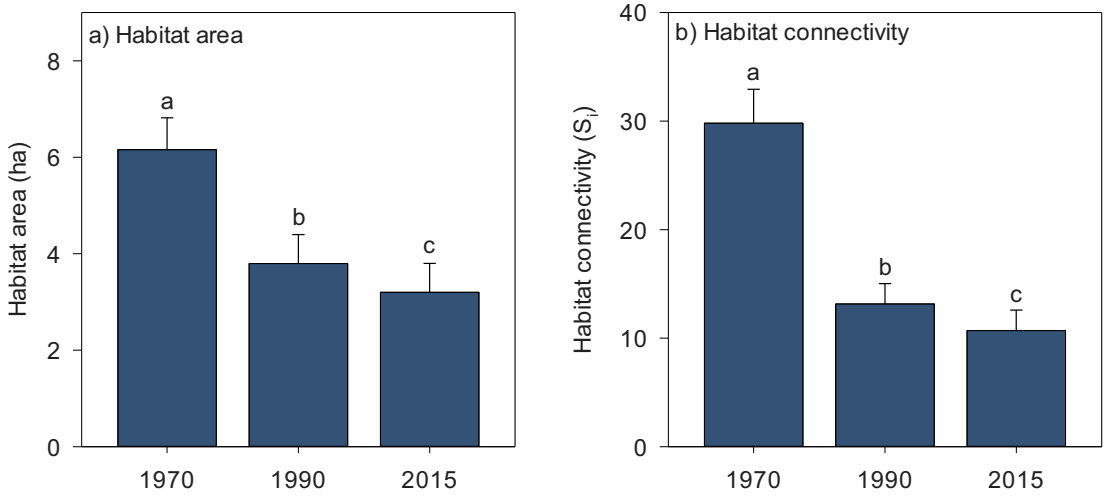

Fig. 1. Changes in (a) habitat area and (b) habitat connectivity (S_i) of the studied calcareous grassland patches ($N = 20$) over the years (1970, 1990 and 2015). Habitat connectivity (S_i) was calculated according to Moilanen and Nieminen (2002) for an average dispersal distance of 1 km (for details, see Section 2.4). The groups were statistically compared using repeated measures analysis of variance (ANOVA), with a paired *t*-test as a post hoc test. Different letters indicate significant differences between the groups ($p < 0.05$).

2.3. Habitat specificity

All species were classified by their habitat specificity. Species whose occurrence in the study area was largely restricted to calcareous grasslands were considered to be habitat specialists (cf. Brückmann et al., 2010; Krämer et al., 2012). All other species that frequently inhabited open habitats in the matrix were defined as habitat generalists. Considering plants, all character species of calcareous grasslands as well as all species regionally restricted to calcareous grasslands were considered to be habitat specialists according to Möseler (1989). Butterfly habitat specificity was ascertained from Brückmann et al. (2010) and Krämer et al. (2012), complemented by additional information provided by Ebert and Rennwald (1991). In the case of grasshoppers, we adopted the classification used by Löffler et al. (2019).

2.4. Habitat area and connectivity

Habitat area and connectivity of the studied calcareous grasslands were ascertained from aerial images taken for the years 1970, 1990 and 2015 using ArcGIS 10.3.1. Patches were regarded as discrete entities when they were isolated from the nearest neighbouring patch by at least 50 m of landscape matrix (non-habitat; e.g. Krämer et al., 2012; Poniatowski and Fartmann, 2010). In addition to patch area, we calculated the connectivity of the studied patches to all neighbouring calcareous grassland patches within a distance of 2 km using Hanski's connectivity index (Hanski, 1999), modified according to Moilanen and Nieminen (2002):

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

where A_i is the area (in ha) of the studied calcareous grassland patch, A_j is the area of the neighbouring patch and d_{ij} is the distance (in km) between the neighbouring patch j and the studied patch i. According to Moilanen and Nieminen (2002), we chose $b = 0.5$ and $c = 0.3$ as scaling parameters for the likelihood of immigration and emigration of species, respectively. The index also considers the average dispersal abilities of the indicator groups. The parameter α scales the effect of distance on dispersal, where $1/\alpha$ is the average dispersal distance. Dispersal ability differs among species groups, and thus we applied different average dispersal values according to each group. The average dispersal capabilities were ascertained from prior fragmentation studies in calcareous grasslands: butterflies ($1/\alpha = 1$ km; Krämer et al., 2012; Moilanen and Nieminen, 2002) and grasshoppers ($1/\alpha = 0.5$ km; Löffler and Fartmann, 2017). Due to usually low dispersal distances among plants (Tamme et al., 2014), their average dispersal capacity was set to $1/\alpha = 0.25$ km. Larger values of the connectivity index S_i indicate higher connectivity.

2.5. Statistical analysis

Differences in habitat area and connectivity among the time points (1970, 1990 and 2015) were tested using repeated-measures analysis of variance (ANOVA), with a paired *t*-test as a post-hoc test. For descriptive statistics, the mean value (Ø) ± the standard error (SE) are presented. The relationship between past and present landscape characteristics (1970, 1990 and 2015) and current species richness was assessed either using generalised linear models (GLM) with a negative-binomial error distribution or linear models (LM) using the package lme4 (Bates et al., 2018). As our data suggested a logarithmic relationship between the number of plant generalists (response variable) and the landscape predictors, the predictors habitat area and connectivity were log-transformed in these models. All statistical analyses were performed using R 3.4.0 statistical package and SigmaPlot 14.0 (R Core Team, 2017; Systat Software, 2017).

3. Results

3.1. Habitat-area and connectivity changes

In 1970, the study area was covered by 420 ha of calcareous grasslands. Up to 1990, their area sharply declined by > 50%, resulting in an area of 205 ha still covered by calcareous grasslands. An additional but smaller decline occurred between 1990 and 2015, with 175 ha of calcareous grasslands remaining up to now.

Both the mean habitat area and connectivity of the patches significantly decreased from 1970 to 2015 (Fig. 1). The mean habitat area declined by almost 40% between 1970 (Ø 6.2 ± 0.7 ha) and 1990 (Ø 3.8 ± 0.6 ha). During the same period, the patch connectivity declined even more severely – by nearly 60% (1970: Ø 29.8 ± 3.1 vs. 1990: Ø 13.1 ± 1.9). In contrast, there was only a slight (but still significant) decline in habitat area and connectivity from 1990 to 2015, resulting in a mean patch area of Ø 3.20 ± 0.6 ha and connectivity of Ø 10.7 ± 1.9.

