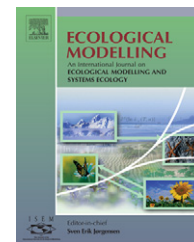


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## Living on the edge—Modelling habitat suitability for species at the edge of their fundamental niche

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### ABSTRACT

Predictive species distribution models have become increasingly common in conservation management. Among them, envelope-based approaches like the Ecological Niche Factor Analysis (ENFA) are particularly advantageous, as they require only presence data. Based on the assumption that the absolute frequency of species presence is a direct indicator of habitat suitability (HS), habitat suitability indices (HSI) are computed. However, this assumption may be misleading when the scarcity of optimal habitat forces most of the individuals to live in suboptimal conditions. This often happens when the environmental conditions in the study area represent only a marginal part of the species fundamental niche.

In this study we propose three new HS algorithms for ENFA models, which address such 'edge of niche' situations. The first algorithm (area-adjusted median,  $M_a$ ) takes the availability of environmental conditions in the study area into account, the second (median + extremum,  $M_e$ ) addresses situations where the species' optimum is at or beyond the extremum of the investigated environmental gradient, and the third (area-adjusted median + extremum,  $M_{ae}$ ) combines both approaches. These algorithms were applied to two populations of capercaillie (*Tetrao urogallus*), situated in different positions relative to the environmental gradient represented in the respective study area, and compared with the classical median algorithm ( $M$ ). We evaluated the models using cross-validation and a comparison with an expert model based on external data.

In both study areas, the HS maps obtained with the three new algorithms differed visibly from those calculated with the median algorithm. Cross-validation and comparison with external data showed that the new algorithms always provided better models, with the extremum-based algorithms ( $M_e$  and  $M_{ae}$ ) performing best. We conclude that the new algorithms can extend the applicability of ENFA-models to a broader range of conservation-relevant species by improving HS calculations for skewed species–habitat relationships in marginal habitats.

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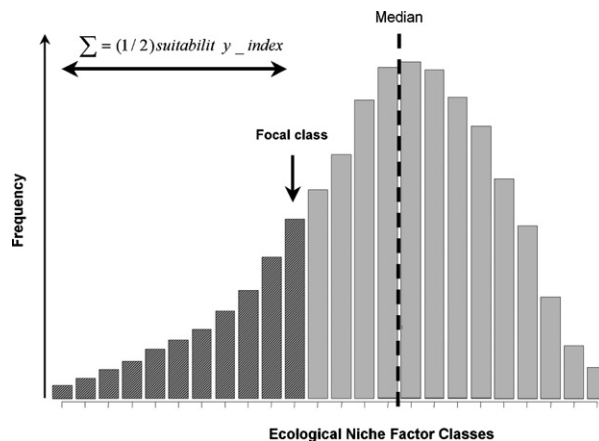
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## 1. Introduction

The rapid development of geographic information systems (GIS) and the growing availability of digital landscape data have increased the importance of predictive species distribution models for the identification of conservation priority sites (e.g., Mladenoff and Sickley, 1998; Schadt et al., 2002; Guisan and Thuiller, 2005; Olivier and Wotherspoon, 2006; Tole, 2006). The basic assumption behind these models is that individuals select sites that offer a suitable set of environmental conditions. Thus, given a set of sites known to host the focal species, it is theoretically possible to reconstruct its habitat selection pattern, i.e., to build the species' environmental niche (*sensu* Grinnell, 1917 and Hutchinson's fundamental niche, 1957) model. Assuming that the frequency of species occurrences reflects habitat suitability (HS), this model allows for the computation of an HS index (HSI) for any site with known environmental conditions, and thus the drawing of a habitat suitability map. Although the details of modelling may vary greatly between methods (Guisan and Zimmermann, 2000), the above assumption remains.

However, various factors can perturb this ideal relationship between habitat suitability and species occurrence (e.g., Holt and Keitt, 2000; Pulliam, 2000; Titeux, 2006). Apart from source-sink dynamics that allow a species to occur in sub-optimal habitats close to a source population (Pulliam, 1988; James et al., 1984), or dispersal limitations that can prevent the colonisation of suitable habitats (Pulliam, 2000), environmental changes and habitat deterioration can force a species to relocate to suboptimal habitats (Austin, 2002). This process, frequently recorded for conservation-relevant species in isolated populations, can lead to a skewed species–habitat relationship, creating a bias in the results of habitat suitability models. In particular, it can have a major effect when the environmental conditions in the study area represent only a marginal part of the species' fundamental niche (Hirzel and Arlettaz, 2003a). Such 'edge of niche' situations often, but not necessarily, occur at the margins of species' geographic distributions.

