



# The generality of habitat suitability models: A practical test with two insect groups

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## Summary

For the design and declaration of conservation areas as well as for planning habitat management it is important to quantitatively know the habitat preferences of the focal species. To take into account the requirements of as many species as possible, it would be of great advantage if one would either (i) find one or several species whose habitat requirements cover those of a large number of other species or if one could (ii) identify a common set of habitat parameters that is important for the occurrence of many species. Ideally such common habitat parameters should be easy to measure. Only then they may be of practical value in applied conservation biology.

In this study, we compared the habitat preferences of different insect species (grasshoppers, bush crickets, butterflies, moths) in the same region by applying identical methods. To identify common explanatory variables that predict the occurrence probability of these species, we first tested the transferability of the specific 'species models' to other species within the same insect group. We tested how well the incidence of one species can be predicted by the occurrence probability of another species. The 'best' models within each group were then tested for transferability between the different groups. Additionally, we tested the predictive power of the predictor variable 'habitat type' as an easy and often available measure for conservation practice.

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Although in the different 'species models' different key factors determine habitat suitability, some models were successfully transferred and were able to reasonably predict the distribution of other species. The habitat preferences of the burnet moth *Zygaena carniolica* were particularly well suited for the prediction of suitable habitats for all other species. In addition, the predictor variable 'habitat type' played a dominant role in all models. Models using this aggregated predictor variable may well predict suitable habitat for all species.

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### Zusammenfassung

Sowohl für die Ausweisung von Naturschutzgebieten als auch für geplante Habitatmanagementmaßnahmen ist es wichtig, die Habitatansprüche der zu schützenden Arten quantitativ und objektiv zu kennen. Um die Habitatansprüche möglichst vieler Arten berücksichtigen zu können, wäre es von großem Vorteil entweder (i) eine Art zu kennen, deren Habitatansprüche die von möglichst vielen anderen Arten abdeckt oder aber (ii) alle gemeinsamen Habitatansprüche identifizieren zu können, die für das Vorkommen vieler verschiedener Arten wichtig sind. Idealerweise sind solche überlappenden Habitatansprüche durch Habitatparameter charakterisiert, die leicht zu messen sind, damit sie im praktischen Naturschutz von Nutzen sein können.

In dieser Untersuchung vergleichen wir die Habitatansprüche verschiedener Insektenarten (Heuschrecken, Tagfalter, Widderchen) im gleichen Untersuchungsgebiet unter Verwendung identischer Methoden. Um Habitatparameter zu identifizieren, die für alle Arten von Bedeutung sind, testeten wir zuerst die Übertragbarkeit von Habitateignungsmodellen für einzelne Arten auf andere Arten innerhalb einer Insektengruppe. Das beste Modell innerhalb einer Gruppe wurde dann auf seine Übertragbarkeit zwischen den Insektengruppen getestet. Zusätzlich testeten wir, wie gut sich das Vorkommen einer Art mit den vorhergesagten Vorkommenswahrscheinlichkeiten einer anderen Art vorhersagen lässt. Neben diesem Vergleich von spezifischen Habitatansprüchen der Insektenarten haben wir auch die Vorhersagekraft der Variable "Habitattyp" getestet. Diese ist ein einfach zu erhebender und häufig schon vorhandener Parameter im Naturschutz.

Obwohl die unterschiedlichen Artmodelle unterschiedliche Schlüsselfaktoren enthielten, ließen sich einige Modelle erfolgreich übertragen. Besonders die Habitatpräferenzen des Esparsetten-Widderchens *Zygaena carniolica* waren geeignet für die Vorhersage geeigneten Habitats der anderen untersuchten Arten. Zusätzlich lieferte der Habitattyp als Prädiktorvariable für alle Arten sehr gute Modelle. Mit dieser aggregierten Prädiktorvariable kann geeignetes Habitat für alle untersuchten Arten bei unterschiedlichem Management vorhergesagt werden.

