

Habitat models and habitat connectivity analysis for butterflies and burnet moths – The example of *Zygaena carniolica* and *Coenonympha arcania*

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Abstract

In this paper, habitat models were used to predict potential habitat for endangered species, which is an important question in landscape and conservation planning. Based on logistic regression, we developed habitat distribution models for the burnet moth *Zygaena carniolica* and the nymphalid butterfly *Coenonympha arcania* in Northern Bavaria, Germany. The relation between adult occurrence and habitat parameters, including the influence of landscape context, was analyzed on 118 sites. Habitat connectivity analyses were carried out on the basis of (1) habitat suitability maps generated from these models and (2) dispersal data from mark recapture studies. Our results showed that (1) the presence of the burnet depended mainly on the presence of nectar plants and of nutrient-poor dry grasslands in direct vicinity, that of the nymphalid on larger areas of extensively used dry grasslands within 100 m vicinity in combination with small patches of higher shrubs and bushes. (2) Internal as well as external validation indicated the robustness and general applicability of the models. Transferability in time and space indicated their high potential relevance for applications in nature conservation, such as predicting possible effects of land use changes. (3) Habitat connectivity analyses revealed a high degree of habitat connectivity within the study area. Thus, we could show no effects of isolation or habitat size for both species.

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1. Introduction

Agricultural intensification on one hand and abandonment of traditional, economically unsustainable land use practices on the other are main reasons for the loss of bio-

diversity in large parts of Europe (Petit et al., 2003; BFN, 2003; Sutcliffe et al., 2003). Today's land use practices strongly promote habitat fragmentation and thus reduce habitat connectivity. Connectivity is the degree to which the landscape facilitates or impedes exchange of individuals with other resource patches (Taylor et al., 1993). Habitat connectivity is assumed to strongly influence species occurrence and population survival in fragmented landscapes (Fahrig and Merriam, 1985; Hanski, 1994; van Langefelde, 2000; Ferreras, 2001; D'Eon et al., 2002).

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In order to stop the decline of species, it is of major importance to assess the effects of land use change. Monitoring can provide a profound basis for the understanding of these effects (Niemi, 2000). Habitat models which formalize the relation between the occurrence of a species and the characteristics of a site (Guisan and Zimmermann, 2000) may be a cost efficient alternative to monitoring (Owen, 1989; Fraser, 1998). Robust models can be used to predict a species' distribution in less well studied regions or assess the effects of future land use changes (Verbyla and Litvaitis, 1989; Schröder and Richter, 1999; Pearce and Ferrier, 2000; Cowley et al., 2001). Since habitat models can also be regarded as a qualitative and quantitative key factor analysis (Austin et al., 1990; Pearce et al., 1994; Kleyer et al., 1999), they are also suited to assess species' persistence probabilities in a specific landscape (Kleyer, 1999).

In our study, we investigated semi-natural, dry grasslands, a largely declining habitat. The study focused on two endangered species that are typical for this habitat: the burnet moth *Zygaena carniolica* LINNAEUS 1761, and the nymphalid butterfly *Coenonympha arcania* SCOPOLI 1763. These species depend on different successional stages of dry grassland and represent different dispersal capabilities (according to Ebert and Rennwald, 1991, 1994; Bink, 1992), thus representing many other endangered (butterfly) species of similar habitats. We hypothesize that: (1) the presence of adults can be predicted by a limited set of habitat parameters; (2) the models can be applied to other regions; (3) both species' habitat is highly fragmented; (4) patch occupancy is affected by isolation and patch size. The aims of our study were: (1) to exemplarily demonstrate the process of model building and validation and its possible implications for habitat connectivity and nature conservation and (2) to generate models that can be implemented into a landscape model for the entire study area (Rudner et al., 2004; Schröder et al., 2004). Within this landscape model, effects of different land-use practices on the habitat and thus on the species under study will be simulated.

2. Materials and methods

2.1. Research areas

The main study area was the nature reserve 'Hohe Wann' in Northern Bavaria (50°03'N, 10°35'E). Elevations range from 240 to 390 m. The geological formation of the region is Middle Keuper, a formation of the Upper Triassic. Average annual temperature is 8.8 °C with an average annual precipitation of 650 mm (Deutscher Wetterdienst, 2002). While agriculture still prevails in flat areas (valleys and plateau sites), slopes are either used extensively or are abandoned. They form a small-

scale mosaic of semi-arid grasslands, thermophile fringes, scattered bushes and – largely abandoned – vine yards (Schröder et al., 2004).

The study area for spatial validation was located 200 km north, near the city of Jena (Thuringia). This study site includes part of the nature reserve 'Leutratal' and adjacent areas and is characterized by the shell limestone layers of the river Saale valley. Elevations range from 190 to 260 m, average annual temperature is 9.3 °C with an average annual precipitation of 587 mm (Heinrich et al., 1998). The area is characterized by extensively used mesophile grasslands in combination with semi-arid grasslands and thermophile fringes. The more or less south-facing slopes are characterized by numerous hedgerows and bushes (Heinrich et al., 1998).

2.2. Species under study

Zygaena carniolica is a xerothermophile species of fallow, moderately grazed or mown dry grasslands. It is listed in the Red Data Books for Bavaria and Germany (e.g., Pretschner, 1998). Within the research areas, larvae feed on *Onobrychis vicifolia* and *Lotus corniculatus*. Adults prefer violet flowering nectar plants like *Knautia arvensis*, *Scabiosa columbaria*, and *Centaurea* species (Ebert and Rennwald, 1994; SBN, 1997; Kreusel and Böhmer, 1998).

