



Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands

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ARTICLE INFO

Article history:

Received 2 November 2011

Received in revised form 15 March 2012

Accepted 26 March 2012

Keywords:

Butterfly conservation
Calcareous grassland
Functional connectivity
Habitat fragmentation
Landscape structure
Land use

ABSTRACT

Habitat size and isolation are considered important drivers for the persistence of insects in fragmented landscapes. In contrast, habitat quality and the composition of the landscape matrix have only recently received more attention. To investigate the effects of habitat area, functional connectivity, landscape context and habitat quality, we analyzed species richness and density of butterfly communities in pre-alpine calcareous grasslands. Through standardized transect walks in meadows ($n = 26$), pastures ($n = 12$), and recently abandoned grasslands ($n = 8$), we sampled butterflies and burnet moths, as well as environmental parameters. Habitat specialist species were found in higher numbers if the habitat patches were surrounded by forests rather than non-habitat grasslands. Furthermore, the number of host plants had a positive influence on butterfly diversity and density. Habitat generalists were not affected by any of the landscape variables, but had higher species numbers and densities if the abundance of nectar plants was higher. In contrast to other studies, we showed that the impact of habitat quality on butterfly communities is more important than landscape effects. The proportion of calcareous grassland in our study region seemed to generally be too high to observe fragmentation effects. Contrary to expectations, surrounding forest increased the species richness of habitat specialists in the habitat patch.

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1. Introduction

Land-use change is a major threat to global biodiversity (Foley et al., 2005; Sala et al., 2000; Stoate et al., 2001; Vitousek, 1994). The transformation of natural or semi-natural landscapes is accompanied by habitat loss and habitat fragmentation (Debinski and Holt, 2000; Fahrig, 2003) but also by deterioration of habitat quality (Fischer and Lindenmayer, 2007; Harrison and Bruna, 1999). Habitat loss and fragmentation usually occur together and lead to reduced habitat area and isolation of the remaining habitat patches from each other (Fahrig, 2003). Deterioration of habitat quality, however, can occur independently, e.g. by abandonment of traditional land use in semi-natural habitats (MacDonald et al., 2000; Strijker, 2005). Habitat size and isolation are considered important drivers of species richness and population density in fragmented landscapes (Dover and Settele, 2009; Hanski, 1999) but the role of habitat quality has only recently received more attention (Krauss et al., 2004; Mortelliti et al., 2010; Thomas et al., 2001).

Butterflies are excellent model organisms for the study of both landscape effects such as habitat size and isolation, and local effects such as habitat quality. This is because many butterflies build

metapopulations, and are therefore influenced by the spatial arrangement of the patches (Dover and Settele, 2009; Hanski, 1999), and also because most species are very specific concerning their local habitat requirements, such as certain host plants (Munguira et al., 2009).

To date, there are no consistent standards for which indicators should be measured to determine habitat quality (Mortelliti et al., 2010). For butterflies, the availability and abundance of nectar plants and host plants are among the most important requirements (Erhardt and Mevi-Schütz, 2009; García-Barros and Fartmann, 2009; Munguira et al., 2009). However, microclimate, which is mediated by vegetation structure and local climate, also has an impact on both adult and larval stages (García-Barros and Fartmann, 2009; Wickmann, 2009). The management regime (land use) of the site influences the above-mentioned parameters, but also affects butterflies directly through the disturbance event (Dover and Settele, 2009). According to Mortelliti et al. (2010), even when taking habitat quality into account, most fragmentation studies did not detect effects, either because inappropriate variables were chosen or the study design did not cover a gradient of habitat quality.

Furthermore, in these studies the landscape is traditionally divided into habitat patches and the landscape matrix, but the composition of the latter is often not considered (Dover and Settele, 2009). However, Dennis et al. (2003) showed that the

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landscape context is crucial because the matrix can provide additional resources for less specialized species. Landscape elements may also act as a barrier or corridor for dispersal of butterflies and thus increase or decrease isolation effects (Öckinger and Smith, 2008; Ricketts, 2001).

Recently, habitat quality has been included in the modeling of butterfly persistence in fragmented landscapes (e.g. Eichel and Fartmann, 2008; Öckinger and Smith, 2006; Thomas et al., 2001; WallisDeVries, 2004), but studies that consider both habitat quality and the landscape context are rare (but see Bergman et al., 2004; Binzenhöfer et al., 2005; Krauss et al., 2003). Furthermore, new tools are available to calculate distances taking the permeability of the matrix for dispersal into account (e.g. least-cost methods). These so-called “functional distances” between patches have successfully been tested in single-species studies (Adriaensens et al., 2003; Chardon et al., 2003). However, the use of functional distances for calculating functional connectivity indices has not yet been applied to butterfly communities.

