Habitat quality matters for the distribution of an endangered leaf beetle and its egg parasitoid in a fragmented landscape

Annette Heisswolf[1], Stefanie Reichmann[1], Hans Joachim Poethke[1], Boris Schröder[2], Elisabeth Obermaier[1]

[1] Field Station Fabrikschleichach, University of Würzburg, Glashüttenstrasse 5, D-96181 Rauhenebrach
[2] Institute of Geoecology, University of Potsdam, P.O. Box 601553, D-14415 Potsdam

Abstract. Fragmentation, deterioration, and loss of habitat patches threaten the survival of many insect species. Depending on their trophic level, species may be differently affected by these factors. However, studies investigating more than one trophic level on a landscape scale are still rare. In the present study we analyzed the effects of habitat size, isolation, and quality for the occurrence and population density of the endangered leaf beetle *Cassida canaliculata* Laich. (Coleoptera: Chrysomelidae) and its egg parasitoid, the hymenopteran wasp *Foersterella reptans* Nees (Hymenoptera: Tetracampidae). *C. canaliculata* is strictly monophagous on meadow sage (*Salvia pratensis*), while *F. reptans* can also parasitize other hosts. Both size and isolation of habitat patches strongly determined the occurrence of the beetle. However, population density increased to a much greater extent with increasing host plant density (= habitat quality) than with habitat size. The occurrence probability of the egg parasitoid increased with increasing population density of *C. canaliculata*. In conclusion, although maintaining large, well-connected patches with high host plant density is surely the major conservation goal for the specialized herbivore *C. canaliculata*, also small patches with high host plant densities can support viable populations and should thus be conserved. The less specialized parasitoid *F. reptans* is more likely to be found on patches with high beetle density, while patch size and isolation seem to be less important.

Keywords. Habitat fragmentation, herbivore, host plant density, metapopulation, multitrophic.

INTRODUCTION

All over the world the persistence of rare animal and plant species is threatened by loss and fragmentation of habitats due to massive human interference in the environment (Fahrig, 2001; Hunter, 2002; Fahrig, 2003; Ewers & Didham, 2006). In Central Germany, insect populations face a fragmented landscape in which suitable habitat patches

are interspersed between areas of intensive agricultural land use. To successfully predict the occurrence patterns of endangered species and in order to choose effective conservation strategies, we need to analyze which patch features are most important for the respective species. In this context, metapopulation variables such as patch size and isolation but also different aspects of habitat quality must be considered (e.g. Dennis & Eales, 1997; Thomas *et al.*, 2001; Fleishman *et al.*, 2002; Tscharntke *et al.*, 2002; Hanski & Gaggiotti, 2004; Dennis *et al.*, 2006).

Metapopulation theory states that the populations of a species are interdependent within a landscape and that long-term persistence depends on a balance across the landscape between local extinctions of individual populations and new colonizations of vacant habitat patches (Hanski, 1998; Moilanen & Hanski, 1998). Based on this theory, the occurrence probability of a species within a patch is supposed to increase with increasing patch size and decreasing isolation, as both raise the probability that dispersing animals will find a patch. Patch size also has a positive effect on the survival probability of a population within a patch, as larger patches usually support larger populations (Hanski & Gaggiotti, 2004).

Additionally, several recent studies emphasized that the quality of a habitat patch also influences its carrying capacity and may thus affect the survival chance of a population (Clarke *et al.*, 1997; Dennis & Eales, 1997; Thomas *et al.*, 1998; Wiegand *et al.*, 1999; but see Haynes *et al.* 2007). Consequently, Thomas *et al.* (2001) suggested that habitat quality is the missing third variable in metapopulation dynamics. They hypothesized that habitat quality and spatial effects operate at different hierarchical levels within the same process: while patch size and isolation can be important for the (re-) colonization probability of a patch, habitat quality is supposed to contribute to species persistence within a patch.

Furthermore, the survival of a species does not only depend on its resources, but also on the impact of natural enemies. Thus, it is of critical importance to take also higher trophic levels into account Hunter (2002); Cronin & Reeve (2005). Still, the majority of studies on insect (meta-)populations focus on just one trophic level and only recently multi-trophic level interactions have been investigated in a metapopulation context (Eber, 2001; van Nouhuys & Hanski, 2002). Our study is one of the first that analyzes the importance of patch size, isolation, and habitat quality for the occurrence and persistence of a herbivore and its parasitoid in a fragmented landscape.

The herbivorous leaf beetle *Cassida canaliculata* Laich. (Coleoptera: Chrysomelidae) has in the past been quite common in Germany (Bach, 1851; Steinhausen, 1949). Today, it is classified as 'vulnerable' (VU) in the red list of Germany (Bundesamt für Naturschutz, 1998) and even as 'critically endangered' (CE) in the red list of Bavaria (Bayerisches Landesamt für Umweltschutz, 2003). However, in the nature re-

serve 'Hohe Wann' in Northern Bavaria, Germany (50° 03' N, 10° 35' E) we found the species to be locally abundant. This gave us an excellent opportunity to study the needs of *C. canaliculata* in relatively favorable conditions.

C. canaliculata is strictly monophagous on meadow sage (*Salvia pratensis* L., Lamiales: Lamiaceae) (Wencker & Silbermann, 1866; Bourgeois & Scherdlin, 1899; Reitter, 1912; Graser, 1984; Trautner *et al.*, 1989; A. Heisswolf and D. Gabler, unpublished data) and can thus only survive on patches where *S. pratensis* occurs. A description of the life cycle of *C. canaliculata* can be found in Heisswolf *et al.* (2005). The egg clutches of the beetle are heavily parasitized (up to 70% of all egg clutches per patch; Heisswolf *et al.* 2006 and unpublished data) by the hymenopteran wasp *Foersterella reptans* Nees (Hymenoptera: Tetracampidae). *F. reptans* can also parasitize other *Cassida* species, e.g., *Cassida rubiginosa* Müller (Bacher & Luder, 2005). However, the occurrence and distribution of other *Cassida* species in the nature reserve 'Hohe Wann' have not yet been investigated.

We tested two hypotheses for both the herbivore *C. canaliculata* and the parasitoid *F. reptans*. (1) The occurrence probability of each species will increase with increasing patch size and with decreasing patch isolation, as both raise colonization success. (2) For both species, population density will increase with increasing patch size and with increasing habitat quality as both determine the carrying capacity of the patch (Thomas *et al.*, 2001; Fleishman *et al.*, 2002; Hanski & Ovaskainen, 2003).