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### Introduction

The increasing and irreversible loss of biodiversity is one of the major current environmental problems. It results in an urgent need for efficient decision making to protect valuable areas. Conservation has to succeed in strong competition with alternative land uses and under substantial constraints (e.g. low monetary funds). This is especially true for grassland systems in Central Europe. Thus, priorities in the declaration of protected areas have to be set. For this aim, appropriate and reliable decision criteria need to be developed to maintain the species diversity in selected conservation areas (with as little expenditure in area and

money as possible, see e.g. Kleyer et al., 2007; Rudner, Biedermann, Kleyer, 2007; 2004; Rudner, Biedermann, Schröder, & Kleyer; 2007).

To reach the aim of protecting as many species as possible in the conservation of grasslands, habitat requirements of a very large number of single species has to be considered simultaneously (Bob-bink & Willems, 1993). To overcome this problem, one could imagine two scientific approaches: (a) the identification of single species – so-called umbrella species – which are representatives for others with respect to habitat requirements (Bonn & Schröder, 2001; Fleishman, Murphy, & Brussard, 2000; Launer & Murphy, 1994; Roberge & Angelstam, 2004), or (b) the combination of single

species habitat requirements in order to find a common set of variables promoting the occurrence of as many species as possible (e.g. Bonn & Schröder, 2001). Both methods would make it feasible to predict suitable habitats and the impact of different management types on the occurrence of a whole set of species. In the past years, habitat requirements of single species have increasingly been identified using habitat suitability models (also known as species distribution models or niche-based model approaches, Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000; Scott, Heglund, Morrison, Haufler, & Wall, 2002). But only seldom these models have been transferred between species and species groups to find one single set of parameters describing the habitat requirements for several species (but see Bonn & Schröder, 2001).

Within the MOSAIK project, the habitat requirements of different insect species inhabiting mesoxerophytic grasslands have been studied (Binzenhöfer, Schröder, Strauss, Biedermann, & Settele, 2005; Hein, Voss, Poethke, & Schröder, in press). In this study, we compare results of these analyses for three orthopteran species, *M. bicolor* (PHILIPPI 1796), *Platycleis albopunctata* (GOETZE 1778), and *S. lineatus* (PANZER 1796) as well as two lepidopteran species, *C. arcania* (LINNAEUS 1761) and *Zygaena carniolica* (SCOPOLI 1763), all typically found in dry grasslands.

We first tested the transferability of the specific 'species' models within one insect group (within-group transfer). The model, which showed the highest transferability in each group ('group model'), was then transferred to the other insect groups (between-group transfer). To determine a representative or 'umbrella' species, we additionally tested whether the predicted occurrence probability of each species can be used to predict incidences of the others just as well (Bonn & Schröder, 2001).

In addition, we tested the categorical explanatory variable 'habitat type' separately for its predictive power and transferability. Although, one might think it is trivial, this variable is of special interest for several reasons. First, although all species under study occur on dry grasslands, their occurrence probabilities on different grassland categories (crop field, mesoxerophytic grassland, fallow land, extensively managed grassland, intensively managed grassland) vary from species to species and can only be predicted accurately by habitat suitability models. Second, the habitat type or derivatives of this parameter, like landscape context (the percentage of a certain habitat type in the surrounding), were included in all single species models (Binzenhöfer et al., 2005; Hein et

al., in press). Additionally, in many parts of the world maps of habitat types may be the only reasonably detailed ecological information available reflecting patterns of biodiversity (Faith, Margules, Walker, Stein, & Natera, 2001; Mac Nally et al., 2002).

## Material and methods

### Study species

#### Grasshopper and bush crickets

The stripe-winged grasshopper, *S. lineatus*, the two-coloured bush cricket, *M. bicolor*, and the grey bush cricket, *P. albopunctata*, are classified as thermophilic and xerophilic (Detzel, 1998; Harz, 1969; Ingrisch, & Köhler, 1998). They typically inhabit dry grasslands as well as broom and juniper heath. *S. lineatus* and *P. albopunctata* are also found on fringes and areas with open soil and sparse vegetation. In contrast, *M. bicolor* is more orientated towards vertical structures and thus prefers habitats with higher vegetation. *S. lineatus* prefers sheep-grazed areas with short vegetation (Detzel, 1998).