Coenonympha arcania inhabits dry grasslands with bushes as well as mesophile grasslands near hedges and forest edges. The species is regarded as near threatened in Bavaria and Germany (e.g., Pretschner, 1998). Larvae preferably feed on nutrient poor grasses like *Holcus lanatus*, *Brachypodium pinnatum*, *Festuca ovina* or *Melica* species. Requirements for nectar plants are unspecific, but also incompletely assessed (Ebert and Rennwald, 1991; SBN, 1991; Settele et al., 2000).

2.3. Sampling design, predictor variables, species data

Within the main study area, we selected 118 sample plots of 30 × 30 m² in a random stratified way (Guisan and Zimmermann, 2000; Hirzel and Guisan, 2002). The strata covered a range of six habitat types which represented the gradient of habitats within the study area (Table 1). A pre-study had shown that, within the study area, fields and forests were unsuitable habitats for the studied species, thus they were not considered further. Habitat types that were expected to have high or low occurrence probabilities (according to published information) were sampled with fewer plots (Table 1). For spatial validation, three plots for each habitat type were selected in the validation area. Since there were no fallow fields in that area, this type remained unsampled for spatial validation (Table 1).

On each plot, we quantified a set of habitat parameters (Table 2). It included parameters describing

Table 1
Incidence of *Z. carniolica* and *C. arcania* within the sampled strata for both study areas

Habitat type	Hohe Wann			Leutratat		
	# of plots	<i>Z. carniolica</i>	<i>C. arcania</i>	# of plots	<i>Z. carniolica</i>	<i>C. arcania</i>
		2001/2002	2001/2002		2002	2002
Fallow field	7(6)	–/–	1/1	–		
Intensively managed grassland	27(23)	–/2	5/6	6		2
Extensively managed grassland	43(37)	13/14	23/20	3	1	2
Semi-arid grassland	24(23)	16/12	13/15	3	2	3
Fringe vegetation, thermophile	11	5/4	11/11	3	2	3
Hedges and shrubs	6	–/–	6/5	3	1	3

Values in brackets refer to the number of plots for the census of *C. arcania*.

Table 2
Habitat parameters measured at all sample plots

Plot parameters	Categories/explanation
Habitat type ^c	Fallow field/intensively managed grassland/extensively managed grassland/semi-arid grassland/fringe, thermophile/hedges and shrubs
Management type	Mowing/cattle grazing and mowing/cattle grazing/shepherding/mulching/fallow
Date of first annual management	Before June 15/before July 15/before August 15/after August 15/fallow
Inclination (°) ^c	
Sine/cosine exposition ^c	
Level of shading	Not shaded/partly shaded/mostly shaded
Potential solar radiation ^c	
Cover (%)/height (m) of bush encroachment fringe species	Single bushes outside hedges present/absent
Hedge length (m)/height (m) cover of hedge (%)	
Cover (%)/height (m) of tree layer	
Cover (%)/height (m) of shrub layer	
Cover (%)/height (m) of vegetation layer	
Cover (%) of moss layer	
Cover (%) of bare ground	
Cover (%) of <i>Lotus corniculatus</i> ^a	
Cover (%) of <i>Onobrychis viciifolia</i> ^a	
Cover (%) of <i>Centaurea jacea</i> ^b	
Cover (%) of <i>Centaurea scabiosa</i> ^b	
Cover (%) of <i>Scabiosa columbaria</i> ^b	
Cover (%) of <i>Knautia arvensis</i> ^b	
Cover (%) of <i>Oreganum vulgare</i> ^b	
<i>Landscape context parameters</i>	
DryGrass.100 (%) ^c	Dry grassland (semi-arid or extensively managed grassland) within a radius of 100 m suitable habitat for <i>Z. carniolica</i> within a radius of 25 m (suitable habitat = semi-arid or extensively managed grassland and thermophile fringes)
Habitat.25 (%) ^c	
PropHedge.25 (%) ^c	proportion of hedges in suitable habitat for <i>C. arcania</i> within a radius of 25 m (suitable habitat = semi-arid or extensively managed grassland, thermophile fringes, hedges)

^a Larvae food plants of *Z. carniolica*.

^b Nectar plants of *Z. carniolica*.

^c Data available area-wide.

landscape context, as a species' presence might also be influenced by the surrounding landscape structure and heterogeneity (Fahrig and Johnson, 1998; Steffan-Dewenter, 2003; Summerville and Crist, 2004). Landscape context parameters were generated based on a map of

habitat types: within a GIS, proportions of each habitat type within a certain distance were calculated for every plot. We tested radii between 25 and 250 m. Later on, explanatory variables were derived from these proportions (Table 2, bottom). Additionally, Schröder et al.

(2004) quantified terrain attributes like exposition, inclination and potential solar radiation based on a digital terrain model (DTM).

For the recording of species' incidence data, our response variable, only adults were considered. All $30 \times 30 \text{ m}^2$ plots were surveyed for a period of 15 min. During this time, two transect walks were performed. If at least one individual was observed, the species was considered to be present on a plot. The surveys were carried out under optimum weather conditions (Pollard et al., 1975; Hermann, 2000) during the species' main flight periods.

2.4. Model building and evaluation

Habitat models were developed on two levels: (1) models based on the whole set of available data; (2) models which were exclusively based on parameters that were available for the whole study area (i.e., all variables derived from the DTM or the map of habitat types). The latter allowed for the generation of area-wide habitat suitability maps.

We used logistic regression to analyze the relationship between species' occurrence and habitat parameters (Manel et al., 1999; Hosmer and Lemeshow, 2000). We started with a careful univariate analysis, as recommended by Hosmer and Lemeshow (2000). In case of unimodal relationships the squared terms of the predictor variable were included. Since maximum likelihood estimation does not converge in case of complete separation (Hosmer and Lemeshow, 2000), categories of variables were combined where necessary. Based on likelihood-ratio-tests of univariate models, non-significant variables ($p > 0.05$) were excluded from further analysis (Hosmer and Lemeshow, 2000). In case of strong correlation between variables (Spearman rank correlation $r_s > 0.5$), only one of them was used to avoid multicollinearity (Capen et al., 1986; Fielding and Hawthorn, 1995; Schröder, 2000).