MATERIALS AND METHODS

Study site

The area of the 'Hohe Wann' nature reserve covers approximately 10 km in NS-direction and 4 km in EW-direction (Rudner *et al.*, 2007). The nature reserve is characterized by a patchwork of different habitat types due to the geological and geomorphological heterogeneity of the area, agricultural land use, and small-scale microclimatic differences resulting from different exposure, inclination, and land use (Elsner, 1994). Crop land (37%) and forest (23%) cover the largest part of the area. Habitat types suitable for the leaf beetle's only host plant meadow sage, *S. pratensis*, are dry grasslands (3% coverage), extensively managed meadows (6%), intensively managed poor meadows (5%), and intensively managed meadows (5%). Absolute and relative coverage of the nine main habitat types (according to Hein *et al.* 2007) occurring in the nature reserve are included in Appendix A. A detailed description of all habitat types can be found in Hein *et al.* (2007) and a map showing the distribution of habitat types in the nature reserve is included in Rudner *et al.* (2007).

Prior to the present study, the occurrence of *S. pratensis* was recorded within the whole nature reserve and a habitat map for *S. pratensis* was developed (S. Reichmann, unpublished data), which consisted of 161 different potential habitat patches for *C. canaliculata*. Within these patches, 77 random points were selected (max. one per patch) using the Geographical Information System Arc View GIS 3.2 (ESRI). These 77 patches belonged to the habitat types dry grasslands (28), extensively managed meadows (30), intensively managed poor meadows (12), and intensively managed meadows (7). The size of the patches ranged from 1.20 to 105.64 ha (mean $\pm$ 95% confidence limit: 18.32 $\pm$ 5.05 ha). In the field, we located the points using a portable GPS. The number of patches which we included in the analyses depended on the variables used (not all predictor variables were available for all 77 patches) and is mentioned separately with each model.

Habitat quality

For *C. canaliculata*, we measured four variables as potential predictors of habitat quality. (1) Mean host plant (*S. pratensis*) size, which was a principal component derived from the variables rosette diameter (cm), rosette height (cm), and number of vegetative cones, (2) host plant density (m^{-2}), (3) patch exposure, which was a principal component derived from the variables cosine-transformed aspect and potential solar irradiation (kWh/m^2), and (4) patch slope (degrees). Appendices B and C show the eigenvectors and eigenvalues of the two principal components analyses. We considered patch exposure and slope as variables describing habitat quality, because they both influence the microclimate of a patch: steep and south-facing patches are expected to have a warmer microclimate and may thus provide better growth conditions for larvae in spring. For obtaining predictors (1) and (2), we randomly selected 10 squares of 1 m^2 size within a circle ($r = 11$ m) around the random point (see above). Within these squares, we counted all host plants and measured the rosette diameter, rosette height, and number of vegetative cones of 30 randomly selected host plants (three per square). The data from the 30 plants per patch were then averaged to obtain one value per patch. Predictors (3) and (4) were obtained from a digital terrain model (grid size 5 m, cf. Rudner *et al.* 2007). Habitat quality variables, which we analyzed for *F. reptans*, were (1) egg clutch density of *C. canaliculata* (see below), (2) density of *S. pratensis* plants, (3) patch exposure, and (4) patch slope.

Patch size

We derived patch size (ha) from aerial photographs by means of GIS analysis. In addition, we used the radius of gyration (m), *R* (Eq. 1), which is defined as the mean distance between the center of each grid cell (x_i, y_i) within a patch (n = number of grid

cells) and the patch center (x, y) (after Keitt *et al.* 1997), to integrate patch shape into a further measure of patch size.

$$R = \frac{1}{n}\sqrt{(x_i - \bar{x})^2 + (y_i - \bar{y})^2} \tag{1}$$

Finally, we calculated the perimeter-to-area ratio of each patch. We obtained both the radius of gyration and the perimeter-to-area-ratio using the software Fragstats 3.3 (McGarigal, 2001).

Patch isolation

To the authors' knowledge, nothing is yet known about dispersal in both *C. canaliculata* and *F. reptans*. This makes it difficult to study isolation effects in both species. As a first approach, we used two different patch isolation metrics for *C. canaliculata*. (1) The shortest edge-to-edge distance (m) to the 'nearest neighbor' patch with *C. canaliculata* occurrence. (2) The connectivity S_i after Hanski (1998) (Eq. 2), where P_j is the occurrence of *C. canaliculata* in patch j, A_j is the size (ha) of patch j, d_{ij} is the shortest center to center distance (m) of patches i and j (which are assumed to be circular), and $\alpha = 1/2D$, where D is the mean dispersal distance (m) of *C. canaliculata*.

$$S_i = \sum_{j=1}^{n} P_j \, e^{(-\alpha \, d_{ij})} \, A_j \tag{2}$$

The mean dispersal distance is also unknown for *C. canaliculata*, but we assumed it to be 50 m, since the beetles move mainly by walking rather than by flying (S. Reichmann and A. Heisswolf, personal observations). *F. reptans*, which has a body length of only 1 mm, is probably not capable of active flight, but may be drifted over far distances with the wind. Thus, any estimation of a mean dispersal distance did not seem reasonable without further information on that species. Therefore, we only used the distance to the nearest neighbor patch with occurrence of *F. reptans* as a first approximation of isolation effects. We obtained variable (1) using the GIS and we calculated variable (2) using the software Isolator 1.3 (R. Biedermann, personal communication).

Species incidence and density

To obtain a measure for egg clutch density of *C. canaliculata* we counted the number of egg clutches on the 30 above-mentioned plants per patch. This measure was also used as a proxy for population density of *C. canaliculata*. If no egg clutches were found on these 30 plants, the whole patch was thoroughly searched for egg clutches to ensure that the patch was truly not occupied by the beetle. To measure parasitism by

F. reptans, we collected 10 egg clutches of *C. canaliculata* per site (if available) and checked them for hatching parasitoids in the laboratory.