Calcareous grasslands are among the most species-rich habitats in Europe, containing 48% of native European butterflies (van Swaay, 2002). Land-use change affects calcareous grasslands in two contrasting ways: intensification and abandonment (Poschold and WallisDeVries, 2002; Settele et al., 2009). Both have led to a severe decline of this habitat type across Europe (WallisDeVries et al., 2002). The same is true of the pre-alpine calcareous grasslands in the Limestone Alps, known in German as “Buckelwiesen” (meaning ‘hummocky meadow’) (Quinger et al., 1994; Embleton-Hamann, 2004). This unique calcareous grassland type is characterized by a pit and mound microrelief of glacial origin: a geomorphologic peculiarity also known for its species richness and thus of great value for biodiversity (Gutser and Kuhn, 1998).

In this study, we analyzed the effects of habitat area, functional connectivity, landscape context, and habitat quality on species richness and density of butterfly communities in pre-alpine calcareous grasslands. We investigated a habitat quality gradient with representative sample sizes of three land-use types, meadow

($n = 26$), pasture ($n = 12$), and abandoned grasslands ($n = 8$), to analyze the effects of different parameters of habitat quality. Furthermore, we focussed on integrating the landscape context into connectivity measures, as well as analyzing edge effects in the surrounding landscape. We studied habitat specialists and generalists separately in order to develop conservation recommendations for this rare habitat type.

The main hypotheses are:

- (i) Species richness and density increase with increasing area, functional connectivity, and quality of the habitat.
- (ii) Habitat specialists and generalists have different requirements on landscape structure and habitat quality.
- (iii) Landscape context has a stronger impact on generalists than on specialists. Grasslands in the surrounding matrix increase species richness and density.

2. Materials and methods

2.1. Study area and sub areas

The study area of 47 km² is located in the northern foothills of the German Alps, approximately 100 km south of the Bavarian capital, Munich (47°26'N, 11°10'E and 47°30'N, 11°17'E) at an elevation of 800–1400 m above sea level (Fig. 1). Due to its location in the Northern Limestone Alps, the climate is generally cold and moist (Rösler, 1997). However, the local climate is favoured by the rain shadow of the Estergebirge mountain range, which results in a lower mean annual precipitation of 1330 mm, and by foehn winds leading to a higher mean annual temperature of 7 °C (station Mittenwald, Rösler, 1997).

The study was carried out on ‘hummocky meadows’. Since the 1920s, the cover of this meadow type in the Alps has declined by more than 95%, mainly due to intensification (flattening and fertilization) and afforestation. The study area contains the biggest remnants of this rare calcareous grassland type within the Alps

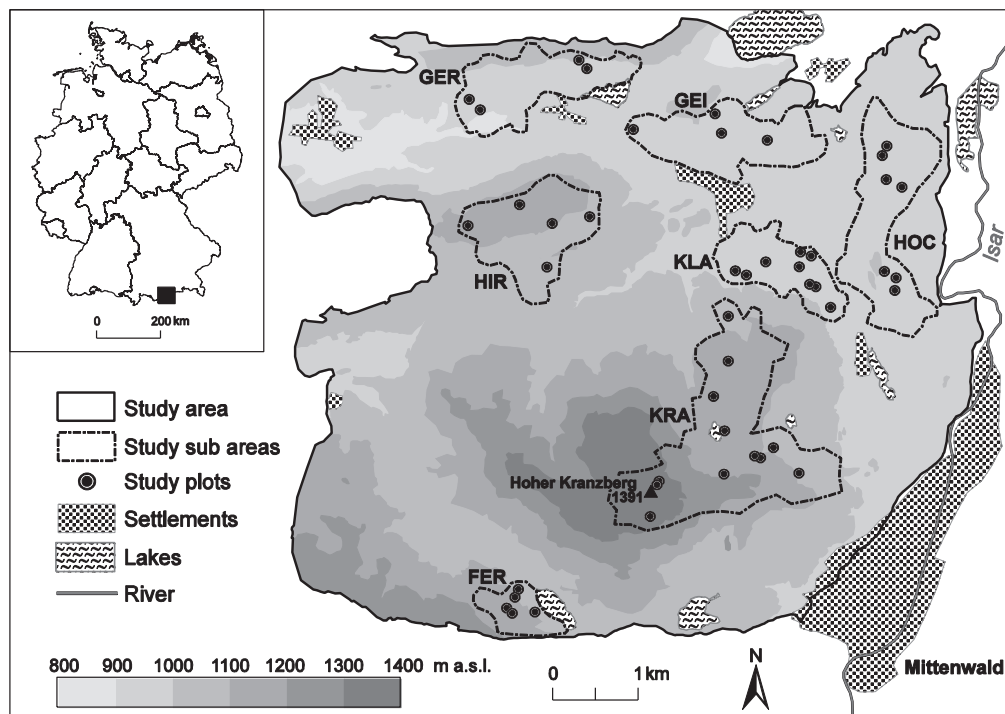


Fig. 1. Study area in southern Germany: sub-areas (FER = Ferchensee, GEI = Geißschädel, GER = Gerold, HIR = Hirzeneck, HOC = Hochfläche, KLA = Klais, KRA = Kranzberg).

(~400 ha), and is part of the Prime Butterfly Area of Karwendel (van Swaay and Warren, 2003).