Multiple models we obtained by performing stepwise backward regression (Hosmer and Lemeshow, 2000). Levels of significance were $p_{\text{in}} = 0.05$ to include and $p_{\text{out}} = 0.10$ to exclude variables (Adler and Wilson, 1985; Schröder, 2000). All statistical analyses were performed with SPSS 11.0™.

We used R_N^2 (Nagelkerke, 1991) to quantify model calibration. The discriminative power of models we assessed via AUC-values (Hanley and McNeil, 1982; Zweig and Campbell, 1993; Fielding and Bell, 1997). According to Hosmer and Lemeshow (2000), a value of 0.7 indicates satisfactory, 0.8 good and 0.9 very good discrimination. In addition, we used Cohen's κ , as it is not negatively affected by the prevalence of species (Manel et al., 2001). Values exceeding 0.4 describe a clear, ones exceeding 0.6 a strong match between predicted and observed occurrences (Sachs, 1999). As a

threshold for discriminating between suitable and unsuitable habitats we applied P_κ which represents that occurrence probability where κ reaches the highest value (Schröder, 2004). For comparison of alternative models we used the Akaike Information Criterion, AIC (cf. Buckland and Elston, 1993; Opper et al., 2004).

2.5. Habitat model validation

For internal validation, we performed bootstrapping (Efron and Tibshirani, 1993; Verbyla and Litvaitis, 1989) with 300 iterations, using Splus 6.1™. Bootstrapping corrects over-optimistic estimates of performance criteria that result from assessing performance on training data (Verbyla and Litvaitis, 1989; Reineking and Schröder, 2003; Opper et al., 2004). AUC and R_N^2 we obtained by using the DESIGN library's 'validate' function provided by Harrell (2001). κ , we calculated based on the 'bootpred' function (Efron and Tibshirani, 1993).

Additionally, we evaluated if models hold for other data and can be transferred in time and space (external validation). Therefore, we applied them to data from the consecutive year (Dennis and Eales, 1999) and from the second study area (Freeman et al., 1997; Manel et al., 1999; Schröder and Richter, 1999). To test the performance of this transfer, we applied significance tests of AUC-values (Beck and Shultz, 1986; Schröder, 2004). We regarded the model transfer as successful if the AUC-value significantly exceeded a threshold of 0.7.

2.6. Habitat suitability maps and habitat connectivity analysis

The regression equations were applied to maps of the predictor variables. Thus, we obtained habitat suitability maps that show predicted occurrence probabilities and – by applying the threshold – suitable habitat patches for the entire study area (Schröder and Richter, 1999; Kleyer et al., 1999).

These binary habitat maps (grain size: 25 m) provided the basis for a habitat connectivity analysis according to Keitt et al. (1997, see also Söndgerath and Schröder, 2002). Depending on the landscape pattern and a species' specific dispersal ability, single habitat patches may be functionally connected to a habitat cluster (With et al., 1997). Within a cluster, gaps between suitable patches may not exceed a critical dispersal distance d_{crit} (Keitt et al., 1997; Schröder, 2000; van Langefelde, 2000). Species specific d_{crit} -values were varied within the range of values obtained from mark recapture studies that were carried out on three sites within the study area in 2001 (Höhfeld unpublished thesis and Holzschuh pers. commun.). Cluster sizes are then expressed as radius of gyration R . Unlike the number of grid cells, it accounts for different shapes. A general measure for a landscape's species specific habitat connectivity is the

correlation length C which represents the area-weighted mean of the radii of gyration over all clusters. It may be interpreted as the mean distance a randomly placed individual can move through the landscape before encountering a cluster's edge (Keitt et al., 1997). Completing this part of the analysis in a further step, we applied the resulting cluster sizes (defined as the clusters' radii of gyration R) as predictor variables in univariate logistic regression models. By this, we checked whether habitat size and small-scale isolation have an effect on species' occurrence. We used $d_{crit} = 25$ m for *Z. carniolica* and $d_{crit} = 100$ m for *C. arcania*, which was a compromise between worst case (i.e., minimum dispersal) assumptions on one hand and landscape context variables considered in the underlying habitat models on the other. For this analysis, only sample plots within

predicted habitat patches were considered ($n = 40$ for *Z. carniolica*, $n = 58$ for *C. arcania*).

3. Results

3.1. Effect of single environmental factors

3.1.1. *Zygaena carniolica*

Prevalence of *Z. carniolica* remained constant in both years with 29% and 27%, respectively. In the validation area 'Leutratl', *Z. carniolica* occurred on 32% of the plots (Table 1).

Eight habitat parameters are significant on the univariate level and thus subject to further analysis (Table 3). The variable 'habitat type' yields high explanatory power

Table 3
Univariate models for *Z. carniolica* and *C. arcania* ('Hohe Wann', 2001): regression coefficients β and R_N^2 -values for all significant predictor variables