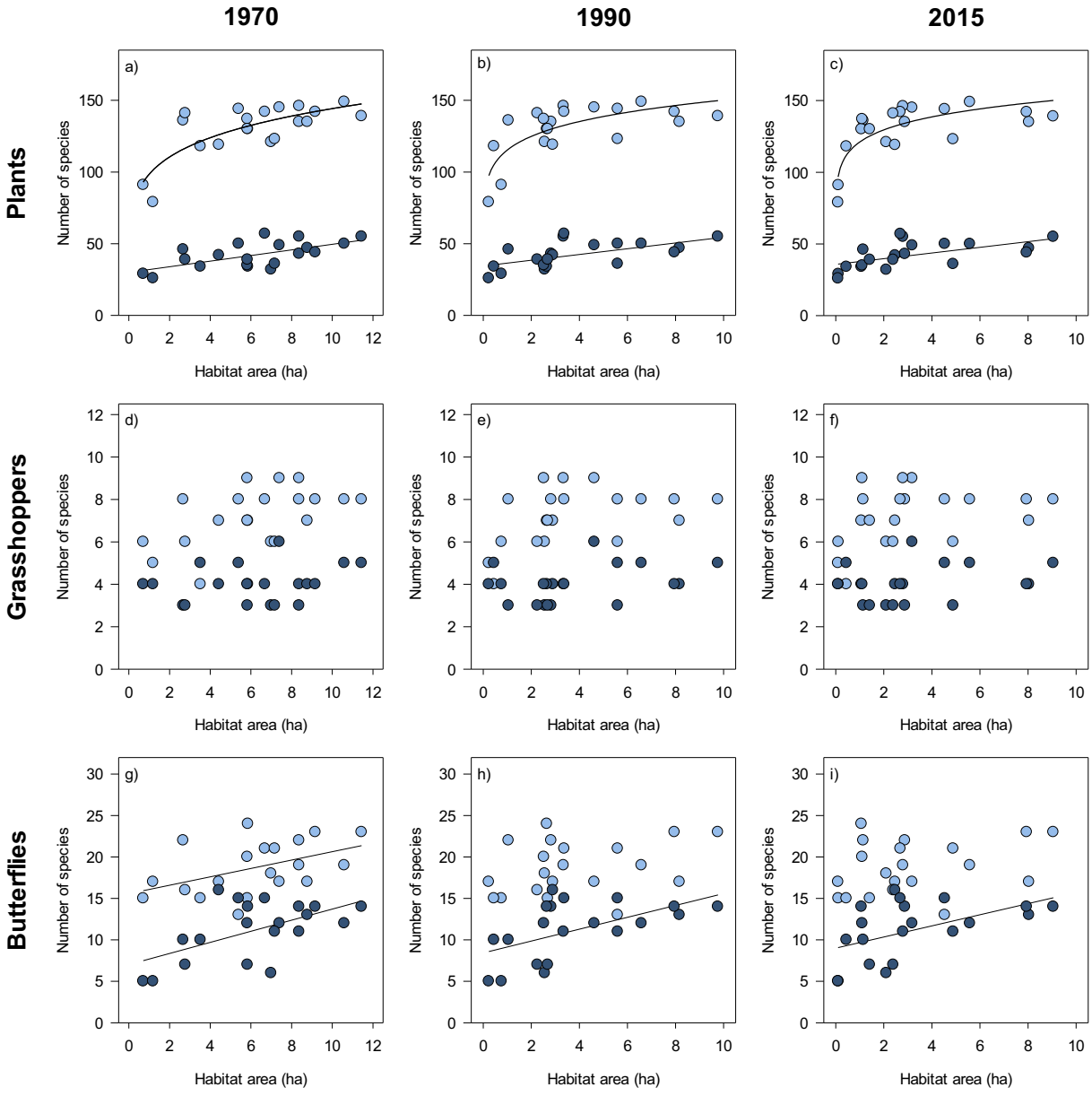

Fig. 2. The relationship between the current number of species (light blue = habitat generalists ∘; dark blue = habitat specialists •) and habitat area of the studied patches ($N = 20$) in the years 1970, 1990 and 2015. The regression lines represent significant relationships ($p < 0.05$), as assessed with single predictor generalised linear models (GLM) using a negative-binomial (habitat generalists: a–f) or linear models (LM) (habitat generalists: g–i; habitat specialists: a–i). The predictor habitat area was log-transformed prior to the analyses regarding panels a–c. For detailed statistics, see Table 1.

3.2. Species richness

In total, we recorded 425 plant, 16 grasshopper and 70 butterfly species in the study area (Tables A1–A3). In the case of plants, we detected a minimum of 114 and a maximum of 224 species per patch (Ø 191.3 ± 6.6). The number of habitat specialists among them varied between 26 and 57 species and on average comprised 22% of the detected species. Overall, the grasshopper species richness in the patches ranged from 9 to 15 species (Ø 11.2 ± 0.4). We found at least 3 but not > 6 grasshopper specialist species per patch, accounting for approximately 36% of all recorded grasshopper species. Regarding butterflies, a minimum of 26 and a maximum of 51 species were detected in the patches (Ø 38.7 ± 1.8). The number of butterfly habitat specialists among them ranged from 5 to 16, resulting in an average share of 28% of the overall butterfly richness.

3.3. Species response to past and present habitat area

The number of plant and butterfly specialists was significantly positively related to the habitat area in 2015, 1990 and 1970 (Fig. 2, Table 1). However, as reflected by decreasing model accuracy from 1970 to 2015, the specialist species richness for both species groups was better explained by past habitat area. In contrast, there was no relationship between the number of grasshopper specialists and habitat area for any of the years. Whereas the number of plant generalists was significantly related to all habitat-area measures, the number of butterfly generalists was only associated with the habitat area in 1970. In contrast, we found no response of grasshopper generalists to the habitat area.