#### Butterfly and burnet moth

Adults of *C. arcania* fly on mesoxerophytic grasslands in the vicinity of hedges and forest edges. Caterpillars feed preferentially on *Holcus lanatus*, *Brachypodium pinnatum*, *Festuca ovina* and *Melica* sp. (Ebert & Rennwald, 1991; SBN, 1997; Settele, Feldmann, & Reinhardt, 2000; Weidemann, 1995).

The burnet moth *Z. carniolica* is a xerothermophilic species and inhabits mainly fallow, extensively grazed or mowed mesoxerophytic grasslands. Preferred larval food plants are *Onobrychis viciifolia* and *Lotus corniculatus*. Adults prefer purple flowering nectar plants like *Knautia arvensis*, *Scabiosa columbaria* and *Centaurea* sp. (Ebert & Rennwald, 1994; Kreusel & Böhmer, 1998; SBN, 1997; Weidemann & Köhler, 1996).

### Field work

All studies were conducted in the field seasons 2001 and 2002 in the nature reserve 'Hohe Wann' in Northern-Bavaria, Germany (latitude 50° 03', longitude 10° 35'). The study area is characterised by abundant sites of mesoxerophytic grasslands, formerly used as vineyards (Elsner, 1994). These patches are separated by agricultural landscape of different use. The whole area covers

approximately 10 km in NS-direction and 4 km in EW-direction.

Incidence of the study species was recorded on 146, 139 and 106 experimental plots for Orthoptera, *Z. carniolica* and *C. arcania*, respectively. Experimental plots were selected by stratified random sampling across the ten main habitat types occurring in the region (i.e. forest, thermophilic forest, hedges, fringes, mesoxerophytic grassland, extensively managed grassland, intensively managed grassland with meagre parts, intensively managed grassland, crop fields, fallow land). To increase the 'resolution' of the logistic regression models we sampled with high effort in habitats with—based on prior knowledge—uncertain status regarding the species' occurrence (i.e. different kinds of mesic open grasslands). To assure comparability of results, the study plots of the grasshoppers and bush cricket studies (15 m × 15 m) were located at a randomly chosen corner of the butterfly/burnet moth plots (30 m × 30 m). Different plot sizes were chosen because butterflies/burnet moths are assumed to be more mobile than grasshoppers or bush crickets.

For the assessment of species incidence, we performed transect counts on the plots. The census was terminated (i) after a species had been recorded or (ii) after a maximum of 15 min (butterfly, burnet moth) or 20 min (grasshopper, bush crickets) of sampling. As the activity of these species strongly depends on weather conditions, censuses were only carried out during appropriate weather conditions – i.e. sunshine, cloud cover < 3/8; air temperature > 17 °C; wind speed < 4 m/s (Settele et al., 2000) – to ensure the same detection probability on all plots.

## Statistical analyses

This study is based on data from different authors (Binzenhöfer et al., 2005; Hein et al., in press). Both studies used the same experimental design to achieve comparable data sets for the different species. In the following, we will give a short summary of the methods used to achieve the models underlying our analysis presented here. For a more detailed description, we refer to the original papers.

In contrast to Binzenhöfer et al. (2005), Hein et al. (in press) do not present any results regarding parameters derived from a digital terrain analysis. In this analysis terrain attributes like potential solar radiation, different measures of disturbance (e.g. frequency and intensity) as well as soil type were quantified. Hence, habitat models were built using

these parameters prior to the analyses of transferability. In addition, we adjusted the analysis of landscape context parameters in Hein et al. (in press) to the approach used in Binzenhöfer et al. (2005). Using GIS (ESRI™ ArcView 3.2), we calculated the proportion of each habitat type in circles of radii ranging from 25 m to 250 m around the experimental plot. To derive explanatory variables from these proportions they were weighted by their predicted occurrence probability determined in the univariate logistic regression analyses with the habitat type as plot parameter.