Variable	Category	<i>Z. carniolica</i>			<i>C. arcania</i>		
		p	R_N^2	β	p	R_N^2	β
Habitat type	Fallow field	<0.001	0.44	Ref. cat.	<0.001	0.25	Ref. cat.
	Int. managed grassland			5.32×10^{-11}			0.328
	Ext. managed grassland			9.367			2.106
	Hedges and bushes			5.32×10^{-11}			} 2.708
	Semi-arid grassland			10.896			
	Fringe, thermopile			10.021			
Management type	Fallow	0.004	0.20	Ref. cat.	–	–	–
	Mowing			0.588			
	Cattle grazing and mowing			–0.916			
	Cattle grazing			–0.693			
	Shepherding			1.668			
	Mulching			–6.908			
Date of first annual management	Before June 15	0.041	0.01	Ref. cat.	<0.001	0.41	} Ref. cat.
	Before July 15			0.588			
	Before August 15			–0.357			} 2.262
	After August 15			1.609			
	Fallow			0.262			
Inclination (°)		–	–	–	<0.001	0.23	0.151
Sine exposition		–	–	–	0.011	0.08	–0.855
Level of shading	Not shaded	–	–	–	0.045	0.05	Ref. cat.
	Partly/mostly shaded						0.863
Bush encroachment (%)		–	–	–	<0.001	0.29	0.321
Hedge cover (%)		0.006	0.12	0.139	<0.001	0.31	0.259
(Hedge cover) ²				–0.003			–
Fringe species	Absent	0.033	0.05	Ref. cat.	<0.001	0.21	Ref. cat.
	Present			0.967			2.136
Tree layer	Absent	–	–	–	0.003	0.10	Ref. cat.
	Present						1.270
Vegetation layer (%)		–	–	–	0.001	0.07	–0.028
Moss layer (%)		<0.001	0.18	0.240	–	–	–
# of nectar plant species		<0.001	0.33	2.188	–	–	–
Habitat.25 (%)		<0.001	0.41	0.052	–	–	–
PropHedge.25 (%)		–	–	–	<0.001	0.42	0.297
(PropHedge.25) ²							–0.003
DryGrass.100 (%)		–	–	–	<0.001	0.34	0.211
(DryGrass.100) ²							–0.003

² indicates that the squared term is included to model a unimodal response. For sigmoid response curves, $\beta > 0$ indicates a positive, $\beta < 0$ a negative correlation, for categorical variables β have to be interpreted with respect to the reference category (ref. cat.).

($R_N^2 = 0.44$). We can see the clear trend that *Z. carniolica* has the highest incidence (67%) in semi-arid grassland, followed by thermophile fringes (46%) and extensively mown grassland (30%). These habitat types we considered as suitable habitat when deriving the landscape context variable ‘habitat.25’. Representing the proportion of suitable habitat types within a radius of 25 m, it has a strong positive association with species’ occurrence. Within radii up to 250 m there still is a positive (but decreasing) influence of suitable habitats with R_N^2 continuously decreasing from 0.41 (25 m radius) to 0.24 (250 m radius). The presence of nectar plants has a strong influence on *Z. carniolica*. Here, highest predictive power is yielded by the variable ‘number of nectar plant species’. It refers to *Centaurea jacea* and *S. columbaria* and represents the number (0/1/2) of these nectar plant species present on a plot. ‘Management type’ proved to be another strong predictor variable. Highest occurrence probabilities are associated with sheep herding, lowest with cattle grazing and mulching. Moss layer as well as the presence of fringe species affirmatively affect *Z. carniolica*’s occurrence, hedge cover shows a unimodal response. The date of first annual management has only weak influence ($R_N^2 = 0.01$). Management after August 15 has the most positive influence on the species’ occurrence, management between mid July and mid August as well as early management before June 15 the most negative.

3.1.2. *Coenonympha arcania*

In the main study area, incidence of *C. arcania* remained constant in both years (56% in 2001, 55% in 2002). In the validation area, *C. arcania* was present on 72% of the sample plots (Table 1). Twelve explanatory variables are significant on the univariate level (Table 3). Eight of them yield high explanatory power with $R_N^2 > 0.20$. Occurrence of *C. arcania* is mostly restricted to the habitat types extensively managed grassland, semi-arid grassland, fringe and hedge. These types, where incidence was between 54% and 100%, we considered as suitable habitat for calculating the landscape context variable ‘PropHedge.25’. Describing the proportion of hedges in all suitable habitat within 25 m, it shows a unimodal response with an optimum between 20% and 80%. R_N^2 is high with 0.42. The second landscape context variable, ‘DryGrass.100’, represents the proportion of dry grassland (extensively managed grassland and semi-arid grassland) within 100 m. Like ‘PropHedge.25’, the relationship is unimodal with a maximum between 20% and 60%. Unlike with *Z. carniolica*, the date of first annual management is a strong predictor ($R_N^2 = 0.41$) for *C. arcania*. Plots that are managed late or are fallow have occurrence probabilities close to 1, whereas early management before mid June cuts them down to less than 0.20. Strong relationships we found for parameters describing succession and marginal structures – bush encroachment,

hedge cover, presence of fringe species and trees increase occurrence probabilities – as well as for increasing inclination.

3.2. Multiple models

3.2.1. *Zygaena carniolica*

The best model obtained from all significant explanatory variables by means of backward selection is based on three predictor variables: occurrence of the nectar plants *C. jacea* or/and *S. columbaria* as well as the landscape context variable ‘habitat.25’ (Fig. 1). Occurrence probability increases with increasing values of ‘habitat.25’ and increasing number of nectar plant species. If at least one of the two plant species is present, *Z. carniolica*’s occurrence probability passes the threshold probability at 70% suitable habitat within 25 m. Without any nectar plants, occurrence probabilities never exceed the threshold. This model shows good performance with $R_N^2 = 0.54$, AUC = 0.90 and $\kappa = 0.66$ (Table 4, Model 1). The model based on parameters that are available area-wide consists of a single variable: the landscape context variable ‘habitat.25’ (Table 4, Model 2). Inclusion of context variables considering larger radii did not lead to significant model improvements. Model 2 yields poorer performance than the best model, especially for R_N^2 and κ . In the model transfers, the AUC-values only slightly deviate from the original models. Both *Z. carniolica* models remain significant after spatial transfer (AUC = 0.89, $p < 0.05$). Model 2 is not transferable in time; the high standard error makes an AUC of 0.78 not significantly different from $AUC_{crit} = 0.7$ ($p > 0.05$).