Table 1
The relationships between the number of species and habitat area of the studied patches ($N = 20$) in the years 1970, 1990 and 2015. Significance and model accuracy were assessed with single predictor generalised linear models (GLM) using a negative-binomial error structur[1] (z-values are given) or linear models (LM)[2] (t-values are given), respectively. The predictor habitat area was log-transformed in the plant-generalist models[3]. The significance levels are indicated as follows: n.s., not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Model group	Habitat area (ha)								
Plants	1970			1990			2015		
	z/t	p	R^2mf	z/t	p	R^2_{MF}	z/t	p	R^2_{MF}
Generalists[1,3]	5.41	***	0.60	5.07	***	0.55	5.67	***	0.65
Specialists[2]	3.54	***	0.41	3.19	***	0.35	3.09	**	0.33
Grasshoppers	**1970**			**1990**			**2015**		
	z/t	**p**	**R^2_{MF}**	**z/t**	**p**	**R^2_{MF}**	**z/t**	**p**	**R^2_{MF}**
Generalists[1]	—	n.s.	—	—	n.s.	—	—	n.s.	—
Specialists[2]	—	n.s.	—	—	n.s.	—	—	n.s.	—
Butterflies	**1970**			**1990**			**2015**		
	t	**p**	**R^2_{MF}**	**t**	**p**	**R^2_{MF}**	**t rowsep="1"**	**p**	**R^2_{MF}**
Generalists[2]	2.26	*	0.22	—	n.s.	—	—	n.s.	—
Specialists[2]	2.92	**	0.32	2.81	*	0.31	2.57	*	0.27

3.4. Species response to past and present habitat connectivity

Both plant and butterfly specialist species richness were significantly and positively related to habitat connectivity in 1970, 1990 and 2015 (Fig. 3, Table 2). Similar to the specialist species' response to habitat area (cf. Section 3.3), models including 1970 habitat connectivity as a predictor also had a higher statistical power compared to those that included this measure from 1990 or 2015. Furthermore, the number of plant generalists was positively related to all habitat-connectivity measures. In addition, the number of grasshopper specialists were only related to increasing habitat connectivity in 1970.

4. Discussion

In this study, we analysed the response of plant, grasshopper and butterfly species richness in calcareous grasslands to habitat fragmentation over the last five decades. Both habitat area and connectivity in the study area underwent a severe decline between 1970 and 1990. However, due to intensified conservation measures, habitat loss and fragmentation has slowed down since the 1990s, as has been shown for other regions in Europe (Carvalheiro et al., 2013; van Strien et al., 2019). In our study, plant and butterfly specialist richness were most strongly related to habitat area and connectivity in the past. Although several studies have shown that habitat generalists are generally less sensitive to habitat fragmentation (Krämer et al., 2012; Löffler et al., 2019; Pöyry et al., 2009), we also found a positive relationship between past habitat area in 1970 and the number of plant and butterfly generalists. These patterns indicate the existence of an extinction debt in both long-lived (plants) and short-lived (butterflies) taxa in the still well-connected landscape of the study area. By contrast, the response to habitat fragmentation was generally weak in grasshoppers.

In our study, species richness of both plant and butterfly specialists increased with increasing habitat area and connectivity. This finding is consistent with previous studies that have shown that habitat specialists suffer from decreasing patch area and connectivity in fragmented calcareous grasslands (e.g. Brückmann et al., 2010; Krämer et al., 2012; Rosin et al., 2012; Poniatowski et al., 2018). However, recent work has suggested that many species can persist in landscapes for a long time after focal habitats have disappeared or became fragmented. Those species might contribute to an extinction debt (e.g. Bommarco et al., 2014; Krauss et al., 2010; Piqueray et al., 2011; Sang et al., 2010). Extinction debt has become particularly evident for long-lived organisms such as plants (e.g. Cousins and Vanhoenacker, 2011; Helm et al., 2006; Kuussaari et al., 2009; Lindborg and Eriksson, 2004; Piqueray et al., 2011). Due to their low dispersal capacity and generally long generation times, it can be assumed that many plant specialists might survive for many years, even if their reproduction is hampered by altered environmental conditions (cf. Helm et al., 2006; Krauss et al., 2010). This applies especially to species with clonal growth (e.g. *Hieracium pilosella*, *Potentilla tabernaemontani* and *Teucrium chamaedrys*; Piqueray et al., 2011). In addition, other traits, including the existence of a persistent seed bank, might also reduce extinction risk among plants (Maurer et al., 2003; Piesens and Hermy, 2006). A study from Sweden revealed time lags of at least 50 years between habitat loss and declines in plant diversity in semi-natural grasslands (Lindborg and Eriksson, 2004). Corroborating these findings, in our study, the model accuracy increased if the past patch area and connectivity were included as predictors of today's plant specialist species richness.

Compared with plants, butterflies are on average characterized by a higher dispersal ability and short life cycles (Bommarco et al., 2014; Brückmann et al., 2010; Kuussaari et al., 2009). Furthermore, many butterfly species strongly depend on metapopulation dynamics for long-term persistence (Anthes et al., 2003; Eichel and Fartmann, 2008; Poniatowski et al., 2018; Stuhldreher and Fartmann, 2014). Although it is predicted that such organisms generally show a faster response to habitat fragmentation (Krauss et al., 2010; Kuussaari et al., 2009), the number of butterfly specialists was more strongly related to past area and connectivity in our study. This phenomenon is probably the result of the maintenance of still large and well-connected habitat patches in the study area (cf. Sang et al., 2010). Cousins (2009) revealed that an extinction debt is most likely to occur in landscapes with > 10% habitat remaining, while studies from more fragmented landscapes did not provide any evidence of an extinction debt (cf. Adriaens et al., 2006). The loss of habitat area and connectivity in the study area was moderate (see Section 3.1) compared to many other parts of Europe (cf. Adriaens et al., 2006; Krauss et al., 2010; Piqueray et al., 2011). It is therefore likely that many butterfly specialists are living just below their extinction threshold and thus they have not yet become extinct; i.e. patch area and connectivity almost meet their minimum habitat demands (cf. Bommarco et al., 2014; Hanski and Ovaskainen, 2002; Salz and Fartmann, 2009; Sang et al., 2010). However, even butterfly species that strongly depend on metapopulation dynamics often start to