## Single species models

The single species models of Binzenhöfer et al. (2005) and the adjusted ones from Hein et al. (in press) that showed the highest AUC (i.e. the area under receiver-operating curves, cf. Hanley & McNeil, 1982; Hosmer & Lemeshow, 2000; Schröder, 2000) and the lowest values for the Akaike information criterion (AIC, see Buckland, Burnham, & Augustin, 1997) were chosen for the tests of transferability (see Table 1). We applied multiple logistic regression analysis with stepwise backward variable selection (Hosmer & Lemeshow, 2000). Model calibration was evaluated using Nagelkerke's  $R^2$  value (Harrell, 2001; Nagelkerke, 1991). Model discrimination was assessed via AUC values (Hanley & McNeil, 1982; Hosmer & Lemeshow, 2000; Schröder, 2000).

To select a final species model from the set of alternative models, we used the AIC (see Buckland et al., 1997), which allows choosing the model with the optimal compromise between goodness-of-fit and model complexity. Models with the lowest AIC were tested for spatial autocorrelation in their residuals by calculating Moran's  $I$  as an index of autocorrelation between different locations (Lichstein, Simons, Shriver, & Franzreb, 2002). Models were internally validated by bootstrapping with 300 iterations (Verbyla & Litvaitis, 1989, cf. e.g. Opper, Schaefer, Schmidt, & Schröder, 2004; Pepler-Lisbach & Schröder, 2004). The bootstrap procedures were performed with the R 1.8.0 software (www.r-project.org, R Development Core Team 2004) using the packages Design (Harrell, 2001) and Hmisc (Harrell, 2001).

## Test of transferability

Each of the single-species models resulting from the separate analyses (Table 1) was tested for transferability in two ways. First, we predicted occurrence probabilities for the species the model

**Table 1.** Overview of the 'best' single-species models with included predictor variables (significant at  $p < 0.05$ ) and model performance criteria:  $R^2_{\text{Nagelkerke}}$  and  $\text{AUC}_{\text{values}}$  after internal validation by bootstrapping with backwards stepwise variable selection

Species	Predictor variables	$R^2_{\text{Nagelkerke}}$	$\text{AUC}_{\text{bootstrapped}}$
<i>S. lineatus</i>	Habitat type Vegetation height (only quadratic term)	0.367	0.735
<i>M. bicolor</i>	Proportion of fringes/mesoxerophytic grassland/ extensively managed meadows within radius = 50 m	0.227	0.723
<i>P. albopunctata</i>	Sinus exposition, vegetation height Potential solar radiation Proportion of fringes within radius = 75 m	0.712	0.941
<i>C. arcania</i>	Time of first management Presence of tree layer Proportion of mesoxerophytic/extensively managed grassland within radius = 100 m Proportion of hedges on suitable area within radius = 25 m	0.640	0.920
<i>Z. carniolica</i>	Presence of <i>Centaurea jacea</i> , Presence <i>Scabiosa columbaria</i> , Proportion of fringes/mesoxerophytic grassland/ extensively managed grasslands within radius = 25 m	0.540	0.900

was estimated for and applied these probabilities to predict the occurrence of the other species (cf. Schröder, 2000; Bonn & Schröder, 2001). This procedure was repeated with a single-predictor model considering 'habitat type' only (altogether 25 possible combinations).

