



# Patch occupancy of grassland specialists: Habitat quality matters more than habitat connectivity

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## ABSTRACT

Land-use change has caused degradation, loss and fragmentation of semi-natural habitats, especially in grassland ecosystems. Today, the remaining habitats are often situated in a matrix of intensively used agricultural land and are therefore more or less isolated from each other. Connectivity, area and quality of habitat patches have been identified as the most important drivers for the persistence of grassland specialists living in metapopulations. However, the relative importance of these factors is still under debate. We used a large-scale, multi-taxon approach to obtain a general pattern which would facilitate conservationists to promote many, instead of one, species. We studied the patch occupancy of 13 grassland specialists belonging to three different insect orders within a Central European landscape with 89 fragments of calcareous grasslands. To disentangle the relative importance of the three metapopulation parameters, generalized linear models (GLM) and variation-partitioning techniques were used. Our study revealed that habitat quality was the most important factor determining the occurrence of specialized species, followed by habitat area. In comparison to habitat connectivity, the variance explained by habitat quality was significantly higher across the studied species. Nevertheless, the persistence of at least six model organisms depended on the degree of habitat connectivity. We conclude that maintaining a high habitat quality on large patches should be the first choice for the conservation of habitat specialist insects in fragmented landscapes. As a secondary measure, conservationists should concentrate on the restoration of relict sites. This increases not only the habitat area, but also contributes to better habitat connectivity.

## 1. Introduction

The global decline of biodiversity has reached an alarming dimension. According to Pimm et al. (2014), the rate of species extinction is currently at least 1000 times higher than the natural background extinction rate. Land-use change is assumed to be the major driver of this development (Sala et al., 2000; Foley et al., 2005). The intensification of agricultural land-use, abandonment, afforestation and urbanization have caused degradation, loss and fragmentation of semi-natural habitats, especially in grassland ecosystems (WallisDeVries et al., 2002; Baur et al., 2006).

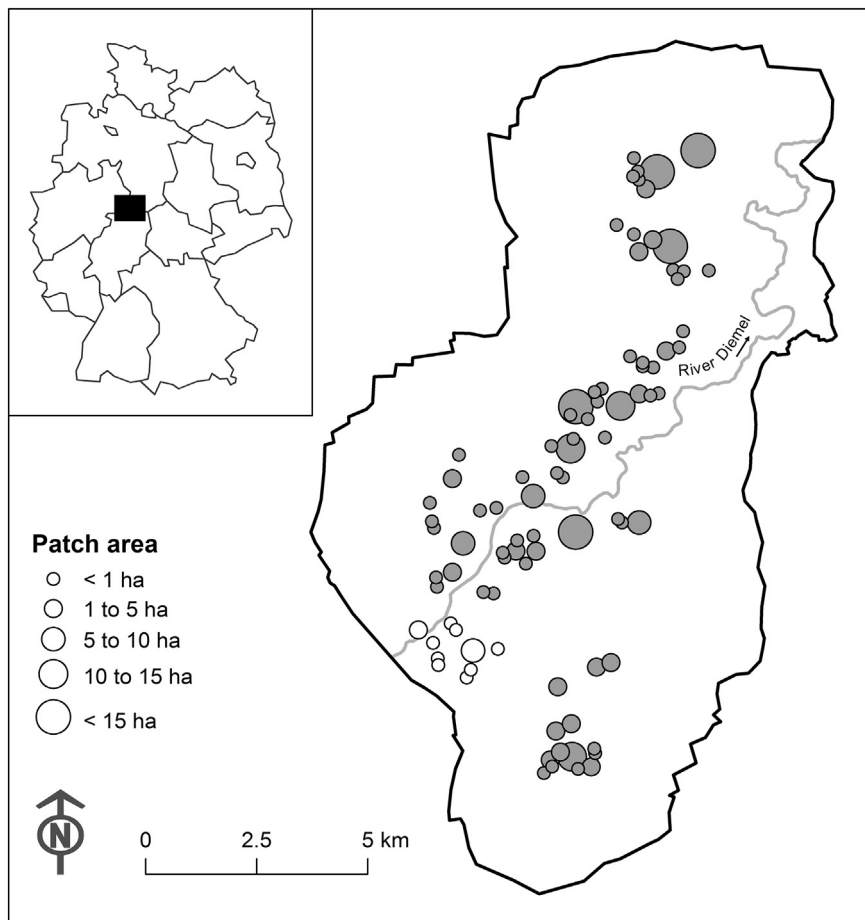
Among grassland ecosystems, calcareous grasslands have an outstanding value for nature conservation due to their very diverse flora and fauna (Poschlod and WallisDeVries, 2002). As a result of the above-mentioned processes, species-rich grasslands have lost much of their original extent and have become increasingly fragmented. Today, they are often situated in a matrix of intensively used agricultural land (Brückmann et al., 2010; Poniatowski et al., 2016) which makes them