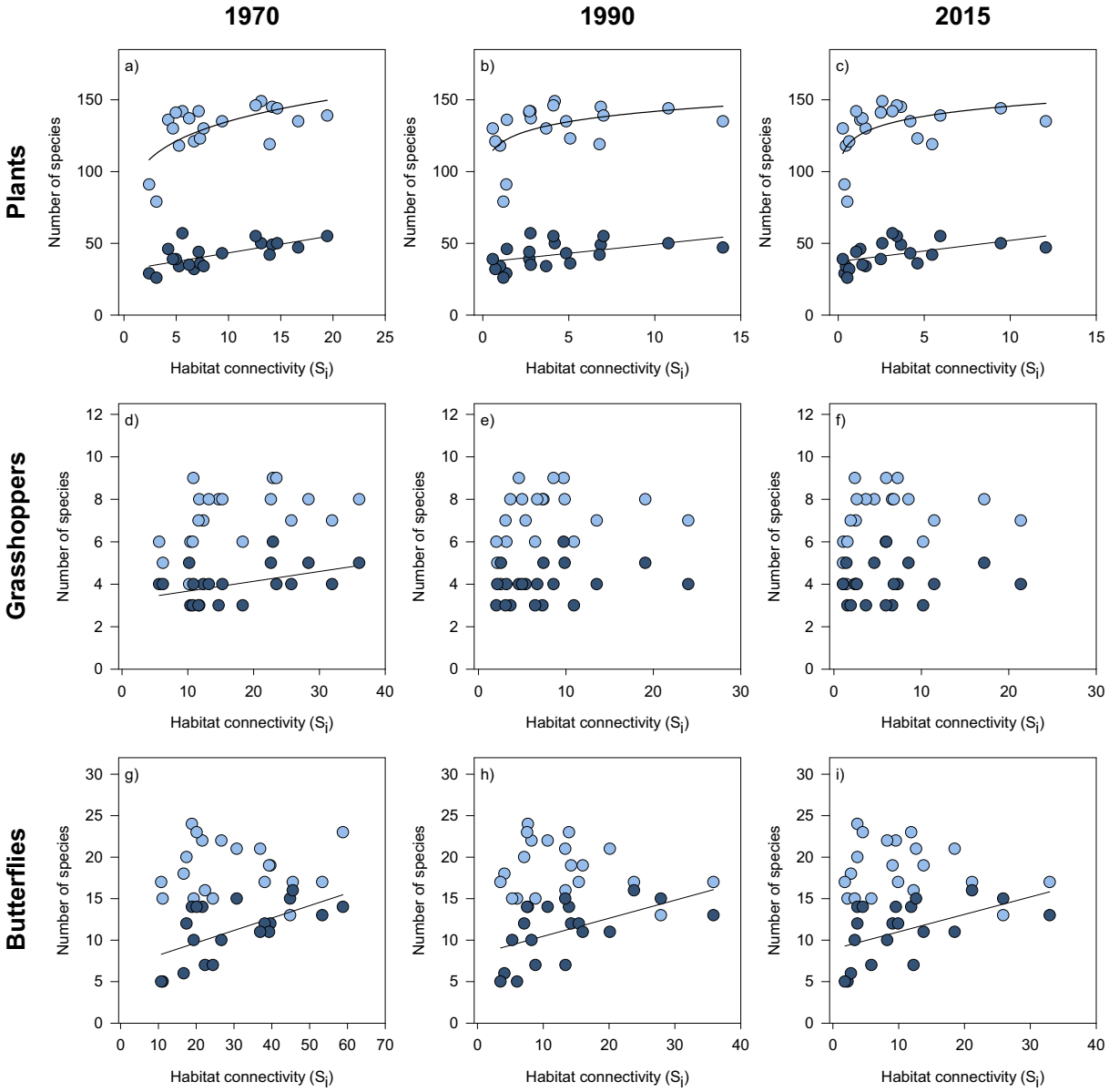

Fig. 3. The relationship between the current number of species (light blue = habitat generalists ○; dark blue = habitat specialists ●) and habitat connectivity (S_i) of the studied patches ($N = 20$) in the years 1970, 1990 and 2015. Habitat connectivity (S_i) was calculated according to Moilanen and Nieminen (2002) by applying different average dispersal distances for each species group (for details, see Section 2.4). The regression slopes represent significant relationships ($p < 0.05$), as assessed with single predictor generalised linear models (GLM) using a negative-binomial error structure (habitat generalists: a–f) or linear models (LM) (habitat generalists: g–i; habitat specialists: a–i). The predictor habitat connectivity (S_i) was log-transformed prior to the analyses regarding panels a–c. For detailed statistics, see Table 2.

decline several decades after habitat loss has occurred (Bulman et al., 2007; van Strien et al., 2011). Therefore, it cannot be excluded that the populations of many butterfly species will decline in the future in response to past habitat fragmentation in the study area, although the habitat area and connectivity have only slightly decreased during the past two decades.

In contrast to plants and butterflies, grasshoppers only weakly responded to habitat fragmentation in the study area. Only the species richness of grasshopper specialists increased with habitat connectivity in the past (1970). This relationship demonstrates that grasshopper specialists can persist in fairly small and often isolated patches (i.e. in closed populations) for a long time (Maes et al., 2006; Poniatowski and Fartmann, 2010). While this finding may also suggest an extinction debt among grasshopper specialists, previous studies revealed that grasshopper patch occupancy is especially driven by habitat quality (Löffler and Fartmann, 2017; Poniatowski et al., 2018). Consistently, Poniatowski and Fartmann (2010) concluded that grasshopper conservation should primarily focus on improving habitat quality, which will also be beneficial for several other taxa in grasslands (cf. Fartmann et al., 2012; Rosin et al., 2012; Poniatowski et al., 2018). Given that the calcareous grasslands in the study area are well-managed today (cf. Brenner et al., 2003), the habitat requirements of most grasshopper species are generally met (Löffler et al., 2019). However, we could not more accurately evaluate the relative impact of habitat quality on extinction debt because information on historic habitat quality was not available for the study area.

Contrary to our expectations, the species richness of plant and butterfly generalists was also more strongly related to habitat area in the past compared to the current times. Due to the rather conservative classification of habitat specialists in our study (see Section 2.3), the

Table 2
The relationships between the number of species and habitat connectivity (Si) of the studied patches (N = 20) in the years 1970, 1990 and 2015. Habitat connectivity (Si) was calculated according to Moilanen and Nieminen (2002) by applying different average dispersal distances for each species group (for details, see Section 2.4). Significance and model accuracy were assessed with single predictor generalised linear models (GLM) using a negative-binomial error structure[1] (z-values are given) or by linear models (LM)[2] (t-values are given), respectively. The predictor habitat connectivity (Si) was log-transformed in the plant-generalist models[3]. Significance levels are indicated as follows: n.s., not significant; * $p < 0.05$; ** $p < 0.01$.