Of the predictive species distribution models, environmental envelope techniques (e.g., Busby, 1991; Walker and Cocks, 1991; Carpenter et al., 1993; Hirzel et al., 2002) represent the most direct implementation of Hutchinson's niche concept, as they strive to enclose the  $n$ -dimensional hypervolume of a species' niche within an environmental envelope. In practical conservation management, where reliable species absence data are often difficult to obtain (e.g., Zaniwski et al., 2002; Ottaviani et al., 2004), these approaches offer a fundamental advantage as they require only presence data. The Ecological Niche Factor Analysis (ENFA, Hirzel et al., 2002), implemented in the Biomapper 4 software (Hirzel et al., 2007) represents such an envelope-based approach to HS modelling. First, redundancies in the environmental predictors are removed as the latter are replaced by a few uncorrelated factors summarising most of the environmental information. To calculate HS scores from these ENFA factors, several algorithms have been developed (Hirzel et al., 2002; Hirzel and Arlettaz, 2003a,b). All of them refer to the species frequency distribution on each factor, and assume that the environmen-

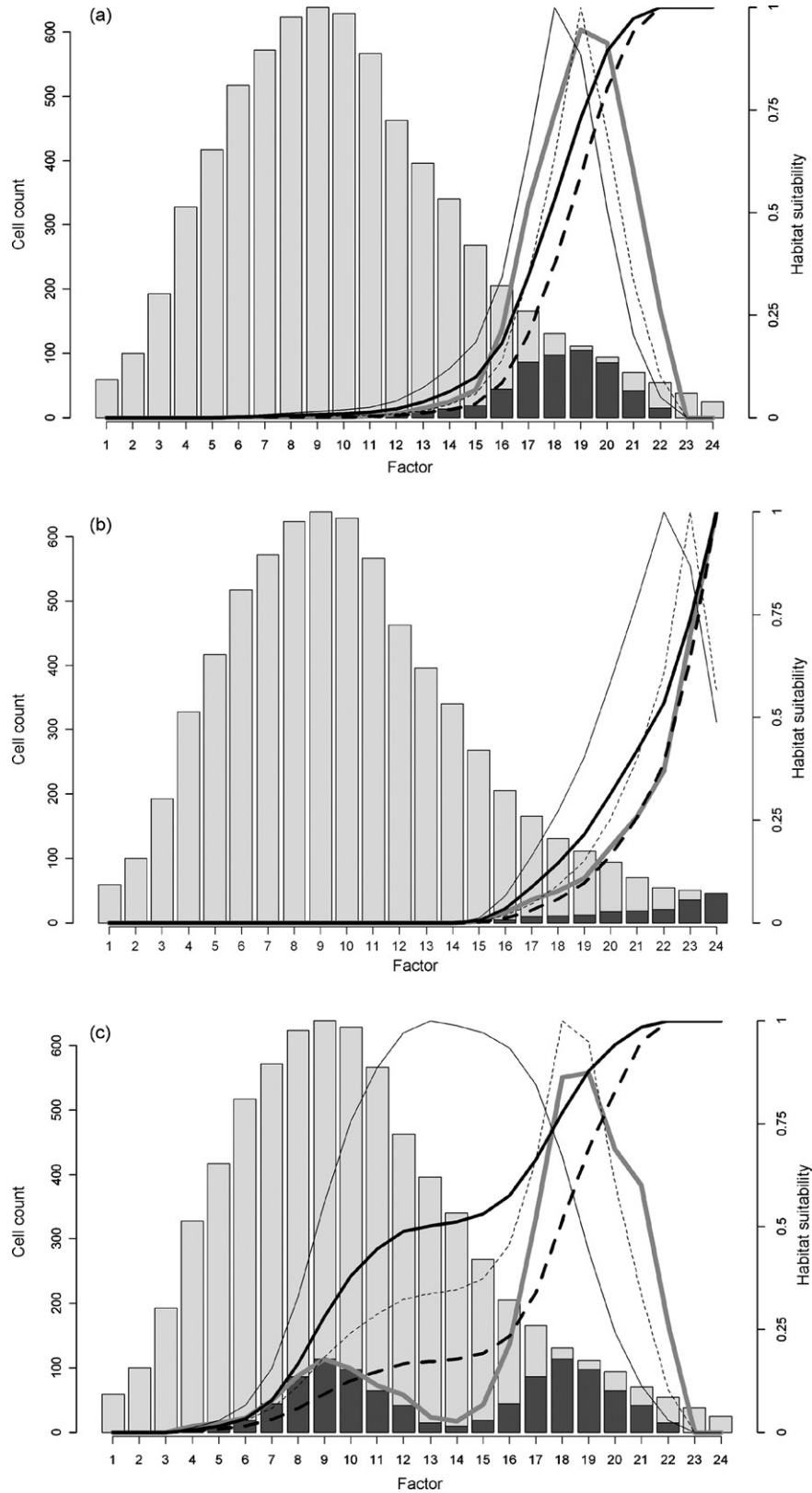


**Fig. 1 – Partial habitat suitability calculation on one factor using the median algorithm. The suitability of any cell in the study area is calculated from its location (arrow) relative to the median (dotted line) and is proportional to the area under the tail (dark grey) of the species distribution (histogram). The final HS is the weighted mean of partial suitability on all factors (from Hirzel et al., 2002, modified).**

tal conditions are optimal where the species is most frequently found. In the 'median algorithm', this optimum is represented by the median of the species frequency distribution, assuming it to be unimodal and symmetrical. The habitat suitability score of each point within the study area is then derived from its distance to the median (Fig. 1). However, when applying these approaches to species occupying marginal habitats situated at the edge of the species' environmental niche, the following problems may occur (see also Sachot, 2002; Hirzel and Arlettaz, 2003a):