refuges for several specialized insect species (Krämer et al., 2012b; Poniatowski et al., 2018). The spatial distribution of such species in cultivated landscapes is determined by several environmental factors operating at two different spatial scales: (i) the landscape level and (ii) the habitat level. Based on metapopulation theory, habitat area and habitat connectivity have been identified as the most important factors determining the persistence of mobile habitat specialists at the landscape level (Hanski, 1999), i.e. these species depend for long-term survival on networks of spatially inter-connected subpopulations (Thomas et al., 1992; Anthes et al., 2003; Stuhldreher and Fartmann, 2014). Due to local extinction and recolonization events, metapopulations are characterized by a dynamic population structure (Leisnham and Jamieson, 2002; Baguette, 2003). The lower the connectivity of a subpopulation, the more prone to extinction it becomes and the less likely it is to be re-established (Carlsson and Kindvall, 2001; Fernández-Chacón et al., 2014). In the long-term, this can lead to extinction of the whole metapopulation (van Strien et al., 2011).

At the habitat level, there is consensus that habitat quality is a

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**Fig. 1.** Study area, the Lower Diemel Valley in central Germany (inlay), and the 89 study patches. Ten patches in the southwestern part of the study area were situated within a 2-km range of adjacent calcareous grasslands in the Middle Diemel Valley. These patches, indicated by white circles, were only used for calculating the functional connectivity of some of the remaining patches (grey circles), and were not used as focal patches. Concerning the 79 focal patches represented by grey circles, all existing calcareous grasslands within a radius of at least 2 km were incorporated in the calculation of the connectivity index.

further important driver of patch occupancy in many insect species (reviewed by Thomas et al., 2011). Habitat quality comprises a multi-factorial complex, which is often dominated by the ecological requirements of the immature stages (eggs, larvae or nymphs, and pupae). This is because the immature stages are often much more sensitive to environmental changes than the adults (García-Barros and Fartmann, 2009). Temperature and humidity at oviposition sites, for instance, are crucial factors for successful egg development (Krämer et al., 2012a; Eilers et al., 2013). Oligo- or monophagous species, additionally, depend on the availability of their host plants (Biedermann, 2004; Eichel and Fartmann, 2008). Moreover, the occurrence of species living in the herb layer is determined by the spatial structure of the vegetation (Poniatowski and Fartmann, 2008; Helbing et al., 2017). In this context, the land-use intensity of the habitat is of particular importance due to its impact on vegetation structure and plant-community composition (cf. Marini et al., 2009; Littlewood et al., 2012). Furthermore, direct effects, such as mowing or trampling, may be crucial for the persistence of a species (Marini et al., 2008; van Klink et al., 2015).

In the early stages of insect conservation, emphasis was placed on reducing rates of local extinctions by maintaining habitat quality (e.g. Thomas, 1984). Somewhat later, in the context of Hanski's metapopulation theory, there was growing evidence that the landscape structure (habitat area and habitat connectivity) has a strong impact on species persistence as well (Hanski, 1994). Finally, both levels were linked to each other (Dennis and Eales, 1997; Thomas et al., 2001; Anthes et al., 2003; Bauerfeind et al., 2009). Even though these studies revealed an impact of habitat area or habitat connectivity, in combination with habitat quality, on patch occupancy, most of them considered only a single species. Large-scale metapopulation studies that take into account several species of different taxonomic orders within the same habitat network are almost completely absent (the only exception being

Maes and Bonte, 2006).

Successful habitat management, in general, considers the ecological requirements of different groups of species (Samways, 2005). For conservationists it is therefore important to know which measure should be the first choice: improving habitat quality, increasing patch area or connecting isolated patches. Survival strategies vary from species to species and may differ regionally. Consequently, Zulka et al. (2014) proposed analysis of the responses of individual species with finely-tuned habitat and matrix variables, followed by aggregation of the results to obtain a general picture. This would help conservation managers to promote many instead of one species (cf. Maes and Bonte, 2006).

In this study, we applied the approach proposed by Zulka et al. (2014). We choose 13 habitat specialists of three different insect orders (Auchenorrhyncha, Lepidoptera and Orthoptera) as model organisms. In the study area, all of them are restricted to calcareous grasslands and exhibit very specific habitat requirements (Poniatowski et al., 2016). They are consequently well-suited to metapopulation and fragmentation studies.

The aim of this study was to quantify the relative importance of the three most important factors determining species persistence in fragmented landscapes. On the basis of our findings, we derive priorities for the conservation of highly specialized insect species.