Model group	Habitat connectivity (Si)								
Plants		**1970**			**1990**			**2015**	
	z/t	**p**	R^2mf	**z/t**	**p**	R^2_{MF}	**z/t**	**p**	R^2_{MF}
Generalists[1,3]	3.54	***	0.36	2.27	*	0.19	2.84	**	0.27
Specialists[2]	3.76	**	0.44	2.36	*	0.24	2.52	*	0.26
Grasshoppers		**1970**			**1990**			**2015**	
	z/t	**p**	R^2_{MF}	**z/t**	**p**	R^2_{MF}	**z/t**	**p**	R^2_{MF}
Generalists[1]	—	n.s.	-	—	n.s.	—	—	n.s.	—
Specialists[2]	2.23	*	0.22	—	n.s.	—	—	n.s.	—
Butterflies		**1970**			**1990**			**2015**	
	t	**p**	R^2_{MF}	**t**	**p**	R^2_{MF}	**t**	**p**	R^2_{MF}
Generalists[2]	-	n.s.	-	—	n.s.	—	—	n.s.	—
Specialists[2]	3.17	**	0.36	2.62	*	0.28	2.50	*	0.26

ratio of habitat generalists in the patches was generally high (Ø 78% of all plant and Ø 72% of all butterfly species). Although the occurrence of generalists was not strictly restricted to calcareous grasslands, it can be assumed that this habitat provides essential resources for many of them. Therefore, it is likely that calcareous grasslands substantially facilitate the persistence of habitat generalists in the overall landscape (cf. Bommarco et al., 2014). For instance, plant species assigned to thermophilic fringe vegetation (e.g. *Agrimonia eupatoria*, *Geranium sanguineum*, *Origanum vulgare* and *Trifolium medium*) still benefit from the nutrient-poor, warm and dry habitat conditions in calcareous grasslands, which can hardly be found in the more intensively used landscape matrix (cf. Ellenberg and Leuschner, 2010). However, our analyses revealed a logarithmic relationship between the number of plant generalists and habitat area, which suggests that there is only a slight increase of plant generalists in larger calcareous grassland patches (see Fig. 2 a–c). Among butterfly generalists in our study, several species such as *Erebia medusa* and *Lasiommata megera* depend on low-intensity land use and heterogeneous habitats, which have now become increasingly threatened across Central Europe (Klop et al., 2015; Stuhldreher and Fartmann, 2018). Bommarco et al. (2014) illustrated that extinction debt among habitat generalists is most likely to exist when their key resources (e.g. lack of pollinators or germination sites for plants, lack of host plants or microhabitats for butterflies) are still available in focal habitats but have become scarce in the matrix. For example, Klop et al. (2015) associated the recent decline of *Lasiommata megera* in the Netherlands with the lack of open and heterogeneous microhabitats in the landscape, even though the host plant is still widespread. Accordingly, we expect that land-use intensification may have led to a decline of generalists with more specific habitat requirements in the matrix, which were still frequently observed in calcareous grasslands of the study area.

5. Conclusions

Our study revealed a similar response of species richness to habitat fragmentation across the three studied taxa. The current species richness was more strongly related to past rather than present landscape conditions. This finding indicates the existence of an extinction debt among both short- and long-lived organisms. Surprisingly, this was also true for habitat generalists among plants and butterflies. We conclude that increased conservation measures since the 1990s have crucially favoured the persistence of species in the still large and well-connected calcareous grasslands, despite earlier severe habitat loss (cf. Carvalheiro et al., 2013; van Strien et al., 2019). In contrast, land-use intensification has probably led to a deterioration of non-protected habitats in the study area, and thus survival in the matrix has become increasingly difficult, even for habitat generalists. Although our study suggests that both specialists and generalists can persist for a long time after habitat loss, many of them might decline in the next decades (cf. van Strien et al., 2011). To inhibit future extinctions, it is necessary to maintain large-scale habitats by traditional land-use practices, such as rough grazing or low-intensity mowing, in calcareous grasslands, as well as restore former habitats to facilitate species dispersal in fragmented landscapes (Cousins, 2009; Rosin et al., 2012; Poniatowski et al., 2018). This is because, larger and well-managed patches are generally characterized by higher species richness or more stable populations of a focal species (Krämer et al., 2012; Löffler and Fartmann, 2017; Poniatowski et al., 2018). However, in highly fragmented landscapes, the conservation of small patches with high habitat quality may also reduce the extinction risk, because they may act as important stepping stones for several species living in a metapopulation network (Poniatowski et al., 2018). Furthermore, increasing landscape heterogeneity and reducing land-use intensity in the matrix would likely promote the dispersal of habitat specialists between patches and additionally increase habitat availability for habitat generalists in fragmented landscapes (Löffler et al., 2019; Streitberger et al., 2016). The application of those measures will ensure the long-term persistence of species and might additionally facilitate species to evade environmental changes such as global warming (Mantyka-Pringle et al., 2015; Streitberger et al., 2016; Stuhldreher and Fartmann, 2014).

CRediT authorship contribution statement

Franz Löffler: Conceptualization, Investigation, Methodology, Formal analysis, Writing - original draft. **Dominik Poniatowski**: Validation, Writing - review & editing. **Thomas Fartmann**: Conceptualization, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. All authors agree with the contents of the manuscript and its submission to the journal. We certify that the submission is original work, has not been published elsewhere in any form, and is not under review by any other publication. Any funding sources are fully acknowledged in the manuscript.

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Appendix A

Table A1
Habitat specificity (Hs; see Section 2.3) and frequency (F) of all recorded vascular plant species in the study area. The nomenclature follows Haeupler et al. (2003).