2.2. Study patches and study plots

In seven sub-areas, we studied 18 patches of calcareous grassland, containing altogether 46 study plots (one to nine study plots per patch). Each plot had a size of 500 m². By definition, a calcareous grassland patch was isolated from other patches by at least 50 m of non-habitat (e.g. forest, other grassland types) (cf. Fartmann, 2006; Poniatowski and Fartmann, 2010). We established the study plots with representative sample sizes of the three land-use types of meadow ($n = 26$), pasture ($n = 12$), and abandoned grasslands ($n = 8$). We conducted a pre-study to apply a gradient of habitat quality to the plots and to spatially intersperse the land-use types throughout the sub-areas and study patches. Vegetation type and structure were always homogeneous within each plot.

2.3. Butterflies

We sampled butterflies (Hesperioidea and Papilionoidea) and burnet moths (Zygaenidae) in 2010 using standardized transect counts (Pollard and Yates, 1993). Unless stated otherwise, “butterflies” includes burnets. We recorded butterflies and their flower visits inside the study plots in loops with a width of 5 m. Each transect walk took exactly 15 min, excluding identification time for butterfly or flower species. We visited all plots five times every three weeks (22 May–26 August 2010), between 10:00 and 17:00 h (GTM + 2) and only during suitable weather conditions (cf. Pollard, 1977). Species numbers and population densities were pooled for each study plot over the sampling period.

We defined butterfly species as habitat specialists ($n = 31$) for calcareous grasslands if they are restricted to or show a preference for calcareous grasslands in the study area. Species that inhabit more than one other habitat type apart from calcareous grasslands, and species with other preferences, were defined as habitat generalists ($n = 31$) (Appendix A). This classification is based on the preferences of the larval stages as described in Ebert (1994) and Ebert and Rennwald (1991a). For alpine species, we used SBN (1997) and Stettmer et al. (2007) as additional references. However, we made some adaptations if species showed different preferences in the field. Similar classifications have been made in other studies (e.g. Krauss et al., 2003; Warren et al., 2001). The butterfly nomenclature follows Karsholt and Razowski (1996).

2.4. Habitat quality

We sampled habitat quality parameters (Table 1) in the study plot once between the end of June and the beginning of July 2010. Only nectar abundance was recorded for each transect walk. All meadows were sampled before mowing.

2.4.1. Nectar sources

We quantified nectar abundance after each transect walk by counting all inflorescences in an area of 12 m² (3 m × 4 m) inside the study plot (Fartmann, 2004). We moved the sampling area to where most of the flowers were found during the transect walk to take the mobility of butterflies into account. We weighted nectar abundance by its use by butterflies derived both from literature data (Ebert, 1994; Ebert and Rennwald, 1991a) and field observations. Flowers which were visited frequently received a higher Preference Class (PC) than unpopular ones (Table 2).

To calculate the weighted nectar abundance (NA_i) of the nectar plant species i , we used the following formula:

$$NA_i = na_i \times \sum \frac{PC_{ij}}{NP_j}$$

where na_i is the absolute nectar abundance of the nectar plant species i , PC_{ij} is the Preference Class of the butterfly species j for the nectar plant species i (Table 2), and NP_j the number of nectar plants of the butterfly species j . The formula is based on Leopold (2001), but also takes the number of flower species used by a butterfly ('niche breath' according to Corwell and Futuyuma, 1971) into account. We calculated the sum of all weighted nectar abundances for each plot at each transect walk, herein called 'nectar sources'. Nectar sources from the different transect walks were pooled by calculating means for each plot.

2.4.2. Larval host plants

We recorded the presence or absence of larval host plant species of mono- and oligophagous butterflies (Ebert, 1994; Ebert and Rennwald, 1991a, 1991b; SBN, 1997) in the study plot. Analogous to the calculation of weighted nectar sources, each host plant was weighted by the number of butterfly species feeding on it, with higher values for mono- than oligophagous larvae. We calculated the weighted number of larval host plants H_k in the plot k using the following formula:

$$H_k = \sum \left(P_{ki} \times \sum \frac{1}{h_j} \right)$$

where P_{ki} is the presence ($P_{ki} = 1$) or absence ($P_{ki} = 0$) of the host plant i in the plot k , and h_j is the number of larval host plants of the butterfly species j . The quotients $1/h_j$ are summarized for each host plant species i ($\sum 1/h_j$). We calculated independent weighted host plant numbers for both specialist and generalist butterfly species. Weighted number of larval host plants are herein called 'larval host plants'.

2.5. Landscape effects

We analyzed landscape effects based on digital thematic maps (Bayerisches Landesamt fur Vermessung und Geoinformation, 2010). Additionally we used maps of protected biotopes (Bayerisches Landesamt fur Umwelt, 2008) to achieve a finer classification of different grassland types. We classified the biotopes in the study area as forests (70%), mesic grasslands (16%), calcareous grasslands (9%), settlements and houses (2%), wet grasslands (1%), and other biotopes (2%). For spatial analysis we used ArcGIS 9.2. Patch connectivity and patch area were calculated for each patch, whereas landscape context was calculated for each plot.