Statistics

We calculated all statistical procedures using the software package R 2.2.1 (R Development Core Team, 2005). Prior to analysis, we tested all predictors for bivariate correlation using Spearman rank-correlations (Appendices D and E). We included only those variables into the same multiple model whose correlation coefficient (ρ_S) was less than 0.1. We combined the correlated variables ($\rho_S \leq 0.5$) mean rosette diameter, rosette height, and number of vegetative cones as well as exposure and potential solar irradiation to principal components using principal components analysis (Mardia *et al.*, 1979; Venables & Ripley, 2002; cf. Appendices B and C).

We estimated the occurrence probability of *C. canaliculata* and *F. reptans* within a patch in two steps. First, we applied hierarchical partitioning methods (Mac Nally, 2000, 2002; Heikkinen *et al.*, 2005) to determine the independent explanatory power of the predictors, using the R package 'hier.part' (Walsh & Mac Nally, 2007). Then, we analyzed all possible combinations of all variables (including interactions) that had a significant independent effect (after bootstrapping) with multiple logistic regression models (Hosmer & Lemeshow, 2000), using the R packages 'Design' (Harrell, 2005) and 'Hmisc' (Harrell 2006). In order to evaluate the goodness-of-fit of the models we considered the pseudo-R^2 after Nagelkerke (1991) ($R^2_{Nagelkerke}$). We used ROC plots (receiver operating characteristics), or more specifically, the area under the resulting curve ('area under curve' = AUC), to determine the classification accuracy of the model (Hanley & McNeil, 1982; Swets, 1988). We calculated AUC-values with a 95% confidence interval applying a software provided by Schröder (2006). This software is used to assess model transferability by testing the significance of AUC-values after applying the model to independent test data (e.g. Binzenhöfer *et al.*, 2005). To achieve unbiased estimates of $R^2_{Nagelkerke}$- and AUC-values for multiple regression models we applied internal validation via bootstrapping (Harrell, 2001).

We tested the correlations between all variables and population density of *C. canaliculata* or rate of parasitism by *F. reptans* using multiple linear regression models. Again, we pre-selected variables for multiple models based on hierarchical partitioning. To evaluate the goodness-of-fit of the models and to compare multiple models, we used the adjusted coefficient of determination R^2 .

For all analyses, we compared different models with the same response variable via the Akaike Information Criterion corrected for small sample sizes (AIC$_c$; Burnham & Anderson, 2002), which allows choosing the model with the optimal compromise between goodness of fit and model complexity.
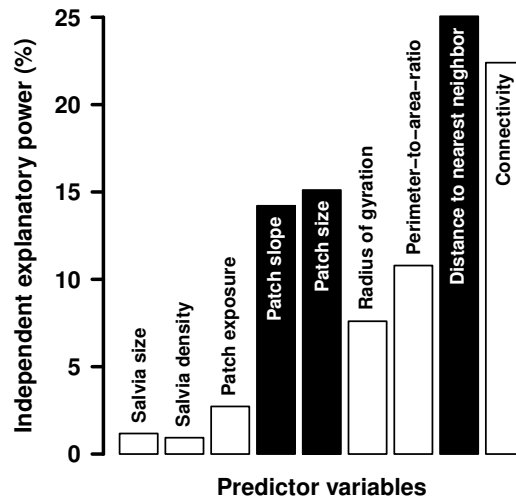
Figure 1: Predictor variables explaining the occurrence of *C. canaliculata*. Percentage distribution of independent explanatory power of all tested predictor variables calculated by hierarchical partitioning. The tested variables were *Salvia* size (principal component), *Salvia* density, patch exposure (principal component), patch slope, patch size, radius of gyration, perimeter-to-area-ratio, distance to the nearest neighbor, and connectivity. Variables that were included in the best multiple logistic regression model are shaded in black.

RESULTS

Occurrence of C. canaliculata

We found egg clutches of *C. canaliculata* on 47 of 77 potential habitat patches (with occurrence of the host plant *S. pratensis*). Consequently, the prevalence of *C. canaliculata* was 61%. Hierarchical partitioning showed that patch isolation (nearest neighbor or connectivity), patch size, and patch slope had a significant independent explanatory power for *C. canaliculata* occurrence, while the other tested variables seemed to be of less relevance (Figure 1).

Subsequent multiple logistic regression modeling resulted in seven significant models (Table 1). The model with the lowest AIC_c-value consisted of the variables patch slope, patch size, and distance to the nearest neighbor (NN) (intercept $\pm$ SE $= -1.08 \pm 1.05$, coefficient [patch slope] $\pm$ SE $= 0.148 \pm 0.080$, coefficient [patch size] $\pm$ SE $= 0.060 \pm 0.029$, coefficient [NN] $\pm$ SE $= -0.007 \pm 0.003$; Table 1). The predicted probability of occurrence calculated by this model and the observed occurrence of *C. canaliculata* for all studied habitat patches match very well for the majority of all studied patches (Figure 2). Furthermore, response surface plots show the predicted occurrence probability of *C. canaliculata* depending on the model predictors patch slope, patch size, and distance to the nearest neighbor patch (Figure 3).

The occurrence probability of *C. canaliculata* increased with increasing patch slope and size, as well as with decreasing distance to the nearest neighbor patch.

Population density of C. canaliculata

Hierarchical partitioning showed that both host plant (*Salvia*) density and patch size strongly influence the population density of *C. canaliculata*, although *Salvia* density had a more than three times higher independent explanatory power (51%) than patch size (15%, Figure 4). A subsequent multiple linear regression model including both variables, *Salvia* density and patch size, highly significantly explained the population density increase of *C. canaliculata* (intercept $\pm$ SE $= -0.140 \pm 0.103$, coefficient [*Salvia* density] $\pm$ SE $= 0.043 \pm 0.012$, coefficient [patch size] $\pm$ SE $= 0.010 \pm 0.002$, $P < 0.0001$, $F = 14.63$, $R^2 = 0.316$, $AIC = 71.52$, $N = 60$ patches).

Parasitism by F. reptans

We observed parasitism of *C. canaliculata* egg clutches by the hymenopteran wasp *F. reptans* on 17 of the 31 patches (55%) where *C. canaliculata* occurred and on which ten egg clutches could be collected. The only variable that significantly explained the occurrence of *F. reptans* was egg clutch density of *C. canaliculata* (intercept $\pm$ SE $= -0.778 \pm 0.588$, coefficient $\pm$ SE $= 1.804 \pm 0.947$, $P = 0.022$, $R_N^2 = 0.207$, $AUC \pm$ 95% CI $= 0.788 \pm 0.186$, $N = 31$ patches), which is a variable describing habitat quality. The percentage of parasitism of the 10 collected egg clutches per site ranged from 10 to 60% (mean: $25.9 \pm 4.4\%$). However, none of the studied variables correlated significantly with the parasitism rate of *F. reptans*.