Species	Hs	F (%)
Acer campestre [b]	-	60
Acer platanoides [b]	-	10
Acer pseudoplatanus [b]	-	50
Achillea millefolium	G	100
Achillea ptarmica	G	5
Acinos arvensis	S	25
Aconitum n. ssp. *napellus*	G	20
Aegopodium podagraria	G	75
Aesculus hippocastanum [b]	-	10
Aethusa cynapium s.l.	G	20
Agrimonia eupatoria	G	95
Agrostis capillaris	G	80
Agrostis stolonifera	G	85
Aira caryophyllea	G	5
Ajuga genevensis	S	25
Ajuga reptans	G	25
Alchemilla monticola	G	25
Alchemilla xanthochlora	G	30
Alliaria petiolata	G	55
Allium oleraceum	S	25
Allium s. ssp. *scorodoprasum*	G	5
Alnus glutinosa [b]	-	5
Alnus incana [a,b]	-	10
Alopecurus pratensis	G	35
Amelanchier ovalis	G	5
Anacamptis pyramidalis	S	5
Anemone nemorosa [b]	-	80
Angelica sylvestris	G	15
Antennaria dioica	S	35
Anthericum ramosum	G	10
Anthoxanthum odoratum	G	75
Anthriscus sylvestris agg.	G	100
Anthyllis vulneraria s.l.	S	85
Apera spica-venti	G	5
Aquilegia vulgaris [b]	-	55
Arabidopsis thaliana	G	5
Arabis hirsuta agg.	S	50
Arctium lappa	G	35
Arctium minus agg.	G	30
Arctium nemorosum	G	5
Arenaria serpyllifolia agg.	G	35
Arrhenatherum elatius	G	95
Artemisia vulgaris	G	5
Arum maculatum [b]	-	20
Asperula cynanchica	S	80
Asplenium ruta-muraria	S	15
Asplenium trichomanes s.l.	S	5
Astragalus glycyphyllos	G	20
Athyrium filix-femina [b]	-	5
Barbarea intermedia [a]	-	5
Barbarea vulgaris s.l.	G	30
Bellis perennis	G	75
Berberis vulgaris	G	25
Betonica officinalis	G	15
Betula pendula [b]	-	40
Bistorta officinalis	G	5
Botrychium lunaria	G	10
Brachypodium pinnatum agg.	S	100
Briza media	G	100

Table A1 (*continued*)

Species	Hs	F (%)
Bromus erectus	S	100
Bromus h. ssp. *hordeaceus*	G	20
Bromus inermis	G	10
Bromus sterilis	G	15
Bunium bulbocastanum	G	55
Calamagrostis epigejos	G	15
Campanula glomerata	S	90
Campanula persicifolia	G	25
Campanula rapunculoides	G	45
Campanula rapunculus	S	5
Campanula rotundifolia agg.	G	90
Campanula trachelium [b]	-	10
Capsella bursa-pastoris	G	10
Cardamine bulbifera [b]	-	5
Cardamine hirsuta	G	25
Cardamine pratensis agg.	G	100
Carduus crispus	G	80
Carex caryophyllea	S	100
Carex demissa	G	5
Carex flacca	S	100
Carex hirta	G	15
Carex montana	S	100
Carex muricata agg.	G	5
Carex panicea	G	5
Carlina vulgaris	S	80
Carpinus betulus [b]	-	45
Carum carvi	G	45
Centaurea jacea agg.	G	85
Centaurea scabiosa	S	100
Centaurium erythraea	S	25
Cephalanthera damasonium [b]	-	15
Cerastium holosteoides	G	95
Cerastium pumilum agg.	G	5
Chaenarhinum minus	G	15
Chaerophyllum temulum	G	30
Chamaespartium sagittale	G	70
Chelidonium majus	G	5
Chenopodium album	G	25
Cirsium acaule	S	100
Cirsium arvense	G	100
Cirsium oleraceum	G	15
Cirsium palustre	G	25
Cirsium tuberosum	G	15
Cirsium vulgare	G	80
Clematis vitalba	G	10
Clinopodium vulgare	G	90
Coeloglossum viride	G	20
Colchium autumnale	G	85
Conium maculatum	G	5
Convolvulus arvensis	G	60
Cornus sanguinea s.l.	G	100
Coronilla vaginalis	S	30
Corylus avellana	G	100
Cotoneaster cf. *integerrimus*	G	5
Cotoneaster spec. [a]	-	5
Crataegus laevigata	G	100
Crataegus monogyna	G	100
Crepis biennis	G	95
Crepis capillaris	G	15
Cruciata laevipes	G	75
Cuscuta e. ssp. *epithymum*	G	5
Cynosurus cristatus	G	65
Cytisus scoparius	G	10
Dactylis glomerata	G	100
Dactylorhiza maculata agg.	G	40
Dactylorhiza majalis	G	5
Danthonia decumbens s.l.	G	35
Daphne mezereum [b]	-	20
Daucus carota	G	100
Deschampsia cespitosa	G	5
Dianthus carthusianorum	S	15
Dipsacus fullonum	G	20
Dryopteris filix-mas agg. [b]	-	25
Echium vulgare	G	10

Table A1 (*continued*)

Species	Hs	F (%)
Elymus repens	G	30
Epilobium angustifolium	G	95
Epilobium ciliatum [a]	-	10
Epilobium hirsutum	G	10
Epilobium montanum [b]	-	20
Epilobium obscurum	G	5
Epipactis atrorubens	G	20
Epipactis helleborine [b]	-	5
Epipactis muelleri	G	5
Equisetum arvense	G	15
Erigeron acris	G	10
Euonymus europaea	G	60
Eupatorium cannabinum	G	5
Euphorbia cyparissias	S	60
Euphorbia helioscopia	G	5
Euphrasia rostkoviana	S	45
Euphrasia stricta	S	65
Fagus sylvatica [b]	-	85
Festuca ovina agg.	G	100
Festuca pratensis	G	85
Festuca rubra agg.	G	80
Filipendula ulmaria	G	20
Filipendula vulgaris	S	10
Fragaria vesca	G	85
Fragaria viridis	G	35
Frangula alnus [b]	-	5
Fraxinus excelsior [b]	-	35
Fumaria o. ssp. *officinalis*	G	10
Fumaria v. ssp. *vaillanttii*	G	15
Galeopsis tetrahit	G	20
Galium aparine	G	80
Galium mollugo agg.	G	100
Galium odoratum [b]	-	20
Galium pumilum	G	60
Galium verum agg.	S	100
Genista pilosa	G	25
Genista tinctoria	S	60
Gentianella ciliata	S	45
Gentianella germanica	S	60
Geranium columbinum	G	10
Geranium dissectum	G	10
Geranium molle	G	10
Geranium pratense	G	5
Geranium pusillum	G	5
Geranium pyrenaicum [a]	-	45
Geranium robertianum	G	75
Geranium sanguineum	G	10
Geranium sylvaticum	G	25
Geum rivale	G	10
Geum urbanum	G	85
Glechoma hederacea	G	100
Globularia punctata	S	80
Gymnadenia conopsea s.l.	S	70
Hedera helix [b]	-	5
Helianthemum nummularium	S	100
Helictotrichon pratense	S	70
Helictotrichon pubescens	G	80
Heracleum s. ssp.	G	95
$^{s}H^{p}e^{h}r^{o}m^{n}i^{d}n^{y}iu^{li}m^{um}$monorchis	S	20
Hieracium lachenalii	G	75
Hieracium murorum	G	35
Hieracium pilosella	G	100
Hippocrepis comosa	S	100
Holcus lanatus	G	95
Hordelymus europaeus [b]	-	10
Hypericum hirsutum	G	65
Hypericum maculatum agg.	G	85
Hypericum perforatum	G	100
Hypochaeris maculata	S	45
Hypochaeris radicata	G	50
Ilex aquifolium [b]	-	30
Inula conyzae	G	5
Inula salicina	G	5
Juncus inflexus	G	10