## 2. Materials and methods

### 2.1. Model organisms

As model organisms we chose four Auchenorrhyncha (*Batrachomorphus irroratus*, *Goniagnathus brevis*, *Kosswigianella exigua* and *Neophilaenus albipennis*), six butterfly (*Argynnis aglaja*, *Cupido minimus*,

*Erynnis tages*, *Hesperia comma*, *Melitaea aurelia* and *Satyrus spini*) and three Orthoptera species (*Metrioptera brachyptera*, *Phaneroptera falcata* and *Stenobothrus lineatus*) (Table A1). The selection of the model organisms followed ecological and methodical criteria:

- (i) Ecological criteria: All model organisms are habitat specialists, i.e. their populations are restricted to calcareous grasslands in the study area (Poniatowski et al., 2016). Due to their high habitat specificity, it can be assumed that the model organisms are sensitive to environmental changes such as deterioration, loss and fragmentation of their habitats.
- (ii) Methodical criteria: For the analysis it was mandatory to know all existing populations of the model organisms. The selection of the model organisms was, therefore, restricted to species whose adult or immature stages are reliably and easily detectable (Table A2). Another important point in the selection of the model organisms was an intermediate frequency in the study area. Extremely rare and very common habitat specialist are not suitable for such studies, as they cannot be used for statistical analyses on a presence-absence level.

## 2.2. Study area

The study area is about 140 km<sup>2</sup> in size and comprises the lower part of the Diemel Valley (Fig. 1). It is located in Central Germany along the border between the federal states of North Rhine-Westphalia and Hesse (51°30'N/9°18'E and 51°36'N/9°24'E) at an elevation of 160 to 280 m a.s.l. The climate is suboceanic with a mean annual temperature of 7.5–9 °C and an annual precipitation of 650–800 mm. Characteristic elements of the study area are calcareous grasslands (covering in total 243 ha) which are isolated within an intensively used agricultural and forested landscape. The study area belongs to the most important network of calcareous grasslands in the northern half of Germany (Fartmann, 2004).

## 2.3. Habitat patches

Calcareous grasslands are well-delimited habitat islands hosting many specialized insects. They are therefore a very suitable system for studying the effect of habitat fragmentation on insect populations. Since knowing all extant populations of a species is required for reliably estimating the degree of isolation of the local populations, all calcareous grasslands within the study area ( $N = 89$ ) were surveyed (Poniatowski et al., 2016). Patch size varied largely between 0.005 ha and 42 ha (mean: 2.7 ha  $\pm$  0.7 SE) and patches were regarded as discrete when they were isolated from the nearest neighboring patch by > 50 m of non-habitat, such as forest, improved grassland or arable fields (e.g. Krämer et al., 2012b). The mean patch isolation (represented by the geometric mean of the three shortest interpatch distances) is 247 m ( $\pm$  16.4 SE). In the case of species that are known to depend on one or two specific host plants (all studied Auchenorrhyncha and butterfly species), only potentially suitable patches, i.e. patches where the host plants were present, were used for the statistical analyses.

## 2.4. Species sampling

From the end of April to the beginning of September 2010, each of the 89 calcareous grassland patches in the study area was sampled five times (end of April, end of May, end of June, end of July/beginning of August and beginning of September) (Table A2). These sampling times ensured that, for each of the selected model organisms, one visit coincided with the time of year when its detectability is highest in the study area. The time spent searching per species varied with the structural heterogeneity of a particular patch. We defined seven structural types that differed with respect to vegetation height and coverage (see Section 2.6) and searched for 0.5 h in each of the structural types that

were present in a patch. The presence of the butterfly species was assessed by searching for adults, larvae or eggs according to the procedure of Fartmann (2004) and Hermann (2006) (see also Table A2). A sweep net was used to sample the Auchenorrhyncha and Orthoptera species living in the herb layer. Furthermore, bare soil and host plants were checked visually to detect geophilic/epigeic species. In order to avoid the results being biased by weather conditions, all sampling of the adult stages was performed on dry, sunny days with low wind speed. A patch was classified as occupied if we found evidence for reproduction (i.e. detection of at least one larva or egg) or at least three adults (as an indicator for an indigenous population) were detected.

## 2.5. Habitat area and habitat connectivity

Habitat area was ascertained from current aerial photographs (taken in 2009) using ArcGIS 10.3.1. For each of the model organisms, we calculated the functional habitat connectivity from each focal patch to all neighboring patches within an area of 2 km around the focal patch in which the species was present (potential source populations). A patch was considered to be a focal patch only if the host plant of the specific species was present (Auchenorrhyncha and butterflies). In the case of the polyphagous Orthoptera, all patches were used for the analyses.