2.5.1. Patch connectivity

We measured edge-to-edge distance from the study patches to neighboring calcareous grassland patches in the study area using the cost-distance model (Adriaensen et al., 2003; Chardon et al., 2003). Instead of Euclidean distances, functional distances were calculated by defining the influence of the biotope type of the matrix elements on butterfly dispersal. Biotope types favouring dispersal received lower resistance values than those that hinder movements (Table 3). Empirical data for the resistance value of the biotopes was not available. Furthermore, the effect is species-specific and difficult to generalize for the whole community. Therefore, we chose the resistance values conservatively, with low differences in the ratio between the biotope types. Non-habitat grasslands may provide resources for butterflies such as nectar plants and were therefore considered as corridors. The surrounding

Table 1
Overview of sampled parameters and their analysis in Generalized Linear Mixed-effects Models (GLMM). Spearman's rank correlation coefficients (r_s) were calculated for all pairs of predictor variables. If a pair strongly correlated ($r_s > \pm 0.6$) one of the two correlated variables was deleted. In the case of several intercorrelated variables, a Principle Component Analysis (PCA: Legendre and Legendre, 1998) was conducted to calculate a single principle component which was used in the subsequent analysis.

Sampled parameter	Correlation		GLMM	Mean (\pm SE)	Min.–Max.
	r_s	Used variable			
Response variables					
Species number ^a	–	–	Model 1 + 2	18.5 \pm 0.6	12–28
Density (individuals/500 m ²) ^a	–	–	Model 1 + 2	50.5 \pm 2.5	21–96
Predictor variables					
<i>Landscape effects</i>					
Patch area (ha) ^b	–	–	Model 1	23.8 \pm 2.4	1–48
Functional connectivity (Index) (see Section 2.5.1)	–	–	Model 1	259 376.4 \pm 23 267.8	892–467 588
Cover of biotopes in 250 m (%) (see Section 2.5.2)					
Forest	1.00	▶ Forest	Model 1	69.3 \pm 4.9	0–100
Mesic grassland	–0.94	▶		28.3 \pm 5	0–99
Wet grassland	–	–	Model 1	2.4 \pm 1.1	0–42
<i>Habitat quality</i>					
Nectar sources (see Section 2.4.1)	–	–	Model 2	569.9 \pm 49.9	121–1521
Larval host plants (see Section 2.4.2)	–	–	Model 2	17.6 \pm 0.4	9–23
Shrub height (cm) ^c	0.81	▶		19.5 \pm 4.6	0–120
Turf height (cm) ^c	0.69	▶		15.2 \pm 0.9	6–30
Horizontal vegetation density (%) ^{c,d}	0.82	▶ Principle component: 'Vegetation density'	Model 2	31.2 \pm 1.4	16–57
Cover of different layers (%)					
Shrubs	0.76	▶		0.8 \pm 0.3	0–8
Litter	0.85	▶		24.2 \pm 5	0–100
Cryptogams	–	–	–	10.3 \pm 2.1	0–60
Herbs and grasses	0.78	▶		94.4 \pm 1.1	70–100
Total vegetation	1.00	▶ 'Vegetation cover'	–	96.5 \pm 0.8	71–100
Bare ground and stony surface	–	–	–	1.4 \pm 0.3	0–10
Potential daily sunshine duration (h) ^e	–	–	Model 2	11.1 \pm 0.2	8–13
Altitude (m a.s.l.)	–	–	–	1049.6 \pm 16.6	920–1375
Land-use type ^f	–	–	Model 2	–	–
Random effects					
Sub area ^g	–	–	Model 1 + 2	–	–
Patch ^g	–	–	Model 1 + 2	–	–

^aHere values for all species, but 'specialists' and 'generalists' were tested separately.

^bCalculated in the digital map.

^cMeasured three times at a randomly chosen location in the study plot. Means were calculated afterwards.

^dMeasured within a frame of 30 cm depth and 50 cm width for different layers in 0–5, 5–10, ..., 25–30 cm height above ground (Poniatowski and Fartmann, 2008), here: mean of all layers.

^eMeasured in the center of the plot with a horizontoscope after Tonne (1954) for June, accuracy: 1/2 h.

^fThree categories: meadow, pasture, abandoned grassland.

^g'Patch' (see Section 2.2) within 'sub area' (Fig. 1) was used as a nested random factor.

Table 2

Preference Class (PC) of butterfly species per nectar plant species. If both literature and field observations existed, we used the higher value.

PC	Classes from Ebert (1994), Ebert and Rennwald (1991a) ("Wertstufen")	Field observations (flower visits during five transect walks)
1	1	–
2	2	–
3	3	1
4	4	2–4
5	5	5–9
6	–	≥ 10

Table 3

Resistance value of the biotope types for the cost-distance model.

Biotope type	Resistance value
<i>Habitat</i>	
Calcareous grassland	0.5
<i>Non-habitat</i>	
Mesic grassland, wet grassland	2
Other biotopes (e.g. water bodies)	3
Settlements and houses	4
Forest	5

coniferous forests, as well as settlements and houses represent physical barriers for butterfly movement. Other biotope types which are neither barriers nor corridors received intermediate resistance values.