Table A1 (*continued*)

Species	Hs	F (%)
Juncus tenuis [a]	-	5
Juniperus communis	S	85
Knautia arvensis	G	95
Koeleria macrantha	S	40
Koeleria pyramidata agg.	S	100
Lamium album	G	55
Lamium maculatum	G	45
Lapsana communis	G	10
Larix decidua [a > b]	-	5
Lathyrus pratensis	G	100
Lathyrus sylvestris	G	15
Leontodon a. ssp. *autumnalis*	G	75
Leontodon hispidus	G	75
Leonurus cardiaca s.l.	G	5
Leucanthemum vulgare agg.	G	95
Ligustrum vulgare	G	20
Linaria vulgaris	G	25
Linum catharticum	S	95
Listera ovata	G	85
Lolium perenne	G	80
Lonicera periclymenum	G	30
Lonicera xylosteum	G	90
Lotus corniculatus agg.	G	100
Luzula campestris agg.	G	75
Luzula multiflora	G	5
Lysimachia vulgaris	G	10
Malus spec. [a]	-	25
Malva moschata	G	40
Medicago falcata	S	85
Medicago lupulina	G	90
Medicago x *varia* [a]	-	10
Melampyrum cristatum	G	5
Melica nutans [b]	-	10
Melica uniflora [b]	-	5
Melilotus alba	G	10
Melilotus officinalis	G	30
Mentha spec. [a]	-	15
Mercurialis perennis [b]	-	55
Minuartia hybrida	S	5
Moehringia trinervia [b]	-	10
Myosotis arvensis	G	55
Narcissus spec. [a]	-	5
Onobrychis viciifolia	S	45
Ononis repens	S	90
Ononis spinosa agg.	S	100
Ophrys apifera	S	5
Ophrys insectifera	S	80
Orchis anthropophora	S	5
Orchis anthrop. x *militaris*	S	5
Orchis m. ssp. *mascula*	S	75
Orchis militaris	S	5
Orchis morio	S	15
Orchis ustulata	S	20
Origanum vulgare	G	85
Orobanche caryophyllacea	G	35
Orobanche cf. *lutea*	G	5
Orobanche elatior	G	15
Papaver rhoeas	G	20
Paris quadrifolia [b]	-	5
Parnassia palustris	S	20
Pastinaca sativa	G	45
Petrorhagia prolifera	S	5
Phleum phleoides	S	10
Phleum pratense agg.	G	80
Phyteuma orbiculare	G	55
Picea abies [a > b]	-	85
Picris hieracioides s.l.	G	60
Pimpinella major	G	25
Pimpinella saxifraga	S	100
Pinus nigra [ab]	-	30
Pinus sylvestris	G	100
Plantago lanceolata	G	95
Plantago major s.l.	G	65
Plantago media	G	100

Table A1 (*continued*)

Species	Hs	F (%)
Platanthera bifolia	G	15
Platanthera chlorantha	G	85
Poa compressa	G	45
Poa pratensis ssp. *angustifolia*	G	95
Poa pratensis ssp. *pratensis*	G	100
Poa trivialis	G	90
Polygala amarella	S	95
Polygala comosa	S	55
Polygala vulgaris s.l.	G	15
Polygonatum multiflorum [b]	-	5
Polygonatum odoratum	G	5
Polygonatum verticillatum	G	5
Polygonum aviculare agg.	G	15
Populus tremula [b]	-	65
Potentilla anserina	G	30
Potentilla erecta	G	45
Potentilla reptans	G	75
Potentilla tabernaemontani	S	100
Primula veris	S	100
Prunella grandiflora	S	85
Prunella vulgaris	G	85
Prunus avium [b]	-	40
Prunus domestica [a,b]	-	5
Prunus spinosa agg.	G	100
Pulmonaria officinalis agg.	G	10
Pulsatilla v. ssp. *vulgaris*	S	85
Pyrola cf. *rotundifolia*	G	5
Quercus petraea [b]	-	25
Quercus robur [b]	-	95
Ranunculus acris	G	55
Ranunculus auricomus agg. [b]	-	60
Ranunculus bulbosus	S	90
Ranunculus ficaria	G	25
Ranunculus polyanthemos	G	75
[a]*Rᵍaᵍnunculus repens*	G	25
Reseda lutea	G	30
Rhamnus catharticus	G	95
Rhinanthus angustifolius	G	70
Rhinanthus minor	G	90
Ribes alpinum	G	75
Ribes uva-crispa	G	75
Robinia pseudacacia a > b	-	5
Rosa arvensis	G	5
Rosa canina agg.	G	95
Rosa corymbifera agg.	G	70
Rosa rubiginosa	G	45
Rosa tomentosa	G	65
Rubus caesius	G	100
Rubus fruticosus agg.	G	70
Rubus idaeus	G	80
Rumex acetosa	G	100
Rumex acetosella s.l.	G	5
Rumex crispus	G	25
Rumex obtusifolius	G	15
Salix caprea b	-	85
Salix cinerea b	-	10
Salix fragilis agg. b	-	15
Salix purpurea a	-	10
Salvia pratensis	S	75
Sambucus nigra	G	60
Sanguisorba minor s.l.	S	100
Sanguisorba officinalis	G	15
Saxifraga granulata	G	40
Scabiosa columbaria	S	95
Scrophularia nodosa b	-	5
Securigera varia	G	5
Sedum acre	S	30
Sedum sexangulare	S	5
Sedum telephium agg. a	-	5
Senecio erucifolius	G	30
Senecio inaequidens a	-	10
Senecio jacobaea	G	95
Senecio ovatus	G	35
Senecio vulgaris	G	15

Table A1 (*continued*)