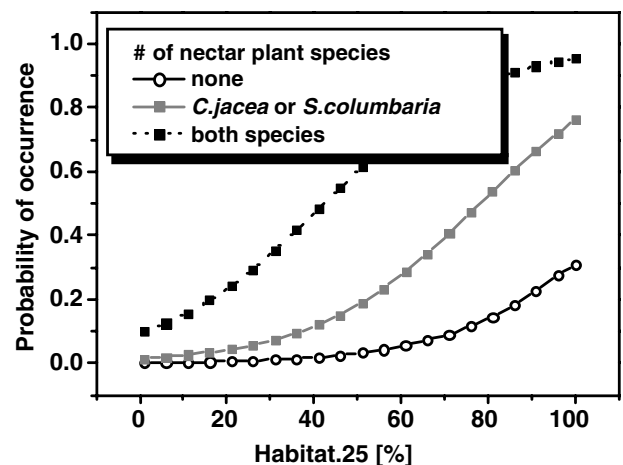


Fig. 1. Response curve for the *Z. carniolica* model based on plot parameters and landscape context. It shows the occurrence probability depending on the proportion of suitable habitat within a radius of 25 m (‘habitat.25’) for different levels of the second explanatory variable ‘number of nectar plant species’ (none, either *Centaurea jacea* or *Scabiosa columbaria*, or both).

Table 4

Bootstrapped performance criteria, threshold probability P_{κ} and parameters considered in multiple models (l.h.s) as well as AUC-values for external validation via spatial and temporal model transfer (r.h.s.)

Species	Model	Parameters	R_N^2	AUC	κ	P_{κ}	Model transfer		In space			
							In time		AUC		AUC	
							AUC	p	AUC	p	AUC	p
<i>Z. carniolica</i>	1	# of nectar plant species, habitat.25	0.54	0.90	0.66	0.40	0.88	<0.0001	0.89	<0.05		
	2	Habitat.25	0.42	0.84	0.48	0.28	0.78	>0.05	0.89	<0.05		
<i>C. arcania</i>	1	First management, tree layer present, DryGrass.100 ⁺² , PropHedge.25 ⁺²	0.64	0.92	0.63	0.63	0.82	<0.01	0.83	>0.05		
	2	DryGrass.100 ⁺² , PropHedge.25 ⁺² , inclination	0.56	0.89	0.54	0.51	0.83	<0.01	0.92	<0.05		

p -values specify the significance level of estimated AUC-values exceeding a critical value of 0.7. ⁺² indicates that the squared term is included to model a unimodal response.

3.2.2. *Coenonympha arcania*

The best model for *C. arcania* is shown in Fig. 2. Optimum habitats for *C. arcania* have a proportion of hedges between 20% and 80% in suitable habitat types within 25 m and between 10% and 60% of dry grassland within 100 m. This span is extended to a maximum under the combination of late management and presence of trees (lower right plot). The model shows high performance ($R_N^2 = 0.64$, AUC = 0.92, $\kappa = 0.63$). The area-wide model is based on the two landscape context variables together with inclination (Table 4, Model 2). Like in Model 1, optimum conditions are at medium levels of ‘PropHedge.25’ and ‘DryGrass.100’, the span being extended with higher levels of inclination. The model performs slightly poorer than the best model. Both models could be transferred in time ($p < 0.01$). A significant spatial transfer was possible for *C. arcania*’s Model 2 (AUC = 0.92, $p < 0.05$) but not for Model 1 (AUC = 0.83, $p > 0.05$).

3.3. Habitat suitability maps and habitat connectivity analysis

Based on the area-wide models, we calculated habitat suitability maps for the entire study area ‘Hohe Wann’. According to these maps, *Z. carniolica* occurs in about 7% of the study area. Nearly half of these patches reach occurrence probabilities over 50%, with a maximum at 63%. The proportion of suitable *C. arcania* habitats is nearly three times higher (19%), with most suitable habitats (13%) exceeding an occurrence probability of 80%.

Our connectivity analysis is carried out based on binary habitat maps (see Fig. 3 as an example). The d_{crit} -values applied correspond to observed dispersal distances (Höhfeld, Holzschuh unpubl. data). Increasing d_{crit} -values yield monotonously decreasing cluster numbers and monotonously increasing correlation lengths since patches separated by larger gaps are successively connected. For specific critical distances the respective correlation lengths were larger for *C. arcania* than for *Z. carniolica* revealing a higher degree of habitat connectivity with respect to the first species. This becomes even more obvious considering the 75% and 95% quantiles of observed flight distances which are 160 m for both species (75% quantile) and 364 m for *Z. carniolica* vs. 332 m for *C. arcania* (95% quantile). Using these quantiles as d_{crit} results in 30 clusters ($C = 422$ m) vs. 10 clusters ($C = 1350$ m) for *Z. carniolica* compared to 3 clusters ($C = 1338$ m) vs. 2 clusters ($C = 1595$ m) for *C. arcania*. If d_{crit} exceeds 550 m in case of *Z. carniolica* and 360 m in case of *C. arcania*, we achieve a single percolating cluster (Fig. 4). In these cases, all habitat patches are connected yielding correlation lengths of $C = 1547$ m for *Z. carniolica*, and $C = 1613$ m for *C. arcania*.