We used the calculated functional distances to calculate a connectivity index I_i for each study patch i , using the following formula:

$$I_i = \sum \exp(-d_{ij}) \times A_j$$

where A_j is the size (in m²) of the neighboring patch j and d_{ij} the (cost-) distance (in km) between the neighboring patch j and the study patch i . This formula was used in several studies with Euclidean distances (e.g. Anthes et al., 2003; Steffan-Dewenter and Tschardtke, 2000) and is based on the formula devised by Hanski (1999). Larger values of the functional connectivity index I indicate better connectivity (and lower isolation) than smaller values. The same formula was also tested with Euclidean distances. Euclidean distances varied from 60 to 1534 m, and functional distances from 251 to 6185 m. The indices were correlated ($r_s = 0.67$, $P < 0.01$) and showed similar effects on the butterfly communities. Therefore, we show only the results with the functional connectivity index.

2.5.2. Landscape context

The proportion of biotope types was calculated for a circle with a radius of 250 m around the study plot. The percentage of calcareous grasslands was correlated with patch area ($r_s = 0.65$, $P < 0.001$). Proportions were therefore calculated excluding areas of calcareous grasslands to reduce the patch area effect. Only the proportions of forest, mesic grassland and wet grassland were used for further analysis, because other biotope types always had low proportions (mean $< 1\%$).

2.6. Statistical analysis

We conducted Generalized Linear Mixed-effects Models (GLMM: Imer, Bates et al., 2010) using R 2.10.1 (R Development Core Team, 2010) to analyze landscape and habitat quality effects on species richness and density of specialist and generalist butterfly species. To deal with multicollinearity, we excluded or summarized some variables prior to analysis (Table 1, for further information see Schroder et al., 2009). We selected two sets of predictor variables to analyze landscape effects (Model 1) and habitat quality effects (Model 2) independently (Table 1). We used all four landscape variables, but chose only five habitat quality parameters a priori to deal with the problem of overfitting and to reduce biases arising from stepwise analysis with too many variables (Schroder et al., 2009). Stepwise backward-selection was used to remove non-significant variables ($P < 0.05$) from the model. We analyzed species richness with a Poisson error structure, and densities with Gaussian error structure after they were square-root transformed to achieve normally distributed residuals. Because the study plots in one study patch were not independent, GLMMs for habitat quality effects were conducted with 'patch' within 'sub area' as a nested random factor. In the landscape effects models, values for functional connectivity and patch area were identical within each patch. However we kept the 46 replicates, because we had individual values for landscape context. Because of that, we used GLMMs with 'patch' within 'sub area' as a nested random factor.

3. Results

In total, we recorded 56 butterfly species and six species of burnet moths, comprising 2325 individuals on the 46 plots. The most frequent and abundant species were *Zygaena filipendulae* and *Coenonympha glycerion*, both occurring in more than 85% of the plots and each comprising around 10% of all individuals.

3.1. Effects of patch size, functional connectivity and landscape context

Generalized Linear Mixed-effects Models (GLMM) revealed that area and functional connectivity of the study patches had no influence on species number (Table 4) or density (Table 5) of specialist or generalist butterflies. The same was true for the connectivity index calculated with Euclidean distances. In all landscape effect models, only species number of specialists could be explained by one of the predictor variables: the number of habitat specialists increased with the share of forest within 250 m around the study plot (Table 4, Fig. 2), simultaneously indicating a negative effect of surrounding mesic grasslands (cf. Table 1). Wet grasslands near the study plot had no influence in any of the models.

3.2. Effects of habitat quality

The habitat quality models showed that both species number and density of specialists were positively affected by the weighted number of larval host plants, whereas generalists had higher species numbers and densities when the weighted nectar abundance was higher (Tables 4 and 5, Fig. 2). Nectar sources had a higher explanatory power for density than for the barely significant number of generalist species (Table 4 and 5, Fig. 2).

4. Discussion

In this study, we tested the influence of landscape structure and habitat quality on specialist and generalist butterfly species in pre-alpine calcareous grasslands. Landscape effects played a minor role in influencing species richness and density, whereas habitat quality had significant effects on both.

Table 4

Statistics of GLMM: Relationship between number of species of specialists and generalists (Poisson error structure) and several environmental parameters (predictor variables) (Table 1). Non-significant predictors were excluded from the final model by stepwise backward-selection ($P > 0.05$). Random factor was 'patch' nested within 'sub-area'.