Table 1: Significant multivariate logistic regression models of the occurrence of *C. canaliculata* depending on combinations of predictors of habitat quality (slope), habitat size (patch size), and habitat isolation (distance to nearest neighbor = NN, connectivity). Given are the *P*-value, χ^2-value, $R_{Nagelkerke}^2$, AIC_c-, and *AUC*-value (after internal validation via bootstrapping), as well as the number (*N*) of study sites that were included in the analysis. The model with the lowest AIC_c is printed in bold letters.

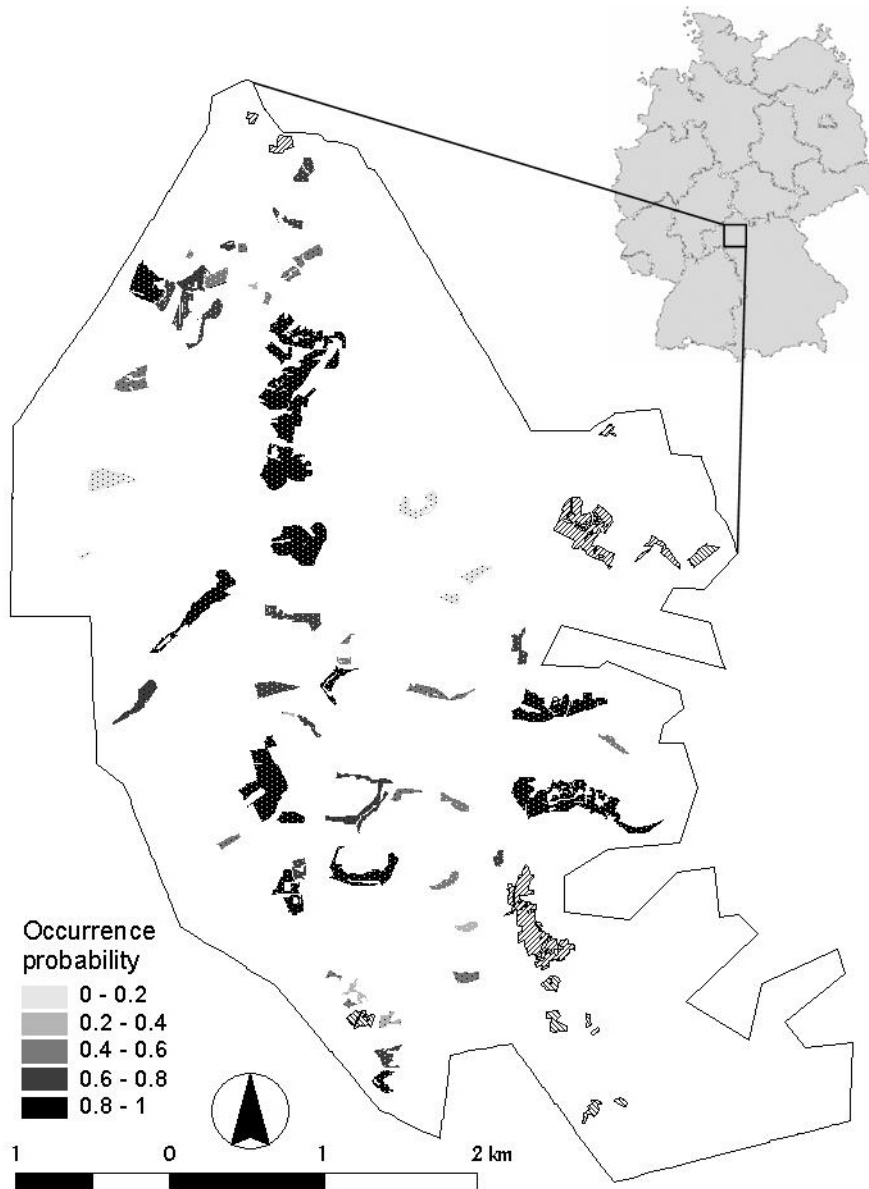| Parameter	*P*	χ^2	R_N^2	*AIC*	*AUC*	*N*
Slope + patch size	0.0055	6.72	0.158	80.67	0.695	64
Slope + NN	0.0015	8.38	0.205	78.07	0.707	64
Slope + connectivity	0.0050	7.46	0.150	80.47	0.720	64
Patch size + NN + patch size $\times$ NN	0.0005	7.77	0.221	93.56	0.731	77
Patch size + connectivity	0.0002	9.55	0.228	92.19	0.748	77
Slope + patch size + NN	**0.0001**	**10.57**	**0.315**	**72.67**	**0.767**	**64**
Slope + patch size + connectivity	0.0003	9.80	0.262	74.49	0.775	64