- (1) Habitat suitability is calculated from the absolute frequency distribution of species occurrence, whereas the availability of habitat conditions is not taken into account. If optimal habitat is rare in the investigated area, and the species is forced to occupy suboptimal areas, the median of the species distribution is shifted towards suboptimal conditions. Consequently, the assumed optimum is misplaced, although 'real' optimal conditions may be more frequently occupied relative to their availability (Fig. 2a and c as a special case).
- (2) If the study area is restricted to an edge of the species' fundamental niche, optimal habitat conditions may lie at or even beyond the observed environmental range. In this case, habitat suitability increases or decreases monotonically with increasing factor values. The median, again, does not indicate optimal conditions but is situated at suboptimal values (Fig. 2b). As the computed habitat suitability decreases to either side of the median of the species distribution, factor values that lie between the median and the 'true optimum' – i.e., the extremum of the global distribution – are underrated.

In this study we propose three modifications of the median algorithm to calculate HS values from ENFA factors in 'edge of niche situations'. Each algorithm deals with one or both



**Fig. 2 – Fictive examples of  $S_f/G_f$  distributions and the corresponding habitat suitability models obtained from the four algorithms. The bars represent cell distribution along the marginality factor (F1) (light grey: all 'global' cells ( $G_f$ ), dark grey: species cells ( $S_f$ )). Three different species frequency distributions ( $S_f$ ) are presented, namely (a) Gaussian, (b) skewed to extreme values on F1, and (c) bimodal. The grey line shows the ratio of species cells to global cells ( $S_f/G_f$ ), rescaled to values between 0 and 1. The black lines represent partial HS computed on the marginality factor by the four algorithms ( $M$ : continuous,  $M_a$ : dashed,  $M_e$ : bold continuous,  $M_{ae}$ : bold dashed).**

of the problems described. The first algorithm ( $M_a$ ) considers the relative availability of habitat conditions, the second ( $M_e$ ) addresses situations where the real optimum is located at an extremum or even outside of the investigated range of environmental conditions. The third ( $M_{ae}$ ) combines both approaches, as both problems can occur at the same time.