For each of the focal patches, connectivity  $I_i$  was calculated using Hanski's index (Hanski, 1999), modified according to Moilanen and Nieminen (2002):

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

where  $A_j$  is the size (in m<sup>2</sup>) of the neighboring calcareous grassland patch and  $d_{ij}$  is the distance (in km) between the neighboring patch  $j$  and the focal patch  $i$ . For the scaling parameter  $b$ , we chose  $b = 0.5$ , as the ratio of patch edge to patch area decreases with  $A^{0.5}$  when the patch size increases (Moilanen and Nieminen, 2002). Larger values of the connectivity index  $I$  indicate better connectivity (and lower isolation) than smaller values. The index also takes into account the dispersal abilities of the model organisms. The parameter  $\alpha$  scales the effect of distance on migration where  $1/\alpha$  is the average migration distance of a species. As there is very little information concerning the dispersal abilities of our model organisms available from the literature, we adopted an empirical method to estimate species-specific values of  $\alpha$  from the data according to the propositions in Oksanen (2004). This approach consisted of fitting (for each of the model organisms) a large number of simple binomial GLMs, with presence/absence as the response and habitat connectivity as the predictor variable. For each of the models, the values of the predictor 'habitat connectivity' were calculated based on a different value of  $\alpha$  between 0.1 and 20, corresponding to average migration distances between 10 km and 50 m (in terms of functional distances, see below). The set of connectivity values that best explained patch occupancy of a species was used in all subsequent analyses that involved the effect of habitat connectivity on that species (Fig. A1).

In order to take into account not only the distance between habitat patches but also the composition of the landscape matrix, habitat connectivity was calculated as functional connectivity based on functional distances (least-cost paths). Functional distances were measured using the cost-distance-tool in ArcGIS 10.3.1 (Adriaenssen et al., 2003). How costly a potential dispersal corridor is depends on its length and on the characteristics of the matrix that an animal has to cross when moving from one patch to another. We therefore generated a cost-grid (resolution 5 m  $\times$  5 m), which included all relevant land-cover types in the study area. The structure of the landscape matrix was derived using land-use data from the German Real Estate Cadastre Information system (ALKIS). In ALKIS, the type of land use is documented for every single parcel of land at a scale of 1:5000. Additionally, we added all calcareous grasslands to this dataset.

Based on the comprehensive study of Poniatowski et al. (2016), a

simple approach of measuring functional connectivity was applied because it had been shown to perform better than all other connectivity measures. This simple approach distinguishes between one habitat and two non-habitat categories. The tall-growing non-habitats (e.g. forest) can act as physical barriers and therefore received a resistance value eight times greater than habitats. Low-growing non-habitats (e.g. mesic grassland) had a resistance value only four times higher than habitats, as they were assumed to be more suitable for inter-patch movements (for more details see Poniatowski et al., 2016).

## 2.6. Habitat quality

As the environmental conditions that constitute a high habitat quality vary from species to species, we sampled a broad range of parameters as follows:

- (i) Vegetation structure (index): In July 2010, the percentage coverage of seven structural types (according to Poniatowski and Fartmann, 2008) was estimated for each patch. The structural types were characterized by increasing vegetation height and density, thus representing a productivity and biomass gradient (for details see Poniatowski and Fartmann, 2008). For each patch, an index of vegetation structure was calculated by multiplying the number (1–7) of each structural type by its percentage coverage. A high value of the index indicates that a patch was dominated by tall-growing and dense structural types. A low value indicates that most of the patch was covered by low-growing and sparse vegetation.
- (ii) Vegetation structure (transformed index): As, in some species, the relationship between patch occupancy and vegetation structure was suspected to be unimodal rather than linear, the values of the vegetation-structure index (see below) were centered and squared and then entered into the statistical models in addition to the raw values.
- (iii) Abundance of host plants: In the case of oligo- and monophagous Auchenorrhyncha and Lepidoptera species, we recorded their host plants during the phenological period of highest detectability in one of two different ways, depending on the distribution of the host plants within the patches (Table A3). In the case of typical fringe species (*Viola hirta*) and very scattered species (e.g. *Rhamnus cathartica*), individuals were counted by randomly walking across the patches for a pre-defined time (10, 20 or 30 min in small, medium-sized and large patches, respectively). Afterwards, the counts were normalized to 10 min. In the case of very abundant species, such as *Brachypodium pinnatum*, *Lotus corniculatus* and *Festuca ovina* agg., their cover was estimated in five randomly selected plots (9 m<sup>2</sup> each). The mean of the five estimates was used for the analysis (Table A3).
- (iv) Microclimate (heat): Aspect and slope of a patch were measured using a compass with an inclinometer. Based on these values and the latitude of the study area, the heat load index was calculated as an approximate measure of the microclimate (McCune and Keon, 2002).
- (v) Microclimate (shade): Shading of a patch, for instance by shrubs and trees, was estimated in percentage.
- (vi) Land use: As detailed data on the intensity of grazing were not available, we assigned only two broad categories, ‘grazed’ and ‘abandoned’.