Figure 2: Predicted and observed occurrence of *C. canaliculata* within the Hohe Wann nature reserve. The map shows the distribution of the 77 studied potential habitat patches with occurrence of the host plant *S. pratensis*. Additionally, a small map of Germany shows the approximate location of the nature reserve within Germany. The studied patches are colored in different shades of gray corresponding to the occurrence probabilities of *C. canaliculata* predicted by the multiple logistic regression model depending on the variables patch slope, patch size, and distance to the nearest neighbor. White (presence) and black (absence) dots on the respective patches indicate the observed occurrence of *C. canaliculata*. Patches on which the presence or absence of *C. canaliculata* were registered, but which could not be included into the multiple model due to the lack of area-wide data are not shaded but are horizontally hatched (presence) or vertically hatched (absence).
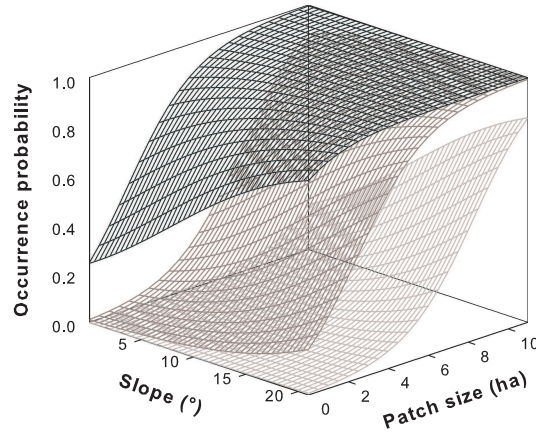
Figure 3: Response surfaces of habitat suitability models for *C. canaliculata* considering the predictor variables patch size (ha), patch slope (°), and distance to the nearest neighbor patch (m), The occurrence probability of *C. canaliculata* is plotted depending on patch slope and patch size for three exemplary distances to the nearest neighbor patch: 10 m (black), 500 m (dark gray), and 1000 m (light gray).
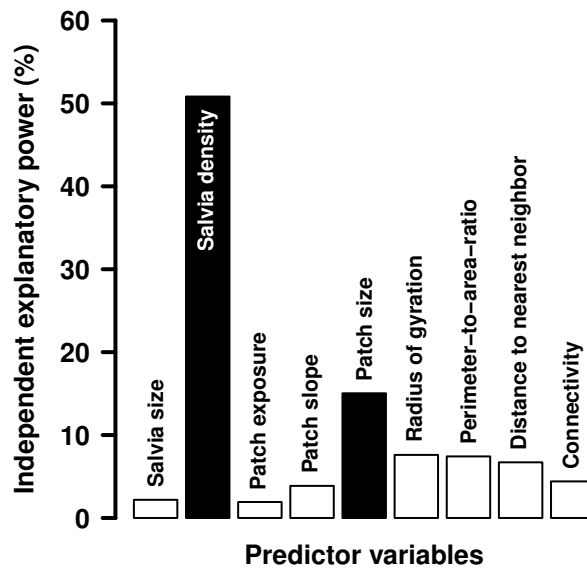

Figure 4: Predictor variables explaining the population density of *C. canaliculata*. Percentage distribution of independent explanatory power of all tested predictor variables calculated by hierarchical partitioning. The tested variables were *Salvia* size (principal component), *Salvia* density, patch exposure (principal component), patch slope, patch size, radius of gyration, perimeter-to-area-ratio, distance to the nearest neighbor, and connectivity. Variables that were included in the best multiple model are shaded in black.

DISCUSSION

Patch size and isolation as well as patch slope were the most important factors determining the occurrence pattern of the endangered leaf beetle *Cassida canaliculata* within the habitat patch network in this study. The population density of the beetles was strongly determined by host plant density and patch size. Patch shape and other habitat quality variables did not contribute significantly to the explanation of beetle occurrence or density. This indicates that a network of large and well-connected habitat patches with high host plant densities is an apparent conservation goal. Nevertheless, as host plant density had a more than three times higher explanatory effect on population density than patch size, also small patches with high host plant densities can support viable populations and should thus be sustained as well. The egg parasitoid *Foersterella reptans* occurred most likely on patches with high population densities of the beetle. However, we could not find any significant correlation between beetle population density and percentage of parasitized egg clutches. Thus, the risk of any single beetle egg clutch being parasitized seemed not to depend on egg clutch density. Patch size, isolation, and other habitat quality variables were not correlated to parasitoid occurrence or density.

In accordance with metapopulation theory (Hanski & Gaggiotti, 2004), the occurrence probability of *C. canaliculata* correlated positively with patch size and negatively with patch isolation. Additionally, patch shape may be essential, as edge effects at the patch border can have a negative impact on species survival within a patch (Tscharntke *et al.*, 2002; Ewers & Didham, 2006). Thus, patches with a small perimeter-to-area-ratio may have a higher occurrence probability. This was, however, not the case in our study. Both this and the fact that patch size had a two times higher independent explanatory power (15%) for the occurrence of the leaf beetle on a patch than the radius of gyration (8%) suggest that linear landscape elements, which may serve as corridors for other species (Rosenberg *et al.*, 1997; Berggren *et al.*, 2002), do not seem to play an important role for *C. canaliculata*.

Concerning patch isolation, the variables distance to the nearest neighbor and connectivity describe the isolation of a patch in a qualitatively different way. The distance to the nearest neighbor patch with *C. canaliculata* occurrence gives no information on the size of this patch and on how many other patches are located nearby, whereas the connectivity integrates the size and distance of all potential source patches within a landscape (cf. Kuhn & Kleyer, 1999/2000). In a recent meta-analysis, Moilanen & Nieminen (2002) recommended that complex connectivity measures should be preferred over simple measures (like the distance to the nearest neighbor), as simple measures often fail to detect effects of isolation, which could be detected with measures that are more complex. In the present study, both the simple measure distance to the

11

nearest neighbor and the more complex measure connectivity could be used to explain the occurrence of *C. canaliculata* within a patch. However, as the distance to the nearest occupied neighbor patch requires no information on the dispersal ability of *C. canaliculata* it should be preferred over the more complex connectivity measure until more detailed knowledge is available on dispersal distances in this species. A still better measure of patch isolation from the beetles' view should also include the structure of the 'matrix' into which the potential habitat patches are embedded (Gustafson & Gardner, 1996; Ricketts, 2001; Goodwin & Fahrig, 2002; Ewers & Didham, 2006). Habitat patches that have the same distances to the 'nearest neighbor' may be differently isolated depending on the surrounding matrix structure. This issue has to be addressed in future studies on *C. canaliculata*.

Regarding habitat quality, only patch slope contributed significantly to the occurrence probability of the beetle. There are several possible explanations for this result. One of them relates to the microclimate of the patch, as steeper patches could have a warmer microclimate favoring the development of the beetle larvae in early spring. However, this holds only for patches facing south and west, whereas slope usually reduces irradiation on north or east facing patches. Moreover, very steep slopes almost always decrease the irradiation of patches. Therefore, it is rather unlikely that slope itself is a good predictor of microclimate. Another possible explanation for the positive correlation between patch slope and beetle occurrence could be that steep patches may be less often disturbed by management than shallow patches and may thus provide better conditions for the long-term survival of populations. A third possibility of an effect of patch slope could be related to the drainage of soil water, which could be important for the abundance and quality of the beetles' host plant *S. pratensis*, which favors dry meadows. However, as we have no detailed information on neither management intensity nor water drainage in relation to patch slope in the study area, both hypotheses remains speculative. Thus, we cannot finally elucidate the meaning of patch slope for the occurrence of *C. canaliculata* within the scope of this study.