Second, we considered the predictors from the minimum-AIC model for each species and estimated new models considering these parameters to explain the incidence of all other species. In both cases, we checked for an agreement between predictions and occurrences by comparing the resulting AUC value with two  $\text{AUC}_{\text{crit}}$  values, 0.5 and 0.7, respectively (Schröder, 2004). The transfer quality of a model is best when all possible combinations result in AUC values significantly exceeding  $\text{AUC}_{\text{crit}}$ . For *within-group* comparisons of transferability, this methods result in five possible combinations for the three Orthoptera species, respectively in three combinations for the two Lepidoptera species. The highest possible number of successful transfers of a single species model for *among-group* comparisons is seven.

## Results

### Adjustment of analyses

After re-analysing the models presented in Hein et al. (in press) according to the approach

presented in Binzenhöfer et al. (2005), there were no changes for *S. lineatus*. In the model for *M. bicolor* the predictor variable 'habitat type of the experimental plot' is replaced by 'proportion of fringes, mesoxerophytic grassland, extensively managed meadows within radius 50 m'. For *P. albopunctata*, we received a strongly better model by including 'potential solar radiation' and 'the proportion of fringes within a radius of 75 m', which decreased the AIC value from 71.98 to 40.84 and increased the bootstrapped AUC value from 0.806 to 0.941.

### Summary of the single-species habitat suitability models

For all three orthopteran species, occurrence probability was highest for fringe vegetation followed by mesoxerophytic grassland. In addition, low vegetation height increases occurrence probability of *S. lineatus*. For *P. albopunctata*, occurrence probability decreases with increasing vegetation height, increasing solar radiation and west faced exposition (Table 1).

The occurrence probability of *C. arcania* was positively influenced by a late start of management measures and the presence of a tree layer (Table 1). Additionally, a high proportion of mesoxerophytic grassland and extensively managed meadows within a radius of 100 m and a high proportion of hedges on suitable habitat within a radius of 25 m

increase the occurrence probability of this species. The highest probability of occurrence for *Z. carniolica* is predicted for areas with a high proportion of mesoxerophytic grasslands, fringes and extensively managed meadows. Additionally, the occurrence of *Scabiosa columbaria* and *Centaurea jacea* has a positive effect on the occurrence probability of *Z. carniolica* (Table 1).

The univariate logistic regression analyses with the additional 'landscape' parameters derived from the digital terrain and landscape model (Schröder et al., 2004; Rudner et al., 2007) resulted in significant univariate models for all species. However, none of these parameters is included into the multiple parameter models for *S. lineatus*, *M. bicolor*, *Z. carniolica* and *C. arcania*. Only the occurrence probability of *P. albopunctata* increased significantly with the inclusion of the factor 'potential solar radiation'.

### Tests of transferability

For grasshoppers and bush crickets, we obtained the best *within-group* transferability applying the *S. lineatus* model (Table 2). The occurrence of *C. arcania* and *Z. carniolica* is best predicted by the *Z. carniolica* model (Table 2).

In the *between-group* transfer of the single species models to the other species the model estimated for *Z. carniolica* showed the highest number of successful transfers to all other species (Table 3a).

Regarding the *between-group* transfer based on parameters from the best group models, the *Z. carniolica*-model performs slightly better than the one based on *Stenobothrus lineatus* (one more

successful transfer; Table 4). Models considering the predictor 'habitat type' alone showed the highest transferability for all species (Table 3b), with 100% (= 25/25) successful transfers.

## Discussion

### Adjustment of analyses

The replacement of the predictor variable 'habitat type of the experimental plot' by 'proportion of fringes, mesoxerophytic grassland, extensively managed meadows within radius 50 m' in the model of *Metrioptera bicolor* yields similar results, because the habitat types, fringes, mesoxerophytic grassland, extensively managed meadows are those with the highest predicted occurrence probabilities of this species in models using the predictive variable 'habitat type of the experimental plot'. The inclusion of landscape context (i.e. the proportion of these habitat types within 50 m) accounts for a larger actual habitat size than the plot size (ca. 1 ha vs. 225 m<sup>2</sup>). The same argument applies to the replacement of predictor variable 'habitat type of the experimental plot' by the factor 'proportion of fringes within a radius of 75 m' in the model of *P. albopunctata*. The additional inclusion of the factor 'potential solar radiation' into the final model for *P. albopunctata* is in agreement with the high temperature requirements of this species for egg and larval development (Detzel, 1998).