## 2.7. Statistical analysis

Intercorrelations of predictor variables were examined prior to regression analyses (see below) by applying a Spearman's correlation matrix that included all metric predictor variables. Collinearity between predictor variables was generally low, with a Spearman's correlation coefficient ( $r_s$ ) of  $|r_s| < 0.5$  for all pairs (cf. Dormann et al.,

2013). However, the comparison of patches with and without land use revealed a significant correlation between the categorical variable land use and several metric environmental variables (vegetation structure, shade and habitat area), using the *t*-test or Mann-Whitney *U* test for significance ( $P < 0.05$ ). We, therefore, excluded the predictor variable ‘land use’ from the analysis.

First, we calculated multiple predictor GLM with a binomial error structure for each species in order to evaluate which of the habitat-quality variables (Section 2.6) best explained the occurrence of our model organisms (habitat-quality models). Dispensable predictors were excluded by stepwise backward-selection based on AIC, as this procedure usually produces sound results and is widely used by scientists (Schröder et al., 2009). The significance of the remaining predictor variables was assessed with likelihood ratio tests (Type III tests).

In a second step, a further binomial GLM was calculated for each species with the presence-absence data of the particular model organism as response variable and the significant variable(s) of the habitat-quality models, as well as habitat area and habitat connectivity, as predictors (metapopulation models). As we aimed to assess the importance of habitat quality as a whole in comparison with the importance of habitat area and habitat connectivity, all predictors relating to habitat quality were simultaneously removed from the model; the reduced model was compared to the full model using a likelihood ratio test (Type III test). Likewise, the significance of the landscape-level parameters was assessed by dropping one parameter at a time and performing a likelihood ratio test of the full and the reduced model.

Afterwards, variation partitioning was applied to each of the model organisms by using the varPart-function of the R-package ‘modEvA’ (Barbosa et al., 2016) to determine the percentage of variance that was exclusively explained by habitat quality, habitat area or habitat connectivity (cf. Heikkinen et al., 2005). Two-sided paired permutation tests with 1000 permutations and *t* as test statistic (Manly, 2007) were then applied to detect significant overall differences in the amount of variance explained by the three parameters. We chose this approach as our model species were deliberately selected from the entirety of insect species living in calcareous grasslands and, hence, do not represent a random sample, which is a precondition for running a classical ANOVA.

All analyses were performed using R 3.3.2 (R Development Core Team).

## 3. Results

### 3.1. Habitat-quality models

For each of the model organisms, the GLM analyses revealed significant relationships between patch occupancy and one to three of the habitat-quality variables (Table 1). Even though it was not used as a predictor in the case of the polyphagous grasshoppers, host-plant abundance was the predictor that was most frequently retained in the final models. It showed a significant positive relationship with the presence of nine species (all Auchenorrhyncha and all Lepidoptera, except for *H. comma*). High values of the heat load index and/or a low degree of shading, both indicating warm microclimatic conditions, favored the occurrence of six species. The index of vegetation structure was significantly related to the presence of six species. However, in two of these species, the transformed index was also a significant predictor, leading to hump-shaped (instead of monotonically decreasing) curves of predicted probabilities of occurrence, with an optimum at intermediate values of the gradient. A similar pattern was observed for one leafhopper in the habitat model in which the vegetation structure was represented by the transformed index alone.

### 3.2. Metapopulation models

Using the metapopulation models (Table 2), we tested which of the parameters, habitat quality, habitat area or habitat connectivity,



**Table 1**

Results of generalized linear models (habitat-quality models): relationship between patch occupancy of the model organisms (binomial response variable) and several environmental parameters relating to habitat quality (see Section 2.7). For each species, the type of relationship (positive or negative z values) between significant predictors and the occurrence of the species, the level of significance ( $***P < 0.001$ ,  $**P < 0.01$ ,  $*P < 0.05$ ) and the performance (McFadden's Pseudo  $R^2$ ) of the model containing only the significant predictors are shown.