While the influence of habitat quality on *C. canaliculata* occurrence remains to be investigated in more detail, there was a clear correlation between habitat quality and population density of *C. canaliculata*. Egg clutch density of *C. canaliculata*, which we used as a measure of population density within a patch, increased not only with patch size but even more with host plant density. Consequently, large habitats with high host plant densities supported larger populations of *C. canaliculata*. In contrast to other studies (Bach, 1988; Connor *et al.*, 2000; Krauss *et al.*, 2004, 2005) patch size and host plant density were not correlated ($\rho_S = -0.008$) in our study area. Consequently, viable populations of *C. canaliculata* may also persist on smaller patches with high host plant densities (cf. Thomas *et al.*, 2001). Therefore, it is not only important to protect large

habitats but also to maintain smaller patches with high host plant densities to facilitate the survival of *C. canaliculata* within fragmented landscapes.

Regarding the egg parasitoid, only the egg clutch density of *C. canaliculata* affected the occurrence of *Foersterella reptans*. The probability of parasitism was positively density dependent. The beetles seem to have a low parasitism risk only when their own population density is low. Above a certain threshold, parasitoids were almost always present. Thus, the beetles do not have very good chances of escaping parasitism within the habitat patch network of this study.

None of the other studied predictors significantly explained variation in the occurrence or density of *F. reptans*. One possible reason for this lack of correlation may be that *F. reptans* can also parasitize other *Cassida* species (e.g., *C. rubiginosa* Müller; Bacher & Luder 2005), and therefore variables of habitat quality, size, and isolation – which were appropriate with regard to its host *C. canaliculata* – may have not been comprehensive enough for the perspective of the parasitoid. To the authors' knowledge, *C. rubiginosa* is the only other potential host of *F. reptans* in the study area. *C. rubiginosa* lives on thistles (Asteraceae: Carduae), which only very rarely grow in the same habitat as *S. pratensis*, the host plant of *C. canaliculata*. Therefore, the patches on which no parasitoids could be found from egg clutches of *C. canaliculata* were most likely really parasitoid-free (keeping in mind that it is per se impossible to 'prove' the absence of a species from a patch). Other potentially suitable patches with *C. rubiginosa* occurrence were not studied. Consequently, we cannot assess their spatial configuration and whether some of them might have been so close to patches classified as 'parasitoid-free' that they might have formed continuous patches from the perspective of the parasitoid. Moreover, even if *F. reptans* would parasitize only *C. canaliculata* the spatial scales affecting herbivore and parasitoid may be nevertheless different (Tscharntke & Brandl, 2004; Cronin & Reeve, 2005; Heisswolf *et al.*, 2006). Therefore, the parasitoid may perceive both patch size and isolation quite differently than its host(s). Only detailed studies on the distribution of all other potential hosts and on the dispersal abilities of *F. reptans* may lead to a better estimation of these variables for the parasitoid.

In summary, our study corroborates the hypothesis of e.g., Dennis & Eales (1997) and Thomas *et al.* (2001) that habitat quality is as important for the survival of insect species in fragmented landscapes as patch size and isolation. While all three variables, patch quality, size, and isolation determined the occurrence of *C. canaliculata*, habitat quality had the strongest effect on population density. Thus, we recommend to preserve not only large habitat patches, but also to maintain large host plant densities in all potential habitat patches independent of patch size to enhance the survival of *C. canaliculata*. In order to reduce isolation effects, more detailed studies on the disper-

sal ability of *C. canaliculata* as well as information about the isolation potential of different matrix types are needed. The egg parasitoid *F. reptans* occurred primarily on patches with high egg clutch densities of *C. canaliculata*. However, as there are still several open questions left regarding the parasitoid, further investigations on this species are necessary to determine how *F. reptans* affects the population dynamics and survival of *C. canaliculata* within the Hohe Wann nature reserve.

ACKNOWLEDGEMENTS

APPENDIX A

Total area and proportion of area covered by the nine main biotope types in the study area, the Hohe Wann nature reserve (Northern Bavaria, Germany; 50° 03' N, 10° 35' E). Classification according to Hein *et al.* (2007). Mapping by J. Eibich (unpublished data).

Biotope type	Area (ha)	Proportion cover (%)
Crop land	772.79	36.46
Fallow land	228.74	10.79
Intensively managed meadows	107.83	5.09
Intensively managed poor meadows	101.25	4.78
Dry grassland	55.59	2.62
Extensively managed meadows	129.80	6.12
Fringe vegetation	18.34	0.86
Hedges	103.93	4.90
Forest	487.43	22.99

APPENDIX B

Eigenvectors, eigenvalues, and explained variance of a principal components analysis including the predictor variables rosette diameter (cm), rosette height (cm), and number of vegetative cones.

	PC 1	PC 2	PC 3
Rosette diameter (cm)	−0.918	0.058	−0.392
Rosette height (cm)	−0.861	0.357	0.364
Number of vegetative cones	−0.407	−0.906	0.114
Eigenvalues	1.748	0.953	0.299
% Variance explained	58.3	31.7	10.0

APPENDIX C

Eigenvectors, eigenvalues, and explained variance of a principal components analysis including the predictor variables potential solar irradiation (kWh/m^2) and exposure (°).

	PC 1	PC 2
Potential solar irradiation (kWh/m^2)	0.985	−0.170
Exposure (°)	−0.985	−0.170
Eigenvalues	1.942	0.058
% Variance explained	97.1	2.89

APPENDIX D

Bivariate Spearman-rank correlations of all predictor variables and principal components (PC) used for explaining the occurrence and density of the herbivore *C. canaliculata*. The correlation coefficient ρ_S is given (values >0.5 are shaded in gray).