Specialists (N = 31)					Generalists (N = 31)				
Parameter	Estimate	SE	Z	P	Parameter	Estimate	SE	Z	P
<i>Model 1: Landscape effects</i>					<i>Model 1: Landscape effects</i>				
Forest 250 m (%)	0.004	0.002	2.781	0.004	n.s.				
Pseudo-R ² [Nagelkerke's] = 0.29; (cf. Fig. 2a)									
<i>Model 2: Habitat quality</i>					<i>Model 2: Habitat quality</i>				
Larval host plants	0.053	0.022	2.477	0.012	Nectar sources/100	0.032	0.017	1.889	0.046
Pseudo-R ² [Nagelkerke's] = 0.23; (cf. Fig. 2b)					Pseudo-R ² [Nagelkerke's] = 0.15; (cf. Fig. 2c)				

Table 5

Statistics of GLMM: Relationship between density (individuals/500 m²) of specialists and generalists (Gaussian error structure) and several environmental parameters (predictor variables) (Table 1). Non-significant predictors were excluded from the final model by stepwise backward-selection ($P > 0.05$). Random factor was 'patch' nested within 'sub-area'.

Specialists (N = 31)					Generalists (N = 31)				
Parameter	Estimate	SE	T	P	Parameter	Estimate	SE	T	P
<i>Model 1: Landscape effects</i>					<i>Model 1: Landscape effects</i>				
n.s.					n.s.				
<i>Model 2: Habitat quality</i>					<i>Model 2: Habitat quality</i>				
Larval host plants	0.212	0.073	2.926	0.006	Nectar sources/100	0.148	0.039	3.787	<0.001
Pseudo-R ² [Nagelkerke's] = 0.16; (cf. Fig. 2d)					Pseudo-R ² [Nagelkerke's] = 0.30; (cf. Fig. 2e)				

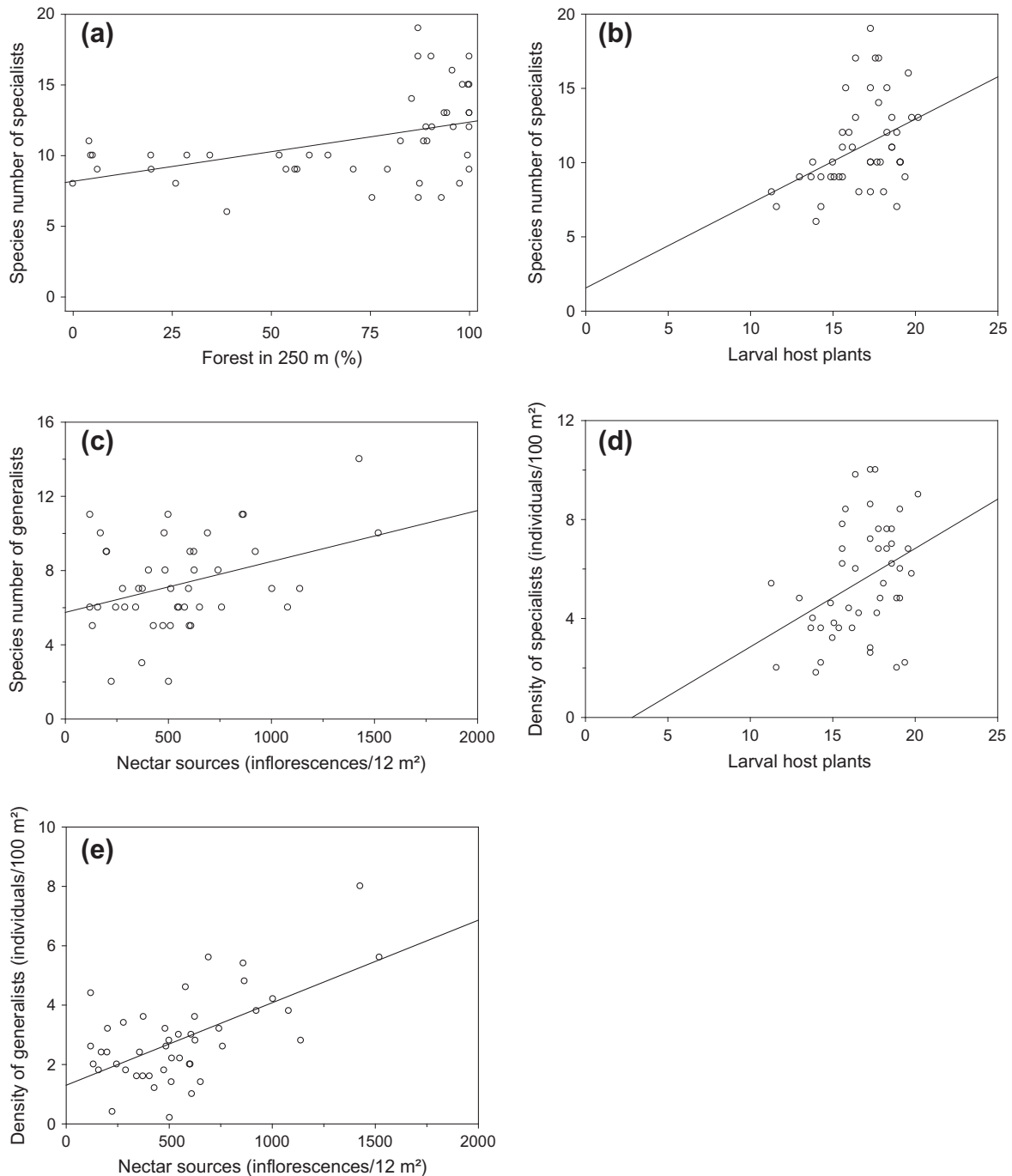


Fig. 2. Results of the GLMMs: Relationship between number of species of specialists and generalists and significant environmental parameters (a–c), as well as the relationship between density (individuals/500 m²) of specialists and generalists and significant environmental parameters (d–e). For details see [Tables 4 and 5](#).