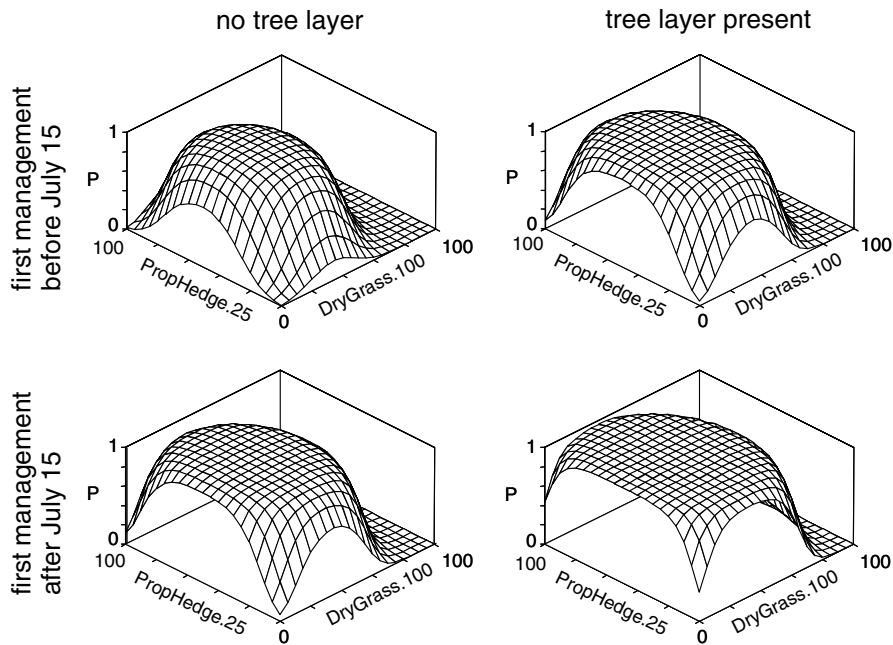


Fig. 2. Response surface for the *C. arcania* model based on plot parameters and landscape context. Occurrence probability depending on landscape context parameters (DryGrass.100: x-axis, PropHedge.25: y-axis). Diagrams show different combinations of tree layer absent/present and first management before/after July 15.

Even for worst case assumptions for d_{crit} , there is no significant relationship between habitat size – calculated as “radius of gyration” for all habitat clusters during habitat connectivity analysis – and the occurrence of neither *Z. carniolica* ($n = 40$, $p = 0.25$), nor *C. arcania* ($n = 58$, $p = 0.07$).

4. Discussion

4.1. Interpretation of habitat models

4.1.1. *Zygaena carniolica*

In both study areas, *Z. carniolica* shows a clear preference for semi-arid grassland, followed by thermophile fringes and extensively mown grasslands. This strongly corresponds with information in the literature, where the species is characterized as a typical representative of arid and semi-arid grasslands (Ebert and Rennwald, 1994; SBN, 1997; Kreusel and Böhmer, 1998). Sporadic encounters of the burnet in otherwise unsuitable habitats can be traced back to available nectar sources: presence of *C. jacea* or *S. columbaria* tremendously improves occurrence probabilities. Nectar plants also seem to play a role in the aggregation behavior of the species. The latter is discussed as a strategy to find mates and to minimize predation risk (Ebert and Rennwald, 1994). Among the nectar plants, only *C. jacea* and *S. columbaria* remained in the best multiple model, the others did not significantly improve the model. Although the preference for nectar plants might vary geographically

as well as phenologically (Smolis and Gerken, 1987; Kreusel and Böhmer, 1998), these two species seem to be sufficient to predict the presence of *Z. carniolica* in other regions as it was shown in the validation area ‘Leutratal’.

According to Thomas et al. (1992), habitat requirements of most insect species are driven by the larvae rather than by the adults. Since *Lotus corniculatus*, one of the larval food sources within the study area, is widespread (B. Reiser, pers. commun.), we could show no effect of larval food plants on *Z. carniolica*’s presence. It remains unclear whether the model would yield comparable predictive power in areas where the rarer *Onobrychis viciifolia* is used as the only larval food resource (Ebert and Rennwald, 1994). On the other hand, Cowley et al. (2001) as well got better results for Lepidoptera habitat models based on habitat composition rather than on the presence of larval food plants. This was particularly true for species with strong habitat associations which can hardly be encountered in unsuitable habitats, but are abundant and widespread in suitable ones. These characteristics are reported for *Z. carniolica* (Smolis and Gerken, 1987; Ebert and Rennwald, 1994; Kreusel and Böhmer, 1998).

The positive relationship between hedge cover and incidence of *Z. carniolica* might be explained by the wind shelter provided by hedges. However, the effect might also be indirect and due to the low land use intensity associated with sites that have a high proportion of hedges. The same is probably true for moss cover.

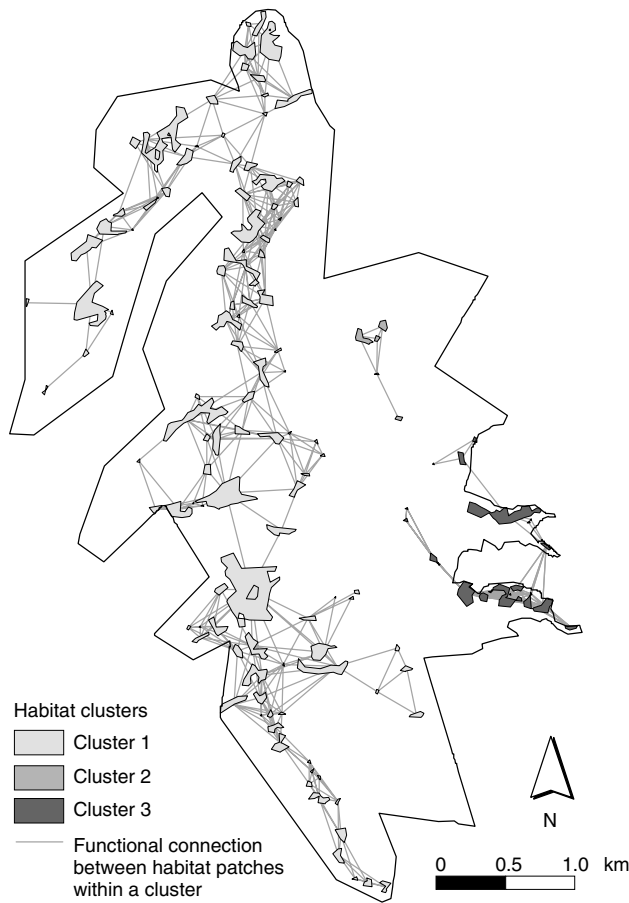


Fig. 3. Binary habitat suitability map of the nature reserve 'Hohe Wann' for *Z. carniolica* after applying $P_k = 0.28$. Lines represent the 'functional linkage' between individual patches of the three clusters resulting from applying $d_{crit} = 360$ m. This distance corresponds to the 95% quantile of observed dispersal distances, i.e., 5% of all individuals that were recaptured covered a distance of 360 m or more.