Model organisms	Habitat-quality models					
	Vegetation structure	Vegetation structure (transformed) <sup>a</sup>	Host-plant abundance <sup>b</sup>	Heat load	Shading	McFadden's Pseudo $R^2$
(a) Auchenorrhyncha						
<i>Batrachomorphus irroratus</i>	.	.	1.7*	.	.	0.16
<i>Goniagnathus brevis</i>	–3.4***	.	2.1*	2.7**	.	0.31
<i>Kosswigianella exigua</i>	.	–1.6*	3.3***	.	.	0.36
<i>Neophilaenus albipennis</i>	.	.	2.8***	.	.	0.18
(b) Lepidoptera						
<i>Argynnis aglaja</i>	–2.5*	.	2.2*	.	–2.1*	0.22
<i>Cupido minimus</i>	1.4**	.	1.4***	.	.	0.52
<i>Erynnis tages</i>	.	.	2.2**	.	–2.5**	0.20
<i>Hesperia comma</i>	–2.9**	–2.3*	.	.	.	0.10
<i>Melitaea aurelia</i>	.	.	3.5***	.	.	0.20
<i>Satyrus spini</i>	–2.2*	.	2.3*	.	.	0.13
(c) Orthoptera						
<i>Metrioptera brachyptera</i>	.	.	.	.	–2.4***	0.13
<i>Phaneroptera falcata</i>	.	.	.	3.1***	–2.0*	0.15
<i>Stenobothrus lineatus</i>	–2.1*	–2.8**	.	.	–2.2*	0.14

<sup>a</sup> Raw data centered + squared (see Section 2.6).

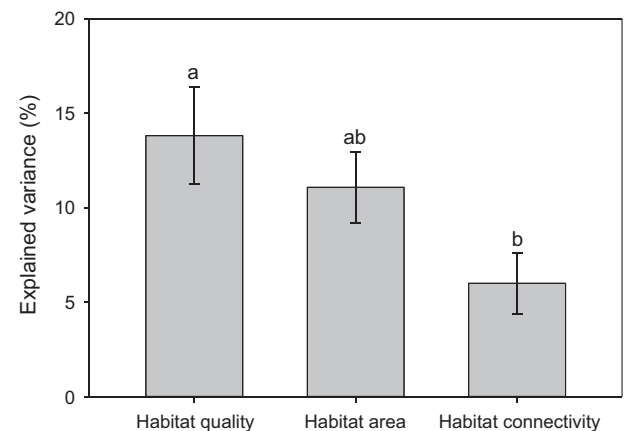
<sup>b</sup> Applies exclusively to oligo- and monophagous Auchenorrhyncha and Lepidoptera species.

**Table 2**

Results of generalized linear models (metapopulation models): relationship between patch occupancy of the model organisms (binomial response variable) and habitat quality (refers to the significant parameters of the habitat-quality models; see Section 2.7 and Table 1), habitat area and habitat connectivity. For each species, the type of relationship (positive or negative z values) between significant predictors and the occurrence of the species, the level of significance ( $***P < 0.001$ ,  $**P < 0.01$ ,  $*P < 0.05$ , n.s. = not significant) and the performance (McFadden's Pseudo  $R^2$ ) of the model containing all three predictors are shown. For the compound predictor 'habitat quality', no overall type of relationship can be given, but the type of relationship between the individual variables that make up this predictor and the occurrence of the species can be read from Table 1.

Model organisms	Metapopulation models			
	Habitat quality	Habitat area	Habitat connectivity	McFadden's Pseudo $R^2$
(a) Auchenorrhyncha				
<i>Batrachomorphus irroratus</i>	*	n.s.	1.9*	0.37
<i>Goniagnathus brevis</i>	***	1.9**	n.s.	0.40
<i>Kosswigianella exigua</i>	**	2.1*	n.s.	0.48
<i>Neophilaenus albipennis</i>	***	1.2*	n.s.	0.27
(b) Lepidoptera				
<i>Argynnis aglaja</i>	*	2.2***	n.s.	0.39
<i>Cupido minimus</i>	***	n.s.	n.s.	0.69
<i>Erynnis tages</i>	**	2.7***	n.s.	0.40
<i>Hesperia comma</i>	n.s.	1.9**	2.8**	0.27
<i>Melitaea aurelia</i>	***	2.0*	2.6***	0.40
<i>Satyrus spini</i>	n.s.	2.3***	1.9*	0.35
(c) Orthoptera				
<i>Metrioptera brachyptera</i>	*	2.4***	2.5**	0.39
<i>Phaneroptera falcata</i>	***	n.s.	n.s.	0.17
<i>Stenobothrus lineatus</i>	n.s.	2.6***	2.9***	0.43

significantly improved the fit of the regression models when both of the other parameters were already contained in the model. Concerning habitat quality and habitat area, this was the case in ten out of the thirteen model species. In contrast, habitat connectivity was significantly related to the occurrence of only six species (Table 2). When



**Fig. 2.** Explanatory power of the metapopulation parameters (habitat quality, habitat area and habitat connectivity) with respect to the occurrence of the 13 model organisms, expressed as the mean proportion of variance explained exclusively by the respective parameter  $\pm$  SE. Different letters indicate significant differences between the metapopulation parameters (two-sided paired permutation tests with 1000 permutations;  $P < 0.05$ ).

comparing the amount of variance explained by the three parameters using variation partitioning and paired permutation tests, distinct differences were detected (Fig. 2). Habitat quality had the highest impact on the occurrence of the model organisms, followed by habitat area and habitat connectivity. However, significant differences were only detected between habitat quality and habitat connectivity.