We chose the capercaillie (*Tetrao urogallus*) to test the algorithms because the aforementioned problems (1) and (2) have been recorded for this species (Sachot, 2002, Braunsch, unpublished data). This large forest grouse is an indicator of structurally rich, continuous forest habitats in cold winter climates (Scherzinger, 1989, 1991; Boag and Rolstad, 1991; Storch, 1993a, 1995; Cas and Adamic, 1998; Suter et al., 2002). Correspondingly, large, continuous populations are found in the boreal forest of Eurasia, whereas the mostly small, isolated (Segelbacher, 2002) and declining populations in Central Europe are restricted to mountain forests (Klaus et al., 1989; Klaus and Bergmann, 1994; Storch, 2000). In these regions, optimal habitat is limited by altitude, extensive habitat degradation and a high degree of topographic and anthropogenic fragmentation. We implemented the algorithms in Biomapper 4.0 (Hirzel et al., 2007) and applied them to two Central European capercaillie populations, situated in different positions relative to the environmental gradient represented in the respective study area. We compared the results to those obtained with the regular median algorithm (M), tested the influence of sample size on algorithm performance and compared the modelled HS maps with the results of an expert model based on independent field data. The practical aim of this study was to enhance the applicability of ENFA models in the context of species conservation by providing a method to calculate habitat suitability in study areas that are restricted to an edge of a species' environmental niche.

## 2. Methods

Before applying the HS algorithms presented here, the environmental predictor variables must be summarised into a few uncorrelated, ecologically relevant factors, by means of the Ecological Niche Factor Analysis (Hirzel et al., 2002). The first factor explains the species' marginality, i.e., the difference between the average conditions in the sites where the species occurs (species distribution) and those in the entire study area (global distribution), thus indicating the position of the niche in the environmental space. The other factors explain the specialisation, i.e., the ratio of global variance to species variance, thus indicating the niche breadth.

### 2.1. Algorithms for HS calculation

Like the median algorithm (M), the three new algorithms (area-adjusted median ( $M_a$ ), median+extremum ( $M_e$ ) and area-adjusted median+extremum ( $M_{ae}$ )) work on a GIS grid representation of the study area. They require three inputs: (1) for all  $N_g$  grid cells in the global study area, the values of  $N_f$  uncorrelated, quantitative, spatial factors computed by the ENFA (Hirzel et al., 2002), reclassified into an even number of equal classes; (2) a set of  $N_s$  grid cells with ascertained species presence; (3) for each of the  $N_f$  factors, a weight  $w_f$  indicating

its importance for the species' niche (factors' eigenvalue provided by the ENFA, Hirzel et al., 2002). All algorithms are based on the frequency distribution of species presence on the factors ( $S_{f,i}$  = number of species presence cells in the  $i$ th class of factor  $f$  divided by the total number of species presences  $N_s$ ). Moreover, the two area-adjusted algorithms also use the frequency distribution of the whole study area ( $G_{f,i}$  = number of cells in the  $i$ th class of factor  $f$  divided by the global number of cells  $N_g$ , or global availability). For each cell  $c$ , the algorithm computes a partial habitat suitability  $H(f, c)$  for each factor  $f$  (see details below), which is weighted by  $w_f$ . The total habitat suitability is given by the weighted mean of all partial suitabilities (Eq. (1)):

$$H(c) = \frac{1}{\sum w_f} \sum_{f=1}^{N_f} w_f H(f, c) \quad (1)$$

The median algorithm (M) makes the assumption that, on all factors, the median of the species distribution indicates the optimal value. Mathematically, the suitability  $H_M(f, c)$  of predictor class  $c$  along factor  $f$  is given by Eq. (2):

$$H_M(f, c) = \begin{cases} 2 \sum_{i=1}^c S_{f,i}, & \text{if } c < \text{median}(S) \\ N_c & \\ 2 \sum_{i=c}^{N_c} S_{f,i}, & \text{if } c > \text{median}(S) \end{cases} \quad (2)$$

The partial suitability increases from 0 at the tails of the species distribution to 1 for the classes bracketing the median.