	NN	Radius of gyration	Area	Slope	Exposure (PC)	Cosine-transformed aspect	Potential solar irradiation	Host plant density	Mean host plant size (PC)	No. vegetative cones	Rosette height	Rosette diameter
Conn.	-0.815	-0.148	-0.107	-0.077	-0.129	0.140	-0.116	0.430	0.142	-0.281	-0.084	-0.122
NN		-0.001	-0.074	0.014	0.092	-0.088	0.094	-0.431	-0.198	0.283	0.130	0.164
Radius of gyration			0.958	0.108	0.232	-0.244	0.216	-0.020	-0.025	0.013	-0.063	0.028
Area				0.096	0.214	-0.232	0.203	-0.008	-0.001	-0.002	-0.102	0.010
Slope					0.030	0.013	0.062	-0.124	0.234	-0.122	-0.256	-0.226
Exposure (PC)						-0.982	0.991	-0.091	0.029	0.105	0.031	-0.131
Cosine-transformed aspect							-0.957	0.032	-0.030	-0.076	-0.058	0.120
Potential solar irradiation								-0.118	0.018	0.116	0.031	-0.130
Host plant density									0.268	-0.551	-0.130	-0.221
Mean host plant size (PC)										-0.639	-0.860	-0.908
No. vegetative cones											0.345	0.573
Rosette height												0.694

APPENDIX E

Bivariate Spearman-rank correlations of all predictor variables and principal compo-nents (PC) used for explaining the occurrence and density of the parasitoid F. reptans. The correlation coefficient ρ_S is given (values >0.5 are shaded in gray).

	Radius of gyration	Area	Slope	Exposure (PC)	Cosine-transformed aspect	Potential solar irradiation	Host plant density	Egg clutch density
NN	0.006	0.000	-0.112	0.207	0.003	-0.052	-0.158	0.073
Radius of gyration		0.938	0.221	0.223	-0.305	0.239	-0.074	0.224
Area			0.142	0.200	-0.323	0.266	-0.091	0.312
Slope				0.234	-0.142	0.104	0.005	-0.421
Exposure (PC)					-0.905	0.882	0.032	0.128
Cosine-transformed aspect						-0.981	-0.090	-0.201
Potential solar irradiation							0.109	0.242
Host plant density								0.430

REFERENCES

Bach, C. E. (1988). Effects of host plant patch size on herbivore density: patterns. *Ecology* **69**: 1090–1102. 12

Bach, M. (1851). Entwickelungs-Geschichte von *Cassida austriaca* Hbr. *Entomologische Zeitung* **12**: 158–159. 2

Bacher, S. & Luder, S. (2005). Picky predators and the function of the faecal shield of a cassidine larva. *Functional Ecology* **19**: 263–272. 3, 13

Bayerisches Landesamt für Umweltschutz (2003). Rote Liste gefährdeter Tiere Bayerns. In: *Schriftenreihe des Landesamts für Umweltschutz*, vol. 166, Bayerisches Landesamt für Umweltschutz, Augsburg, Germany. 2

Berggren, A., Birath, B. & Kindvall, O. (2002). Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeseli*). *Conservation Biology* **16**: 1562–1569. 11

Binzenhöfer, B., Schröder, B., Strauss, B., Biedermann, R. & Settele, J. (2005). Habitat models and habitat connectivity analysis for butterflies and burnet moths – The example of *Zygaena carniolica* and *Coenonympha arcania*. *Biological Conservation* **126**: 247–259. 6

Bourgeois, J. & Scherdlin, P. (1899). *Catalogue des Coléoptères des Vosges et des regions limitrophes*. Decker, Colmar. 3

Bundesamt für Naturschutz (1998). Rote Liste gefährdeter Tiere Deutschlands. In: *Schriftenreihe für Landschaftspflege und Naturschutz*, vol. 55, Landwirtschaftsverlag, Münster, Germany. 2

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York. 6

Clarke, R. T., Thomas, J. A., Elmes, G. W. & Hochberg, M. E. (1997). The effects of spatial patterns in habitat quality on community dynamics within a site. *Proceedings of the Royal Society B: Biological Sciences* **264**: 347–354. 2

Connor, E. F., Courtney, A. C. & Yoder, J. M. (2000). Individuals-area relationships: the relationship between animal population density and area. *Ecology* **81**: 734–748. 12

Cronin, J. T. & Reeve, J. D. (2005). Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proceedings of the Royal Society B: Biological Sciences* **272**: 2225–2235. 2, 13

Dennis, R. L. H. & Eales, H. T. (1997). Patch occupancy in *Coenonympha tullia* (Müller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. *Journal of Insect Conservation* **1**: 167–176. 2, 13

Dennis, R. L. H., Shreeve, T. G. & van Dyck, H. (2006). Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity and Conservation* **15**: 1943–1966. 2

Eber, S. (2001). Multitrophic interactions: The population dynamics of spatially structured plant-herbivore-parasitoid systems. *Basic and Applied Ecology* **2**: 27–33. 2

Elsner, O. (1994). *Geplantes Naturschutzgebiet "Südlicher Haßbergetrauf" im Landkreis Haßberge. Gutachten im Auftrag der Regierung von Unterfranken*. Institut für Vegetationskunde und Landschaftsökologie, Hemhofen-Zeckern. 3

Ewers, R. M. & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* **81**: 117–142. 1, 11, 12

Fahrig, L. (2001). How much habitat is enough? *Biological Conservation* **100**: 65–74. 1

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**: 487–515. 1

Fleishman, E., Ray, C., Sjögren-Gulve, P., Boggs, C. L. & Murphy, D. D. (2002). Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology* **16**: 706–716. 2, 3

Goodwin, B. J. & Fahrig, L. (2002). How does landscape structure influence landscape connectivity? *Oikos* **99**: 552–570. 12

Graser, K. (1984). Thüringer Funde von *Cassida* (U. G. Lordiconia RTTR) *canaliculata* LAICH. 1781 (Col., Chrysomelidae). *Entomologische Nachrichten und Berichte* **28**: 86–87. 3

Gustafson, E. J. & Gardner, R. H. (1996). The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* **77**: 94–107. 12

Hanley, J. A. & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* **143**: 29–36. 6

Hanski, I. (1998). Metapopulation dynamics. *Nature* **396**: 41–49. 2, 5

Hanski, I. & Gaggiotti, O. E. (eds.) (2004). *Ecology, Genetics, and Evolution of Metapopulations*. Elsevier Academic Press, Amsterdam. 2, 11

Hanski, I. & Ovaskainen, O. (2003). Metapopulation theory for fragmented landscapes. *Theoretical Population Biology* **64**: 119–127. 3

Harrell, F. E. J. (2001). *Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis*. Springer, New York. 6

Harrell, F. E. J. (2005). *Design: Design package.* R package version 2.0-12, URL `http://www.r-project.org`. 6