#### 4. Discussion

Our study revealed that – at the scale studied – habitat quality was the most important driver of patch occupancy in specialized species of calcareous grasslands, followed by habitat area. In comparison to habitat connectivity, the variance explained by habitat quality was significantly higher across the studied species. Our findings are consistent with the results of some previous studies that also found only a subordinate importance of habitat connectivity for species persistence in comparison to habitat quality (Dennis and Eales, 1997; WallisDeVries, 2004; Thomas et al., 2001; Fleishman et al., 2002).

#### 4.1. Habitat connectivity

There is no doubt that patch occupancy of some highly specialized insects, as has been shown in our study (Table 2), depend on habitat connectivity (Littlewood et al., 2009; Brückmann et al., 2010). This is especially true for species living in spatially inter-connected subpopulations, i.e. in a metapopulation network (Anthes et al., 2003; Maes and Bonte, 2006; Bauerfeind et al., 2009). However, several specialists are able to survive over a long period in permanent habitats with less or without exchange of individuals (Kuussaari et al., 2009; Poniatowski and Fartmann, 2010; Sang et al., 2010).

Our study revealed that habitat connectivity played only a minor role in determining patch occupancy of most of the studied species, although the importance of this factor was possibly overestimated due to  $\alpha$ -optimization (see Section 2.5 and Fig. A1). The absence of significant effects may be accounted for by the dispersal ability of the species. On the one hand, the mobility of small species, such as *Goniagnathus brevis* and *Neophilaenus albipennis*, is probably so low that they fail to reach most of the other suitable patches in the study area. A previous metapopulation study on *Neophilaenus albipennis* (Biedermann, 2004), which found significant effects of connectivity on patch occupancy, was conducted at a much smaller spatial scale. In Biedermann's study, patches were regarded as discrete when they were only 5 m apart. In contrast, we specified a minimum of 50 m for patch separation. On the other hand, highly mobile species, such as *Argynnis aglaja* and *Phaneroptera falcata*, may have no difficulties in colonizing other habitat patches (Poniatowski et al., 2016), especially if the overall degree of habitat fragmentation is relatively low, as in our study area (cf. Fig. 1 and Section 2.3). Hence, the occurrence of these species is more strongly influenced by habitat quality and/or habitat area (Table 2).

#### 4.2. Habitat area

The importance of the habitat area for the persistence of a species has often been emphasized (Biedermann, 2004; Bauerfeind et al., 2009; Pasinelli et al., 2013). One disadvantage of small patches is that they frequently harbor only small populations (Leisnham and Jamieson, 2002), especially when habitat quality is low (cf. Heisswolf et al., 2009; Kalarus and Nowicki, 2015). In such small populations, adverse events of genetic or environmental stochasticity are much more likely to entail serious consequences than in large populations (Sutcliffe et al., 1997; Schtickzelle et al., 2005). The risk of extinction in small patches is correspondingly high (Thomas et al., 2011; Fernández-Chacón et al., 2014). Furthermore, the emigration rates associated with small patches are often higher than with large patches (Schtickzelle and Baguette, 2003). This may be attributed to the limited resources (Fleishman et al., 2002; Baguette et al., 2011) and the lower edge-to-size ratio of small patches (Sutcliffe et al., 1997; Leisnham and Jamieson, 2002). The latter factor means that, in small patches, migrating individuals reach the border of the habitat more quickly and more frequently and are thus more likely to leave the breeding site than in large patches.

In addition, the structural diversity of a patch usually increases with increasing habitat area (e.g. Löffler and Fartmann, 2017). Consequently, large patches often exhibit larger areas of suitable habitat structures, refuges or host plants that enable the occurrence of the respective species (cf. Sutcliffe et al., 1997). This is a possible reason why we observed a relationship between habitat area and patch occupancy in small species with low actual demands of habitat area. However, there are also some species, e.g. *Argynnis niobe* or *Hipparchia semele*, which generally have very high habitat-area requirements (Maes et al., 2006; Salz and Fartmann, 2009). Additionally, the habitat-area requirements of a certain species are often a function of habitat quality within the patches. Salz and Fartmann (2017), for instance, showed that *Argynnis niobe* is able to occupy small patches when the abundance of the host plant is high, while the minimum habitat area was much larger in landscapes with low abundance of host plants. Accordingly,

several metapopulation studies reported no, or only weak, correlations between habitat area and patch occupancy (Dennis and Eales, 1997; Thomas et al., 2001; Stuhldreher and Fartmann, 2014). In these cases, habitat quality was the more important predictor of species occurrence.