The area-adjusted median algorithm ( $M_a$ ), by contrast, compares habitat use to habitat availability to evaluate habitat selection. If a species is distributed randomly, the proportion of species records in the  $i$ th class of factor  $f$  ( $S_{f,i}$ ) is equal to its global availability ( $G_{f,i}$ ), i.e., the ratio  $S_{f,i}/G_{f,i} = 1$ . A ratio  $S_{f,i}/G_{f,i} > 1$  indicates positive selection, whereas  $S_{f,i}/G_{f,i} < 1$  indicates negative. The area-adjusted median algorithm ( $M_a$ ) assumes for all factors that the median of the ratio  $S_f/G_f$  indicates the optimal value. Mathematically, the suitability  $H_{Ma}(f, c)$  of predictor class  $c$  along factor  $f$  is given by Eq. (3):

$$H_{Ma}(f, c) = \begin{cases} 2 \sum_{i=1}^c \left( \frac{S_{f,i}}{G_{f,i}} \right), & \text{if } c < \text{median} \left( \frac{S}{G} \right) \\ N_c & \\ 2 \sum_{i=c}^{N_c} \left( \frac{S_{f,i}}{G_{f,i}} \right), & \text{if } c > \text{median} \left( \frac{S}{G} \right) \end{cases} \quad (3)$$

In this way, the class where the species is most abundant relative to the global availability is accorded the maximum suitability.

The median+extremum algorithm ( $M_e$ ) differentiates between the suitability explained by the marginality (marginality factor alone) and by the specialisation (all specialisation factors + specialisation part of the marginality factor) and assumes that, on the marginality factor, either the lowest or highest value indicates the optimal value, whereas on all specialisation factors it is the median (as in the M algorithm). Mathematically, the suitability  $H_{Me}(1, c)$  of

predictor class  $c$  along the marginality factor is given by Eq. (4):

$$H_{Me}(1, c) = \begin{cases} \sum_{i=1}^c S_{1,i}, & \text{if } \text{mean}(S) > \text{mean}(G) \\ \sum_{i=c}^{N_c} S_{1,i}, & \text{if } \text{mean}(G) > \text{mean}(S) \end{cases} \quad (4)$$

The marginality part of the suitability has a weight of 1. The specialisation part of the suitability is given by Eq. (2). Thus, on the marginality factor, the maximum suitability is given to the last (respectively first) class if the species distribution is biased towards the high (respectively low) values. For the other factors, partial suitability behaves as in the median algorithm.

The area-adjusted median + extremum algorithm ( $M_{ae}$ ) is a combination of the  $M_a$  and  $M_e$  algorithms. The marginality part of suitability is therefore given by Eq. (5):

$$H_{Mae}(1, c) = \begin{cases} \sum_{i=1}^c \frac{S_{1,i}}{G_{1,i}}, & \text{if } \text{mean}(S) > \text{mean}(G) \\ \sum_{i=c}^{N_c} \frac{S_{1,i}}{G_{1,i}}, & \text{if } \text{mean}(G) > \text{mean}(S) \end{cases} \quad (5)$$

with a weight of 1. The specialisation part of the suitability is given by Eq. (3). Examples for different patterns of  $S_f/G_f$  distributions and for the resulting habitat suitability models are given in Fig. 2.

## 2.2. Studied species

Due to its broad spatial and specific habitat requirements (e.g., Klaus et al., 1989; Storch, 1993a,b, 1995), and owing to its function as an umbrella species (e.g., Suter et al., 2002), the capercaillie is a popular model species for the analysis of species–habitat relationships in the field of conservation biology. The habitat requirements of capercaillie have been comprehensively investigated, primarily at the local scale (e.g., Gjerde et al., 1989; Helle et al., 1990; Storch, 1993a, 1995; Bollmann et al., 2005). At the landscape scale used in this study, species occurrence depends on a high proportion of forest cover dominated by conifer trees in regions with cold winter climate conditions. In addition, habitat suitability is positively influenced by the absence of human disturbance (e.g., roads, settlements) and agricultural land, as well as by gentle slopes and pronounced topographic exposition (Ménoni, 1994; Sachot, 2002; Storch, 2002; Graf et al., 2005; Braunisch and Suchant, 2007). However, regional differences in absolute predictor importance were observed (Sachot, 2002; Graf et al., 2006; Braunisch and Suchant, 2007).