Habitat requirements of *Z. carniolica* in terms of management correspond to present knowledge (Ebert and Rennwald, 1994; SBN, 1997) but could be defined more precisely by our study. Sheep herding and hay harvesting promote the species, whereas cattle grazing and mulching are unfavorable management types. Management seems to have a negative impact during the main flight period of the adults, i.e., between 15th of July and 15th of August.

According to our study, the presence of *Z. carniolica* is predominantly driven by habitat quality in the direct surroundings of the patches (25 m radius). Although, within radii up to 250 m distance there still is a positive (but decreasing) influence of suitable habitats. This might be due to the species' dispersal behavior. Even though it was shown to be extremely sedentary in different MRR studies (Kreusel and Böhmer, 1998; Holzschuh, pers. commun., Smolis and Gerken, 1987), there were observations within these studies that *Z. carniolica* can fly for several kilometers across unsuitable habitat and thus colonize remote habitats.

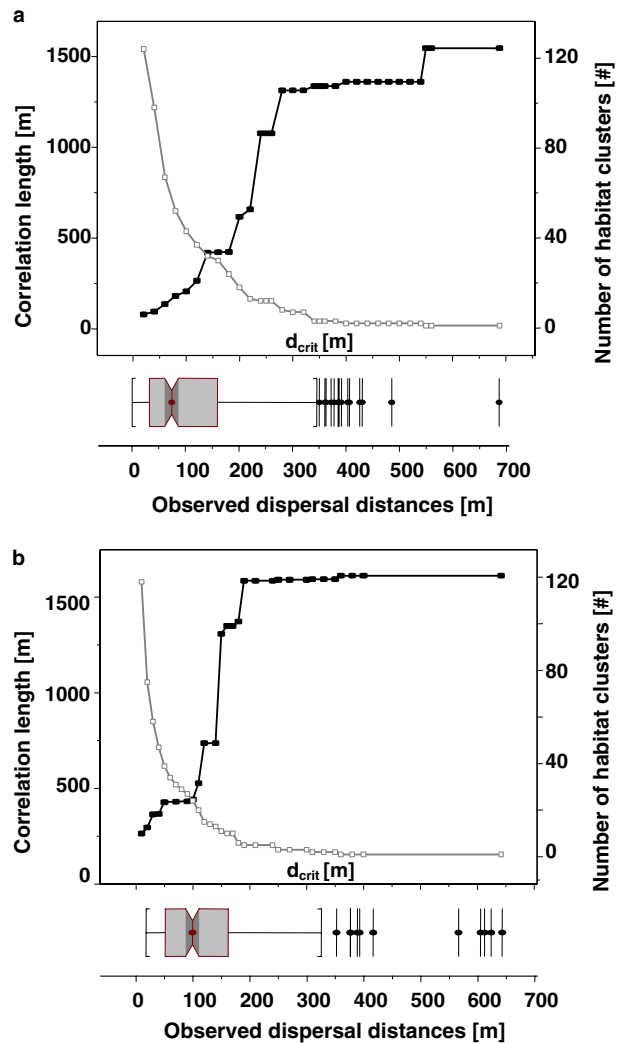


Fig. 4. Correlation lengths (black) and number of habitat clusters (gray) for different d_{crit} -values as well as boxplots of observed dispersal distances for (a) *Z. carniolica* ($n = 244$), and (b) *C. arcania* ($n = 216$).

4.1.2. Coenonympha arcania

According to Ebert and Rennwald (1991), *C. arcania* has a preference for abandoned or extensively used grasslands, thermophile fringes and bush complexes. This agrees well with our results. On early used patches the preferred nutrient poor grasses are missing. The preferred larval food plant *Brachypodium pinnatum* (Hermann pers. commun.) typically grows in semi-arid grasslands (Oberdorfer, 2001). Bink (1992) states a preference for ecotones of open land, hedges and forest margins which offer more balanced microclimatic conditions favored by the species. The high percentage of woody elements found in the preferred habitat types confirms this assumption. Furthermore, shrubs are used for territorial behavior and sun basking (Ebert and Rennwald, 1991). This might be another reason for the positive influence of succession (see also Ebert and Rennwald, 1991, Höhfeld unpubl. data). Within the research area,

steeply inclined hills are preferred habitats of *C. arcania*. On the one hand, slopes might provide a warmer and thus more favorable microclimate (Weiss and Weiss, 1998). On the other hand, this preference might rather reflect the low land use intensity on these sites.

We could not show a significant influence of management type. This might be due to the limited number of plots that were not mown. Ebert and Rennwald (1991) assume that *C. arcania* is particularly sensitive to fertilization and mowing. SBN (1991) recommends partial mowing or low intensity grazing, as strong bush encroachment or succession also may pose a threat to the species. This is reflected in our models where 'Prop-Hedge.25' shows a unimodal response. In the (thermophile) forests covering parts of the research area we did not encounter any *C. arcania* adults. Pre-forest stages as well as forest margins however are inhabited by the species (Ebert and Rennwald, 1991; Feldmann et al., 2000).