From the fact that for the other species, no terrain-related factors are included into the final models, it may not be concluded that disturbance

**Table 2.** Results of *within-group* transfers, only the results for the model with the most successful transfers are shown. For Orthoptera the model of *Stenobothrus lineatus* showed the best transferability (five successful out of five possible transfers)

Model of species	Species incidence used for model calibration	Species incidence to be predicted	Model outcome – transferability	
			AUC	Lower–upper confidence bound
<i>S. lineatus</i>	<i>S. lineatus</i>	<i>S. lineatus</i>	0.762*	0.677–0.848
		<i>M. bicolor</i>	0.632*	0.525–0.739
		<i>P. albopunctata</i>	0.870**	0.794–0.946
	<i>M. bicolor</i>	0.771*	0.680–0.862	
<i>Z. carniolica</i>	<i>Z. carniolica</i>	<i>Z. carniolica</i>	0.991**	0.870–0.969
		<i>C. arcania</i>	0.613*	0.507–0.719
	<i>C. arcania</i>	<i>C. arcania</i>	0.898**	0.837–0.960

For Lepidoptera, the model of *Z. carniolica* was best transferable. AUC-values significantly ( $\alpha = 0.05$ ) exceeding  $AUC_{crit} = 0.7$  are indicated by \*\*, those significantly exceeding  $AUC_{crit} = 0.5$  by \*.

**Table 3.** Results of (a) *between-group* transfer with the 'best' model of each species and the predicted probabilities of these species used to predict the occurrence of the other species and (b) transferability tests with the single predictor variable 'habitat type' from 15 m × 15 m experimental plots

Species incidence used for model calibration for models with	Species incidence to be predicted	(a) Model outcome – transferability		(b) Model outcome – transferability	
		AUC	Lower–upper confidence bounds	AUC	Lower–upper confidence bounds
(a) Species specific predictor variables ('best model')	<i>S. lineatus</i>	0.762*	0.677–0.848	0.846**	0.787–0.904
	<i>M. bicolor</i>	0.632*	0.525–0.739	0.802**	0.734–0.870
	<i>P. albopunctata</i>	0.870**	0.794–0.946	0.846**	0.769–0.922
	<i>Z. carniolica</i>	0.640*	0.525–0.755	0.803**	0.727–0.880
	<i>C. arcania</i>	0.596*	0.476–0.715	0.711*	0.624–0.799
(b) The single predictor variable 'habitat type'	<i>S. lineatus</i>	0.727*	0.628–0.827	0.842**	0.780–0.904
	<i>M. bicolor</i>	0.740*	0.641–0.839	0.806**	0.739–0.873
	<i>P. albopunctata</i>	0.619	0.496–0.742	0.842**	0.762–0.922
	<i>Z. carniolica</i>	0.767	0.672–0.862	0.807**	0.734–0.879
	<i>C. arcania</i>	0.521	0.392–0.651	0.736*	0.650–0.821
<i>P. albopunctata</i>	<i>S. lineatus</i>	0.630	0.488–0.772	0.807**	0.740–0.873
	<i>M. bicolor</i>	0.418	0.286–0.551	0.766*	0.693–0.839
	<i>P. albopunctata</i>	0.949**	0.893–1.0	0.855**	0.785–0.925
	<i>Z. carniolica</i>	0.377	0.241–0.512	0.777*	0.696–0.859
	<i>C. arcania</i>	0.557*	0.419–0.695	0.678*	0.589–0.766
<i>Z. carniolica</i>	<i>S. lineatus</i>	0.760*	0.681–0.839	0.847**	0.785–0.910
	<i>M. bicolor</i>	0.766*	0.681–0.839	0.803**	0.730–0.877
	<i>P. albopunctata</i>	0.738*	0.650–0.826	0.840**	0.773–0.906
	<i>Z. carniolica</i>	0.919**	0.870–0.969	0.820**	0.754–0.887
	<i>C. arcania</i>	0.613*	0.507–0.719	0.745*	0.659–0.831
<i>C. arcania</i>	<i>S. lineatus</i>	0.527	0.412–0.642	0.773*	0.692–0.854
	<i>M. bicolor</i>	0.537	0.425–0.649	0.762*	0.68–0.845
	<i>P. albopunctata</i>	0.751*	0.650–0.851	0.832**	0.756–0.907
	<i>Z. carniolica</i>	0.584	0.462–0.706	0.770*	0.696–0.844
	<i>C. arcania</i>	0.938**	0.896–0.981	0.811**	0.741–0.880