## 2.3. Study areas

The study areas were selected so as to represent two contrasting parts of the environmental gradient. (1) The ‘Swiss Alps’ area is located in eastern Switzerland and comprises the biogeographic regions ‘eastern pre-Alps’ and ‘eastern central Alps’ (Gonseth et al., 2001). It covers 13,600 km<sup>2</sup>, with an eleva-

tion ranging from 350 to 4200 m a.s.l. Capercaillie habitats are located entirely between the two extremes of the altitudinal gradient in the study area, in the forested regions above 1000 m a.s.l. up to the upper natural tree line at 2300 m a.s.l. (Graf et al., 2005). The population size of capercaillie in the study area is estimated at about 320–380 males (Mollet et al., 2003). (2) The ‘Black Forest’ area is a forest-dominated lower mountain range in south-western Germany, defined by the eco-regions ‘Schwarzwald’ and ‘Baar-Wutach’ (Aldinger et al., 1998). It covers an area of about 7000 km<sup>2</sup>, with an elevation ranging from 120 to 1493 m a.s.l. Capercaillie is currently present on about 510 km<sup>2</sup> at the higher altitudes (above approximately 700 m a.s.l.), which represent extreme conditions in the study area with regard to the variables that are important to capercaillie (i.e., climate (low temperatures), forest fragmentation (low) and density of human infrastructure (low)). A total of 308 males were counted in 2006 (Braunisch and Suchant, 2006).

## 2.4. Species data

Capercaillie presence data for the Swiss Alps area stemmed from the capercaillie research project of the Swiss Federal Research Institute (WSL) and from regional inventories covering the period 1990–2004. Capercaillie data for the Black Forest originated from the grouse monitoring programme of the Forest Research Institute of Baden-Wuerttemberg (FVA). The programme assesses all direct and indirect evidence of capercaillie provided by foresters, hunters and ornithologists, as well as data collected during research projects (Braunisch and Suchant, 2006). Presence data were sampled from areas consecutively inhabited from 1988 to 2003. We chose a minimum distance of 300 m between presence points in both study areas to reduce biases from spatial autocorrelation. A total of 639 and 1600 presence points were used for the Swiss Alps and the Black Forest areas, respectively.

## 2.5. Environmental variables

We focused on indirect variables (Austin and Smith, 1989; Austin, 2002) at the landscape scale, which are often closely linked to the availability or development of direct resource variables and thus can replace a combination of them in a simple manner (Guisan et al., 1999; for capercaillie: Braunisch and Suchant, 2007). As the available data for the two study regions differed, we did not use the same set of environmental variables (EV) for both areas (Table 1a and 1b). We used the variables that were found to predict the species’ occurrence in the respective regions in earlier studies (Swiss Alps: Graf et al., 2005, 2006; Black Forest: Braunisch and Suchant, 2007). However, the most important EVs, namely the proportion of forest and its fragmentation, the macroclimate, the density of human infrastructure (roads) and topography (slope) were included in both models.

All EVs were prepared in raster maps with a 100 m × 100 m (Swiss Alps) and 30 m × 30 m (Black Forest) grid size. To convert the Boolean maps into continuous maps, the mean value for each variable within a 10-ha circular moving window was calculated, as this resolution was found to provide the best results in a previous study (Braunisch and Suchant, 2007). As multinormality was required for the ENFA, all variables were

**Table 1a – Environmental variables included in the model in the Swiss Alps (from Graf et al., 2005, modified)**

Variable category	Code	Variable description	Unit	Data source
Climate	TAVE	Average temperature (June)	°C × 100	DEM
Topography	SLOPE	Slope	°	DEM
	TOP	Topographic exposure	Index	DEM (Zimmermann and Roberts, 2001)
Forest	PFOR	Proportion of forest	% of area	PK25®2004, SWISSTOPO, DV033594
	FE	Density of forest edges	% of area	PK25®2004, SWISSTOPO, DV033594
Linear infrastructure	ROD	Density of roads	m/ha	Vector25®2004, SWISSTOPO, DV033594

**Table 1b – Environmental variables included in the model in the Black Forest (from Braunisch and Suchant, 2007, modified)**