Species	Hs	F (%)
Serratula t. ssp. tinctoria	G	5
Seseli annuum	S	5
Sesleria albicans	S	60
Silaum silaus	G	10
Silene dioica	G	15
Silene latifolia	G	10
Silene vulgaris	G	75
Sisymbrium officinale	G	10
Solanum dulcamara	G	10
Solidago canadensis a	-	5
Solidago gigantea a	-	15
Solidago virgaurea	G	25
Sonchus arvensis	G	10
Sonchus asper	G	40
Sonchus oleraceus	G	25
Sorbus aria agg.	G	85
Sorbus aucuparia [b]	-	55
Sorbus torminalis	G	30
Stachys sylvatica [b]	-	25
Stellaria graminea	G	70
Stellaria holostea [b]	-	70
Stellaria media agg.	G	20
Succisa pratensis	G	10
Symphoricarpos albus [a]	-	10
Symphytum officinale s.l.	G	5
Tanacetum vulgare	G	15
Taraxacum laevigatum agg.	S	25
Taraxacum officinale agg.	G	95
Teucrium botrys	S	10
Teucrium chamaedrys	S	50
Teucrium montanum	S	10
Thesium pyrenaicum	G	65
Thlaspi arvense	G	15
Thlaspi perfoliatum	G	70
Thymus pulegioides	S	100
Tilia platyphyllos [b]	-	15
Torilis japonica agg.	G	70
Tragopogon pratensis	G	85
Trifolium arvense	G	5
Trifolium dubium	G	45
Trifolium hybridum	G	15
Trifolium medium	G	100
Trifolium montanum	S	100
Trifolium pratense	G	100
Trifolium repens	G	95
Trisetum flavescens	G	95
Tussilago farfara	G	30
Urtica dioica	G	95
Valeriana officinalis agg.	G	45
Valerianella locusta	G	40
Verbascum lychnitis	G	20
Verbascum nigrum	G	20
Verbascum thapsus	G	50
Veronica arvensis	G	40
Veronica chamaedrys	G	95
Veronica hederifolia	G	5
Viburnum lantana	G	85
Viburnum opulus	G	80
Vicia angustifolia	S	55
Vicia cracca	G	100
Vicia hirsuta	G	65
Vicia sepium	G	95
Vicia tenuifolia	G	50
Vicia tetrasperma	G	20
Viola arvensis	G	10
Viola tricolor agg.	G	5
Viola hirta	G	100
Viola odorata a	-	5
Viola reichenbachiana b	-	55
Viola riviniana	G	35

[a] Alien species as well as regionally non-resident species (according to Haeupler et al., 2003) were excluded from the analyses. [b] Species strongly associated with woodlands (according to Ellenberg et al., 1992) were excluded from the analyses.

Table A2
Habitat specificity (Hs; S = habitat specialists, G = habitat generalists; see Section 2.3) and frequency (F) of all recorded grasshopper species in the study area. The nomenclature follows Fischer et al. (2016).

Species	Hs	F (%)
Bicolorana bicolor	S	95
Chorthippus biguttulus	G	100
Chorthippus brunneus	G	70
Chrysochraon dispar	G	90
Decticus verrucivorus	S	10
Metrioptera brachyptera	S	95
Myrmeleotettix maculatus	S	20
Nemobius sylvestris	S	5
Omocestus viridulus	G	95
Pholidoptera griseoaptera	G	85
Pseudochorthippus parallelus	G	100
Roeseliana roeselii	G	90
Stenobothrus lineatus	S	100
Tetrix tenuicornis	S	75
Tetrix undulata	G	25
Tettigonia viridissima	G	70

Table A3
Habitat specificity (Hs; S = habitat specialists, G = habitat generalists; see Section 2.3) and frequency (F) of all recorded butterfly species in the study area. The nomenclature follows Reinhard and Bolz (2011) and Rennwald et al. (2011).

Species	Hs	F (%)
Adscita geryon	S	70
Adscita statices	G	25
Aglais io[a]	-	65
Aglais urticae[a]	-	95
Anthocharis cardamines	G	90
Apatura iris[b]	-	10
Aphantopus hyperantus	G	95
Aporia crataegi[a]	-	60
Araschnia levana	G	80
Argynnis aglaja	S	50
Argynnis paphia[b]	-	55
Aricia agestis	S	85
Boloria selene	G	10
Brenthis ino	G	10
Callophrys rubi	G	65
Carcharodus alceae	G	15
Carterocephalus palaemon	G	40
Celastrina argiolus	G	30
Coenonympha arcania	G	95
Coenonympha pamphilus	G	95
Colias alfacariensis	S	55
Colias crocea[a]	-	40
Cupido minimus	S	80
Cyaniris semiargus	G	75
Erebia ligea	G	15
Erebia medusa	G	95
Erynnis tages	S	80
Gonepteryx rhamni[a]	-	90
Hamearis lucina	S	80
Issoria lathonia[a]	-	10
Jordanita cf. *globulariae*	S	5
Lasiommata maera	S	15
Lasiommata megera	G	90
Leptidea juvernica	G	65
Limenitis camilla[b]	-	15
Lycaena hippothoe	G	20
Lycaena phlaeas[a]	-	25
Lycaena tityrus	G	45
Maniola jurtina	G	100
Melanargia galathea	G	95
Melitaea aurelia	S	45
Melitaea cinxia	S	10
Nymphalis polychloros	G	5
Ochlodes sylvanus	G	90
Papilio machaon	G	10

Table A3 (*continued*)

Species	Hs	F (%)
Pararge aegeria [b]	-	65
Phengaris arion	S	20
Pieris brassicae [a]	-	65
Pieris napi [a]	-	100
Pieris rapae [a]	-	75
Plebeius argus	S	35
Polygonia c-album	G	30
Polyommatus coridon	S	95
Polyommatus icarus	G	100
Pyrgus alveus	S	15
Pyrgus malvae	S	90
Satyrium pruni	G	10
Spialia sertorius	S	75
Thecla betulae	G	35
Thymelicus acteon	S	10
Thymelicus lineola	G	95
Thymelicus sylvestris	G	95
Vanessa atalanta [a]	-	80
Vanessa cardui [a]	-	70
Zygaena filipendulae	G	80
Zygaena lonicerae	S	50
Zygaena loti	S	50
Zygaena purpuralis	S	45
Zygaena transalpina	S	50
Zygaena viciae	G	70

[a] Migratory species (including both true migrants and highly mobile species which frequently occur outside their breeding range according to Ebert and Rennwald, 1991) were excluded from the analyses.

[b] Species strongly associated with woodlands (according to Ebert and Rennwald, 1991) were excluded from the analyses.

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