AUC-values significantly ( $\alpha = 0.05$ ) exceeding  $AUC_{crit} = 0.7$  are indicated by \*\*, those significantly exceeding  $AUC_{crit} = 0.5$  by \*.

factors like 'disturbance frequency' or 'disturbance intensity', have no influence on habitat suitability for these species. Especially, adult butterflies are sensitive to changes in temperature, light and humidity levels, parameters that are often affected by habitat disturbance (Wood & Pullin, 2002). We assume that other factors already included in the models cover the effects of disturbance or other 'landscape' parameters. The integrating predictor variable 'habitat type' may be such a factor; for instance, extensively and intensively managed meadows differ in the degree of management (i.e. disturbance) frequency.

### Tests of transferability

Models based on the incidence of *C. arcania* are not applicable to predict other species' distribution. Furthermore, the incidence of *C. arcania* can only be poorly predicted by other species' occurrences. This may be due to the comparatively broad niche properties of *C. arcania*. This species is mesophilic, i.e. its habitats cover a broad range of habitat types. Habitats suitable for *Z. carniolica* and the grasshopper and bush cricket species only cover a small part of habitats suitable for *C. arcania*.

**Table 4.** Results of *between-group* transfer with the parameters of the Lepidoptera 'group' model (*Z. carniolica*) used to predict the occurrence of the other species

Species incidence used for model calibration	Species incidence to be predicted	Model outcome – transferability	
		AUC	Lower–upper confidence bounds
<i>S. lineatus</i>	<i>S. lineatus</i>	0.775*	0.688–0.862
<i>M. bicolor</i>	<i>M. bicolor</i>	0.747*	0.659–0.835
<i>P. albopunctata</i>	<i>P. albopunctata</i>	0.787*	0.674–0.900

AUC-values significantly ( $\alpha = 0.05$ ) exceeding  $AUC_{crit} = 0.7$  are indicated by \*\*, those significantly exceeding  $AUC_{crit} = 0.5$  by \*. Original models are marked in grey.

Occurrence probabilities of all five species studied can be best predicted with the model of the burnet moth *Z. carniolica*. This species may thus act as a representative or 'umbrella species' for others. However, this point needs further investigations. In the models, the predictor variables 'habitat type', 'vegetation height' as well as 'occurrence of the nectar plants *Centaurea jacea* and *Scabiosa columbaria*' play an important role. The two plant species may not directly influence grasshoppers and bush crickets, but they indicate extensively managed areas, which are preferred by the species.

Generally, stenoecious but mobile species may be best suited as 'umbrella' or surrogate species (New, Pyle, Thomas, Thomas, & Hammond, 1995). They exactly represent habitat requirements of species typically found in specific habitats and can reach all potential habitats better than species with low mobility. Thus, we would have expected the bush cricket *P. albopunctata* to be a good representative species as it represents a species with narrow niche properties and is the most endangered and most stenoecious species among the species of this study. In addition, Schmeller (1995) could show a high mobility of this species and did not find any genetic differences between populations in the study region. However, models of *P. albopunctata* are not suited to predict occurrence of the other species. This indicates that species with a too narrow niche may not be suitable as good representatives for other species.