The combination of the two landscape context variables clearly shows the strong association of *C. arcania* to a complex of habitat types. An extended area of shrubs without nutrient poor grassland reduces butterfly occurrence as well as nutrient poor grassland without any shrubs. The best habitats of *C. arcania* are larger complexes of extensively managed and semi-arid grasslands (within a radius of 100 m), with locally high shrub/hedge cover (up to 80%). Irregular or late management (after mid July) as well as presence of single trees increase occurrence probability. This fits into the general characterization of the species as limited to mosaic-structured landscapes (Bink, 1992). Landscape context regarding distances larger than 100 to 150 m seems to have low impact on the presence of *C. arcania*. This agrees with the results of the MRR study of Höhfeld (unpubl. data), where most adults reached home ranges between 100 and 150 m. Bink (1992) estimates the area requirements for a population of *C. arcania* to be approximately 4 ha (which equals a radius of 110 m).

4.2. Model validation

The models of *Z. carniolica* could both be transferred in space but the simple model which yields the weakest performance failed the test of temporal transferability. In case of *C. arcania*, transfer in time was significant. For the complex model however, spatial transfer to the Leutratl was not significant. This might be mainly due to the low number of sampling sites ($n = 18$) and the low variability of habitat conditions regarding management and inclination (cf. Hein et al., unpublished). Overall, after internal validation the best multiple models show an outstanding performance, the simpler area-wide models performed still excellent. Even though not every model transfer was successful, the models are quite robust.

4.3. Habitat connectivity analysis

In addition to habitat quality, species' occurrence probability is also influenced by spatial factors, like isolation and patch size affecting spatial population dynamics (Thomas et al., 1992, 2001; Hanski and Gilpin, 1997; Wahlberg et al., 2002). In our approach, population dynamic factors were not considered due to the static nature of habitat models (Guisan and Zimmermann, 2000). However, by carrying out a habitat connectivity analysis based on habitat model derived suitability maps and mark recapture studies, we considered the spatial arrangement of landscape elements. Our results show that the resulting habitat pattern is more connected for *C. arcania* than for *Z. carniolica*. Nonetheless, in this context, we have to consider the scale on which the organisms interact with landscape patterns (van Langefelde, 2000; D'Eon et al., 2002). On a comparatively small spatial scale the studied species are significantly affected by the area of suitable habitat. This can be seen by the strong influence of landscape context variables (radii of 25–100 m). The correlation lengths however were far larger than the scale on which landscape context had an effect. Considering the distribution of observed flight distances found in the mark recapture studies (Fig. 4 bottom panels), suitable patches are highly connected for both species. Thus, a closely linked habitat network among all subpopulations is extremely likely. Additionally, we did not find a negative impact of small patch sizes and small-scale isolation on butterfly presence. Evidently, for both species a comparatively low proportion of habitat (7% for *Z. carniolica*, and 19% for *C. arcania*) may be sufficient to allow for connectivity, if habitat patches are adequately arranged like in the landscape under study. Dennis and Eales (1997) assume that isolation becomes a prominent factor only in case of large-scale site extinction. This is confirmed by Krauss et al. (2004) for *Cupido minimus*: while isolation did not play an important role for patch occupancy in landscapes with general high habitat quality, distribution was clearly more scattered in sub-optimal landscapes (see also Baguette et al., 2000; Binzenhöfer, 2005).

4.4. Implications for nature conservation

Our results show, that simple models – taking into account only a few predictor variables – yield good to very good predictive performances for both species. The models estimated for area-wide application had poorer, but still reasonable quality compared to the 'best' models. For these models, all variables could be derived from a map of habitat types and the DTM. This information is available for many regions. Our models agree very well with literature information on habitat requirements of the studied species, which makes them meaningful not

only from a statistical, but also from an ecological point of view. They are validated in time and space. This implies that the models (1) enable reliable predictions for other regions with similar biotope configurations and comparable management regimes in a fast and cost-effective manner and (2) can be implemented into a landscape model to simulate the effects of land use changes on an ensemble of plant and animal species (Rudner et al., 2004; Schröder et al., 2004). Therefore, these habitat models are highly relevant for species and nature conservation.

Referring to observed dispersal distances of single individuals our results demonstrate that the surveyed landscape is highly connected regarding both species, although it shows considerable fragmentation on smaller spatial scales especially for *Z. carniolica*. The habitat network of *C. arcania* is considerably larger, due to a higher amount of suitable habitat for this species and a suitable spatial configuration of these patches. Therefore, connectivity is species and landscape specific (Wiens et al., 1997; Tischendorf and Fahrig, 2000; D'Eon et al., 2002); it depends on the species' habitat requirements (see habitat models) and vagility (see results from mark recapture studies) as well as the spatial configuration of habitat patches (see habitat connectivity analysis). These aspects should be taken into account for nature conservation.

5. Conclusions

In regions with high density of suitable habitat patches, habitat quality is the main driving factor for patch occupancy of butterflies and moths. Even if an effect of isolation and habitat size on species occurrence is not detectable, landscape context might still play an important role on smaller and larger scales. Therefore, investigations of habitat preferences should always be taken on different spatial scales (cf. e.g., Fischer et al., 2004; Oppel et al., 2004). Although this paper shows results for only two target species, the methods proposed can easily be transferred to other species and taxa. Habitat distribution modelling by means of logistic regression is an established method (cf. e.g., Deng and Zheng, 2004; Gibson et al., 2004a,b; Hilbert et al., 2004; Poirazidis et al., 2004; Posillico et al., 2004; Shriver et al., 2004; Silva et al., 2004). We encourage wider application of the powerful connectivity analysis via landscape graphs in ecological research (e.g., van Langefelde, 2000; Roshier et al., 2001; Söndgerath and Schröder, 2002; Pyke, 2005).

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