Variable category	Code	Variable description	Unit	Data source
Climate	SNOWD	Number of days per year with snow cover > 10 cm	Days	Digital elevation model (DEM) (Schneider and Schönbein, 2003), Soil condition database
Soil conditions	SCVAL	Soil conditions, evaluated according to their potential to support suitable forest types	Index (1–15)	Soil condition database
Topography	SLOPE	Slope	°	DEM
Forest	FOALL	Proportion of forest	% of area	Landsat 5
	FCOMI	Proportion of coniferous and mixed forest	% of area	Landsat 5
	AGFOR	Proportion of forest edges bordering agricultural land (200 m width)	% of area	Landsat 5
Agriculture	AGALL	Proportion of agricultural land	% of area	Landsat 5
	AGDIST	Distance to agricultural land	m	Landsat 5
Settlements	URB	Proportion of settlements and urban area	% of area	Landsat 5
	URBDIST	Distance to settlements and urban area	m	Landsat 5
Linear infrastructure	STALL	Proportion of area influenced by roads (roads with 100 m buffer)	% of area	ATKIS
	STTRA	Roads weighted according to average traffic/day	% of area × traffic-index	ATKIS/Ministry of Traffic
	STDIST	Distance to roads	m	ATKIS

normalised using the Box–Cox algorithm (Box and Cox, 1964; Sokal and Rohlf, 1981). Maps were prepared in ArcView 3.3 (ESRI, 1996) and then converted to IDRISI (Eastman, 1990) format for use in Biomapper (Hirzel et al., 2007).

## 2.6. ENFA models

We calculated an ENFA model for each study area. As the  $S_f/G_f$  ratio might be sensitive to the sample size, we reduced the number of species records in the Swiss Alps ( $N = 639$ ) by recursively subsampling 320, 160 and 80 records, from which we calculated another three models. For all models, the number of significant factors retained for habitat suitability calculation was chosen according to the broken-stick heuristics (Jackson, 1993; Hirzel et al., 2002). Four habitat suitability maps were calculated from each model using each of the four algorithms ( $M$ ,  $M_a$ ,  $M_e$  and  $M_{ae}$ ).

## 2.7. Algorithm evaluation—cross-validation

We used 10-fold cross-validation (Fielding and Bell, 1997) to evaluate the HS models resulting from the four different algorithms. The presence data set was spatially split into 10 equal partitions, of which nine were used sequentially to calibrate the model, with the remaining partition used to evaluate it.

This provided 10 independent estimates of the evaluation index. Pairs of models were then compared by means of bootstraps with 1000 replicates.

The model quality was quantified using the continuous Boyce index (Hirzel et al., 2006), a threshold independent modification of the Boyce index (Boyce et al., 2002), which quantifies the relationship between the observed and expected number of validation points for different values of the HSI.

## 2.8. Algorithm evaluation—model comparison using external data

As model evaluation should preferably be based on both cross-validation techniques and independent data (Manel et al., 1999; Guisan and Zimmermann, 2000), we evaluated the HS maps by comparing them with the results of an expert model based on independent field data. For a subunit (98 km<sup>2</sup>) of the Black Forest study area we mapped capercaillie-relevant resource variables in the field: forest stand type, canopy closure, successional stage, height of ground vegetation, bilberry (*Vaccinium myrtillus*) cover and cover of naturally regenerated tree growth. In addition, we assessed slope and relative elevation above the farmland valley floor, as defined by Storch (2002). All variables were recorded for forest stand units, which

represent homogenously structured habitat patches of 1–50 ha in size. For each forest stand ( $N = 2211$ ), we combined the variables to a habitat suitability index for capercaillie ( $HSI_{year}$ ) using the expert model developed by Storch (2002). In addition, we calculated the mean HSI score for each forest stand with each of the four algorithms. We then correlated the expert HSI with each of the four ‘modelled’ HSIs using least square linear regression and Pearson’s  $R$  and used a two-sided test for differences between correlation coefficients (STATISTICA, StatSoft, 1999) to compare Pearsons’  $R_s$ . As the mapped resource variables defining the habitat suitability ( $HSI_{year}$ ) are largely determined by the variables included in the ENFA model (Braunisch and Suchant, 2007), it could be expected that the correlation between the expert HSI and a ‘modelled’ HSI would be the stronger, the better the respective algorithm performs in modelling habitat suitability.