Several studies have shown the importance of habitat size on butterfly communities (e.g. Krauss et al., 2003; Steffan-Dewenter and Tschamtko, 2000), whereas Thomas et al. (2001) found that the effects of isolation and especially habitat quality on their six studied butterfly species were more important than habitat area. Our results are in accordance with those of Binzenhöfer et al. (2005), which did not find an effect of either habitat size or isolation because of the high density of suitable habitat patches in their study region. Dover and Settele (2009) conclude that isolation is more important in highly modified landscapes. Therefore, we suspect that there is no impact of either habitat area or functional connectivity because of the generally high proportion and low isolation of calcareous grasslands in our study region (see Section 2.5).

To our knowledge, this is the first study that uses an isolation or connectivity index on the community level that is based on functional distances (least-cost modeling, cf. Adriaensen et al., 2003). Because we failed to prove an effect of functional connectivity as well as Euclidean connectivity, we recommend testing this method in a more fragmented landscape. Although Brückmann et al. (2010) advise against the use of such complex connectivity measures in community studies, we expect more precise results from functional distances, compared to Euclidean distances, in landscapes with strong differences in permeability of the matrix habitats for butterfly dispersal (cf. Öckinger and Smith, 2008). Empirical data on dispersal through different habitat types would improve the fitting of the resistance values (Baguette and Van Dyck, 2007).

Contrary to our expectations, the landscape context had no effect on generalists, but did have an effect on specialists, and species richness was increased by forest rather than mesic grassland surrounding the habitat patches. Forest is a barrier for grassland butterflies (Roland et al., 2000; Schmitt, 2000) thus inhibiting dispersal to other calcareous grassland patches. However, dispersal of an individual carries the risk of failing to reach a suitable habitat, hence draining the population in the patch rather than promoting genetic exchange (Hovestadt and Nieminen, 2009). Intensively used grasslands may act as a sink habitat for specialist species that cannot reproduce in the matrix, although some resources such as nectar plants are available. Consequently, in high-quality patches of sufficient size to support viable populations, it is better for specialists not to emigrate. Such effects have been shown by Kuussaari et al. (1996), demonstrating that open-patch boundaries have positive effects on emigration rates of *Melitaea cinxia*, thus leading to negative effects on the persistence of the population. However, three alternative explanations need to be considered: (i) preference of forest–grassland ecotones; (ii) sheltering from wind by forests which leads to building-up of heat; and (iii) eutrophication by neighboring fertilized grasslands. For the first two explanations we would expect that the effect is limited to either (i) forest and fringe-species, or (ii) to thermophilous species, but this could be refuted by our species data (results not shown). The third explanation is also unlikely because the neighboring grasslands are not highly fertilized (personal observation) and because the eutrophication effect should be reflected through the habitat quality parameters. Although more detailed data would be necessary to conclude that mesic grasslands act as a sink in our study area, we assume that it is the best explanation for our results.

Only one of the four landscape models showed a significant impact on butterflies, whereas all habitat quality models explained species richness and density of both specialists and generalists. This supports the finding of other studies (e.g. Mortelliti et al., 2010; Thomas et al., 2001; WallisDeVries, 2004) that habitat quality is at least as important as landscape factors. Larval food sources influenced habitat specialists, because they were usually host plant specialists (mono- or oligophageous according to Ebert, 1994; Ebert and Rennwald, 1991a,b) and remain in the same habitat type throughout their life-cycle. In contrast, habitat generalists were more strongly affected by adult food sources, because they are more mobile (Warren et al., 2001) and their larval development can take place in another patch or even habitat type. Some of the generalists are simply nectar visitors that cannot reproduce on calcareous grasslands due to lack of their host plants (e.g. *Aglais urticae* or *Inachis io* feeding on *Urtica dioica*, own observation). Other habitat quality parameters such as vegetation structure, local climate and land use were not relevant in this study. On the species level, however, we observed that species had different optima in these parameters (results not shown), but there was no general pattern that was reflected up to species richness and density on the community level.

5. Implications for conservation

Our data emphasize the importance of habitat quality for the butterfly community, whereas landscape effects play a secondary role. This supports the results of Binzenhofer et al. (2005) that in landscapes with a lower degree of fragmentation, habitat quality is the main driver of species occupancy. However, the high amount and connectivity of habitats remains an important value, as it is the reason for the persistence of species with high demands for space that are rare or extinct elsewhere (e.g. *Argynnis niobe*, Salz and Fartmann, 2009). The analysis of habitat specialists and generalists revealed the importance of food sources for butterflies. Conservation strategies should aim to provide a great variety of different

larval host plants, because this is key to the protection of habitat specialists, which are usually of greater conservation concern than widespread generalists (Warren et al., 2001). Nectar resources are also important (Erhardt and Mevi-Schutz, 2009) but, according to this study, increasing their abundance will mainly affect densities of habitat generalists.