Although one would expect that, based on its higher mobility, the burnet moth *Z. carniolica* were much better suited as representative species for xerothermophilic species living on dry grasslands, we found the transferability of the model of *Z. carniolica* only slightly different (one more successful transfer) from the one of the grasshopper *S. lineatus*. This may be due to the fact that mobility is not a decisive factor for the survival of this species in the nature reserve 'Hohe Wann', as connectivity is probably very high for *S. lineatus*. To

really quantify this argument, a landscape-wide mapping of *S. lineatus* for the determination of connectivity would be necessary (cf. connectivity analyses for *Z. carniolica*, Binzenhöfer et al., 2005). Alternatively, one could test and compare the predictive quality of both models in other landscapes. Provided that *S. lineatus* would be as suitable as *Z. carniolica*, it would be much easier to determine the occurrence of *S. lineatus* than that of *Z. carniolica* from a practical point of view. This grasshopper is easily recognised by its songs and its activity is less dependent on weather conditions than that of the burnet moth.

## Implications for nature conservation

In contrast to general or expert statements on species' habitats (Detzel, 1998; Settele et al., 2000; Ingrisch & Köhler, 1998), the developed habitat suitability models allow for a quantitative and spatially explicit prediction of occurrence probability of the studied species in different grassland types.

In the past, different approaches like indicator, umbrella, focus and keystone species (cf. e.g. Andelman & Fagan, 2000; Simberloff, 1998) have been utilised in conservation biology to protect as many species as possible. Lambeck (1997), for example, suggested the use of a combination of focal species that represent the most limited species (e.g. dispersal limited, element limited, area-limited, etc.). But unfortunately, most often the baseline data for this kind of study are not available and, hence, such an approach has been criticised as being non-operational in a planning sense (Lindenmayer et al., 2002).

Our models for the grasshopper *S. lineatus*, the bush cricket *M. bicolor* and the burnet moth *Z. carniolica*, particularly those including the variable 'habitat type', can predict the occurrence of other species very well. Obviously, the predictor 'habitat type' reflects an aggregation of different para-

meters ranging from geological and topographical prerequisites (e.g. soils, slope) to anthropogenic influences (e.g. disturbance). This result is supported by studies on biodiversity management (Faith et al., 2001; Margules & Pressey, 2000). They showed that using ecological categorisations instead of single species yields better surrogates for biodiversity. In practical work, it is also much easier to map habitat types than any of the insect species studied by us, as the recording of all species is weather dependent to a certain extent and is restricted to a short adult season. In contrast, vegetation can be monitored under nearly all weather conditions and over a longer time period.

Several recent papers on modelling species distribution at larger scales have found that models using climatic or terrain variables work far better than those including habitat type (Thuiller, Lavorel, & Araujo, 2005). These findings are in contrast to our results, but may be routed in the different scales of the studies. Our study was conducted at a small spatial scale compared to studies of large environmental, geographical and climatic gradients (Guisan & Thuiller, 2005; Thuiller et al., 2005). In these studies, climatic factors often reflect ecological properties of the species very well and can be used for extrapolation. These variables are then also often closely related to resource availability (Mackey & Lindenmayer, 2001) and are often the only predictors available at larger scales. Nevertheless, our results may be particularly helpful in conservation biology, as the habitat type can easily be determined in contrast to costly analyses of vegetation structure and composition. Additionally, information on the habitat type already exists for many regions of conservational interest.

With reference to the MOSAIK project (Kleyer et al., 2002) or other approaches aiming at optimising the management of dry grasslands, a prediction of habitat types resulting from different management regimes, as implemented in the MOSAIK landscape model INGRID (Rudner et al., 2007), allows for an objective classification of suitable and unsuitable areas for threatened species according to the management regime. Based on these data, a comparison and assessment of different management regimes and their influence on species composition and biodiversity is possible (see Schroder et al., 2004; Rudner et al., 2007).

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