Harrell, F. E. J. & contributions from many other users (2006). *Hmisc: Harrell Miscellaneous*. R package version 3.1-1, URL `http://www.r-project.org`. 6

Haynes, K. J., Dillemuth, F. P., Anderson, B. J., Hakes, A. S., Jackson, H. B., Jackson, S. E. & Cronin, J. T. (2007). Landscape context outweighs local habitat quality in its effects on herbivore dispersal and distribution. *Oecologia* **151**: 431–441. 2

Heikkinen, R. K., Luoto, M., Kuussaari, M. & Pöyry, J. (2005). New insights into butterfly-environment relationships using partitioning methods. *Proceedings of the Royal Society B: Biological Sciences* **272**: 2203–2210. 6

Hein, S., Voss, J., Poethke, H. J. & Schröder, B. (2007). Habitat suitability models for the conservation of thermophilic grasshoppers and bush crickets – simple or complex? *Journal of Insect Conservation* **11**: 221–240. 3, 15

Heisswolf, A., Obermaier, E. & Poethke, H. J. (2005). Selection of large host plants for oviposition by a monophagous leaf beetle: nutritional quality or enemy-free space? *Ecological Entomology* **30**: 299–306. 3

Heisswolf, A., Poethke, H. J. & Obermaier, E. (2006). Multitrophic influences on egg distribution in a specialized leaf beetle at multiple spatial scales. *Basic and Applied Ecology* **7**: 565–576. 3, 13

Hosmer, D. W. & Lemeshow, S. (2000). *Applied Logistic Regression*. Wiley, New York. 6

Hunter, M. D. (2002). Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology* **4**: 159–166. 1, 2

Keitt, T. H., Urban, D. L. & Milne, B. T. (1997). Detecting critical scales in fragmented landscapes. *Conservation Ecology [online]* **1**: 4, URL `http://www.consecol.org/vol1/iss1/art4/`. 5

Krauss, J., Steffan-Dewenter, I., Müller, C. B. & Tscharntke, T. (2005). Relative importance of resource quantity, isolation and habitat quality for landscape distribution of a monophagous butterfly. *Ecography* **28**: 465–474. 12

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2004). Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. *Biological Conservation* **120**: 355–361. 12

Kuhn, W. & Kleyer, M. (1999/2000). A statistical habitat model for the Blue Winged Grasshopper (*Oedipoda caerulescens*) considering the habitat connectivity. *Zeitschrift für Ökologie und Naturschutz* **8**: 207–218. 11

Mac Nally, R. (2000). Regression and model-building in conservation biology, biogeography and ecology: The distinction between – and reconciliation of – "predictive" and "explanatory" models. *Biodiversity and Conservation* **9**: 655–671. 6

Mac Nally, R. (2002). Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodiversity and Conservation* **11**: 1397–1401. 6

Mardia, K. V., Kent, J. T. & Bibby, J. M. (1979). *Multivariate Analysis*. Academic Press, London. 6

McGarigal, K. (2001). *Fragstats: Spatial Pattern Analysis Program for Quantifying Landscape Structure. Version 3.3.* URL http://www.umass.edu/landeco/research/fragstats/fragstats.html. 5

Moilanen, A. & Hanski, I. (1998). Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* **79**: 2503–2515. 2

Moilanen, A. & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology* **83**: 1131–1145. 11

Nagelkerke, N. J. D. (1991). A note on the general definition of the coefficient of determination. *Biometrika* **78**: 691–692. 6

R Development Core Team (2005). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.r-project.org. 6

Reitter, E. (1912). *Fauna Germanica, Käfer*. Lutz, Stuttgart. 3

Ricketts, T. H. (2001). The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* **158**: 87–99. 12

Rosenberg, D. K., Noon, B. R. & Meslow, E. C. (1997). Biological corridors: form, function, and efficacy. *BioScience* **47**: 677–687. 11

Rudner, M., Biedermann, R., Schröder, B. & Kleyer, M. (2007). Integrated Grid Based Ecological and Economic (INGRID) landscape model – A tool to support landscape management decisions. *Environmental Modelling & Software* **22**: 177–187. 3, 4

Schröder, B. (2006). *ROC & AUC-Calculation – evaluating the predictive performance of habitat models*. URL http://brandenburg.geoecology.uni-potsdam.de/users/schroeder/download.html. 6

Steinhausen, W. (1949). *Morphologie, Biologie und Ökologie der Entwicklungsstadien der in Niedersachsen heimischen Schildkäfer (Cassidinae Chrysomelidae Coleoptera) und deren Bedeutung für die Landwirtschaft*. Ph.D. thesis, Technische Hochschule Braunschweig. 2

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science* **240**: 1285–1293. 6

Thomas, J. A., Bourn, N. A. D., Clarke, R. T., Stewart, K. E., Simcox, D. J., Pearman, G. S., Curtis, R. & Goodger, B. (2001). The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society B: Biological Sciences* **268**: 1791–1796. 2, 3, 12, 13

Thomas, J. A., Clarke, R. T., Elmes, G. W. & Hochberg, M. E. (1998). Population dynamics in the genus *Maculinea*. In: Dempster, J. P. & McLean, I. F. G. (eds.) *Insect Population Dynamics: In Theory and Practice*, Chapman & Hall, London, pp. 261–290. 2

Trautner, J., Geigenmüller, K. & Bense, U. (1989). *Käfer beobachten, bestimmen*. Neumann-Neudamm, Melsungen. 3

Tscharntke, T. & Brandl, R. (2004). Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology* **49**: 405–430. 13

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002). Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research* **17**: 229–239. 2, 11

van Nouhuys, S. & Hanski, I. (2002). Multitrophic interactions in space: metacommunity dynamics in fragmented landscapes. In: Tscharntke, T. & Hawkins, B. A. (eds.) *Multitrophic Level Interactions*, Cambridge University Press, Cambridge, pp. 124–147. 2

Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S*. Springer, New York. 6

Walsh, C. & Mac Nally, R. (2007). *hier.part: hierarchical partitioning. R package version 1.0-2*. URL `http://www.r-project.org`. 6

Wencker, J. & Silbermann, G. (1866). *Catalogue des Coléoptères de l'Alsace et des Vosgues*. Silbermann, Strasbourg. 3

Wiegand, T., Moloney, K. A., Naves, J. & Knauer, F. (1999). Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *American Naturalist* **154**: 605–627. 2