The well-connected, traditionally used and nutrient-poor grasslands in our study area (Gutser and Kuhn, 1998) provide the habitat for species-rich butterfly and burnet moth communities. Calcareous grasslands are semi-natural grasslands that need human disturbance to remain open (Poschlod and WallisDeVries, 2002). In the case of our study region, the focus should be on preserving traditional mowing on sites known to have been mown for centuries, because flora and fauna have adapted to this practice used by landowners (Gutser and Kuhn, 1998). Long-term succession on abandoned grasslands should be halted by some form of management. Grazing or mowing every few years are cost-effective alternatives to annual mowing on these sites.

Acknowledgements

This study was partly funded by the 'Bayerisches Landesamt fur Umwelt' (LfU). Regional support was provided by the 'Landratsamt Garmisch-Partenkirchen' (W. Kraus and K. Streicher). We are grateful to R. Bolz and S. Hafner for the determination of some critical butterfly and burnet moth species. Moreover, we would like to thank C. Muller, C. Sanz Perucho, A. Zielisch and two anonymous reviewers for valuable comments on an earlier version of the manuscript.

Appendix A

See Table A1.

Table A1
Specialist and generalist butterfly and burnet moth species on the 46 pre-alpine calcareous grassland plots.

Taxon	Constancy (%) ($N_{\text{patches}} = 46$)	Number of individuals (5 walks, 500 m ² plot)
Specialists		
<i>Coenonympha glycerion</i>	98	224
<i>Erebia aethiops</i>	80	202
<i>Erebia medusa</i>	76	101
<i>Cupido minimus</i>	72	136
<i>Melitaea aurelia</i>	67	112
<i>Hesperia comma</i>	61	81
<i>Polyommantus coridon</i>	61	55
<i>Colias alfacariensis</i>	61	53
<i>Erebia oeme</i>	50	63
<i>Brenthis ino</i>	48	41
<i>Argynnis niobe</i>	46	43
<i>Zygaena loti</i>	43	41
<i>Erebia pronoe</i>	39	134
<i>Polyommantus bellargus</i>	39	37
<i>Zygaena purpuralis</i>	33	30
<i>Melitaea athalia</i>	26	29
<i>Hamearis lucina</i>	26	13
<i>Maculinea arion</i>	24	18
<i>Pyrgus alveus</i> agg.	24	12
<i>Aricia artaxerxes</i>	22	14
<i>Euphydryas aurinia aurinia</i>	22	14
<i>Argynnis aglaja</i>	15	8
<i>Plebeius argus</i>	15	8
<i>Adscita geryon</i>	11	9
<i>Argynnis adippe</i>	11	5
<i>Pieris bryoniae</i>	11	5
<i>Pyrgus malvoides</i>	11	4

(continued on next page)

Table A1 (continued)

Taxon	Constancy (%) ($N_{\text{patches}} = 46$)	Number of individuals (5 walks, 500 m ² plot)
<i>Erynnis tages</i>	9	5
<i>Polyommantus dorylas</i>	4	3
<i>Coenonympha arcania</i>	2	1
<i>Zygaena lonicerae</i>	2	1
Generalists		
<i>Zygaena filipendulae</i>	87	227
<i>Maniola jurtina</i>	74	176
<i>Pieris rapae</i>	54	42
<i>Zygaena viciae</i>	52	61
<i>Papilio machaon</i>	50	33
<i>Aglais urticae</i>	43	37
<i>Colias croceus</i>	37	24
<i>Anthocharis cardamines</i>	33	19
<i>Ochlodes sylvanus</i>	26	14
<i>Gonepteryx rhamni</i>	26	11
<i>Pieris napi</i>	22	12
<i>Inachis io</i>	22	9
<i>Vanessa atalanta</i>	22	8
<i>Aphantopus hyperantus</i>	20	16
<i>Polyommantus icarus</i>	17	9
<i>Coenonympha pamphilus</i>	15	10
<i>Thymelicus lineola</i>	13	20
<i>Vanessa cardui</i>	13	8
<i>Thymelicus sylvestris</i>	11	11
<i>Polyommantus semiargus</i>	11	6
<i>Lasiommata maera</i>	11	4
<i>Aporia crataegi</i>	9	7
<i>Melitaea diamina</i>	9	5
<i>Erebia ligea</i>	9	4
<i>Lasiommata petropolitana</i>	9	4
<i>Maculinea nausithous</i>	9	4
<i>Lycaena hippohoe eurydame</i>	4	4
<i>Minois dryas</i>	4	4
<i>Boloria euphrosyne</i>	4	2
<i>Boloria titania</i>	4	2
<i>Agrynnis paphia</i>	2	1

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