#### 4.3. Habitat quality

Our approach underlines the outstanding relevance of habitat quality for the persistence of specialized insects in fragmented landscapes. Patch occupancy of all of the model organisms was correlated with at least one of the habitat-quality parameters (Table 1). Additionally, habitat quality had generally more explanatory power than habitat connectivity (Fig. 2). These results are in accordance with the findings of Thomas et al. (2011), who concluded in their review on butterflies that the larval-habitat quality explained slightly more examples of patch occupancy than site isolation. In this context, special attention must be paid to the abundance of host plants (cf. Samways and Lu, 2007). In our study, a significant effect on patch occupancy was observed for nine out of ten oligo- and monophagous species. The high importance of the host-plant abundance for species persistence was also demonstrated in other studies (Anthes et al., 2003; Biedermann, 2004). Bauerfeind et al. (2009), for example, identified the abundance of host plants as the most important parameter within a set of eight habitat-quality variables. However, for some of our model organisms, other habitat-quality parameters had a much greater relevance for patch occupancy than host-plant abundance. The occurrence of *Goniagnathus brevis*, for instance, was mainly determined by a sparse vegetation structure and a high heat load. Low vegetation coverage was also responsible for the persistence of *Hesperia comma*, and *Erynnis tages* preferred sites with little shading. These examples illustrate the complexity of the factor 'habitat quality'. It is therefore essential to include various habitat-quality parameters in order to identify the most important factors involved in the occurrence of a species.

#### 4.4. The relative importance of the three metapopulation parameters

Habitat quality was the most important driver determining patch occupancy of habitat specialists in our study. Our finding based on a large-scale, multi-taxon approach in a representative, fragmented European agricultural landscape. Hence, we assume that the observed pattern is valid for a wide range of specialized insects living in fragmented, semi-natural grasslands. Indeed, several other studies corroborate this assumption (Anthes et al., 2003; Biedermann, 2004; WallisDeVries, 2004; Bauerfeind et al., 2009; Pasinelli et al., 2013).

It is even very likely that a more differentiated view of the habitat-quality parameters would have led to a higher explanatory power of the models used. The suitability of a host plant as oviposition site and as larval food, for example, is determined by several factors, such as prominence, biomass, nitrogen content or microclimate (García-Barros and Fartmann, 2009; Krämer et al., 2012a; Eilers et al., 2013; Kurze et al., 2017). Nevertheless, the accuracy of our habitat-quality models, with McFadden's Pseudo  $R^2$  values between 0.10 and 0.52 (mean value 0.22), indicates a good, or even a very good, model performance (Bennett, 1999).

A high habitat quality per se, however, is usually not sufficient for the persistence of habitat specialist insects living in fragmented landscapes. The species-specific minimum requirements for habitat area and/or habitat connectivity must also be fulfilled (Eichel and Fartmann, 2008; Pasinelli et al., 2013; Stuhldreher and Fartmann, 2014). However, depending on the degree of habitat fragmentation their relative importance varies. In moderately fragmented landscapes like the study area, for instance, habitat connectivity is hardly limiting (cf. Krämer et al., 2012b). In contrast, its impact increases distinctly in much more fragmented landscapes (Maes and Bonte, 2006).

## 5. Conclusions

For the conservation of habitat specialist insects in fragmented landscapes, the maintaining of a high habitat quality on large patches, which are generally able to harbor larger and, therefore, more stable populations than small patches, should be the first choice. This recommendation has also been expressed in several former studies (Heisswolf et al., 2009; Kalarus and Nowicki, 2015) and can thus be considered as a general rule that is valid for most habitats and regions. Specifically, this means conserving patches with a high structural diversity and different aspects (microclimates) that provide favorable conditions for a variety of animal and (host) plant species (Samways, 2007; Helbing et al., 2017; Löffler and Fartmann, 2017). As a secondary measure, conservation managers should create additional habitats or enlarge existing ones by restoring relict sites (cf. Littlewood et al., 2009). This will help species with high demands on the minimum habitat area to persist there or to recolonize them. In addition, an increase of the habitat area also contributes to better habitat connectivity. Although habitat connectivity played a subordinate role in the persistence of species in our study, its importance should not be underestimated. On the one hand, it had a significant influence on the occurrence of at least six of our model organisms. On the other hand, its impact increases distinctly in much more fragmented landscapes (Opdam and Wascher, 2004). Especially in highly fragmented landscapes, the conservation of small patches with high-habitat quality is also of great importance for maintaining specialists (Heisswolf et al., 2009; Kalarus and Nowicki, 2015). This is because small patches may act as stepping stones or island (satellite) habitats for mobile species living in a metapopulation network (mainland-island and core-satellite populations, respectively), as well as providing permanent habitats for sedentary species with low demands on the minimum habitat area.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.07.018>.

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