### 3. Results

#### 3.1. ENFA results

Capercaillie exhibited a similar pattern of habitat selection in both study areas. Its habitats were characterised by a high proportion of forest cover (Swiss Alps (SA): PFOR mean: 74.8, S.D.: 25.6, Black Forest (BF): FOALL mean: 97.6, S.D.: 9.0) a low propor-

tion of area impacted by roads (SA: ROD mean: 10.6, S.D.: 20.6; BF: STALL mean: 5.2, S.D.: 17.4), an intermediate proportion of forest edge (SA: FE mean: 7.9, S.D.: 5.8; BF: AGFOR mean: 9.7, S.D.: 2.1), a moderate slope (SA: SLOPE mean: 19.5, S.D.: 7.1; BF: SLOPE mean: 12.9, S.D.: 7.1) and cold climate conditions (SA: TAVE mean: 1006.1, S.D.: 122.4; BF: SNOWD mean: 59.4, S.D.: 11.3). However, as the variables do not originate from the same source, their absolute values are not statistically comparable. The range of environmental conditions differed greatly between study areas and as capercaillie is situated in different positions with regard to the environmental gradient, major differences in the variables’ contributions to marginality and specialisation were recorded (Table 2). In the Swiss Alps the marginality factor was correlated most with the proportion of forest, which also revealed the highest contribution to explained specialisation (Table 2a). In The Black Forest the proportion of forest explained a high amount of specialisation as well, but marginality was mostly related to climate conditions, i.e., the number of days with snow (Table 2b).

#### 3.2. Species vs. global distribution—location of the species optimum

In both study areas the median of the species frequency distribution  $Med(S_f)$  on the marginality factor diverged from the median of the  $S_f/G_f$  distribution  $Med(S_f/G_f)$ . As expected from

**Table 2 – Contribution of the environmental variables to marginality (F1), specialisation (F1–F4) and explained information (F1–F4), presented for the significant factors of the ENFA models in (a) the Swiss Alps and (b) the Black Forest**

	F1 marginality (53.3%)	F2 spec. 1 (25.3%)	F3 spec. 2 (11.4%)	F4 spec. 3 (6.5%)	F1–F4 explained specialisation (96.5%)	F1–F4 explained information (98.3%)
<b>(a)</b>						
PFOR	0.772	0.222	0.356	−0.196	0.540	0.662
FE	0.464	0.027	0.171	−0.041	0.286	0.385
TOP	0.314	0.029	−0.609	0.502	0.287	0.304
SLOPE	−0.224	0.014	0.687	0.528	0.244	0.236
TAVE	0.195	−0.974	−0.048	0.646	0.412	0.308
ROD	−0.051	0.010	−0.014	−0.109	0.040	0.057
	F1 marginality (30.4%)	F2 spec. 1 (22.9%)	F3 spec. 2 (19.8%)	F4 spec. 3 (9.2%)	F1–F4 explained specialisation (82.3%)	F1–F4 explained information (91.2%)
<b>(b)</b>						
SNOWD	0.443	−0.066	−0.102	−0.009	0.171	0.320
AGDIST	0.334	0.002	0.115	0.010	0.126	0.240
STDIST	0.321	0.008	−0.005	0.001	0.101	0.221
URBDIST	0.314	−0.011	−0.021	−0.033	0.106	0.220
SCVAL	0.311	0.001	−0.022	−0.009	0.100	0.216
FCOMI	0.304	−0.022	−0.012	0.004	0.100	0.212
AGALL	−0.274	0.634	−0.799	−0.553	0.449	0.353
FOALL	0.271	0.770	−0.527	−0.701	0.441	0.348
AGFOR	−0.229	−0.002	0.237	0.056	0.123	0.181
STALL	−0.198	−0.008	0.039	−0.137	0.085	0.147
STTRA	−0.187	0.011	−0.036	0.129	0.081	0.139
URB	−0.151	−0.002	−0.031	−0.404	0.098	0.127
SLOPE	0.064	0.002	0.003	−0.010	0.022	0.045

Positive coefficient values in the marginality factor column indicate positive selection, whereas negative values indicate negative selection relative to the mean conditions in the study area. Variables are sorted by decreasing absolute coefficient values on F1. The numbers in parentheses indicate the amount of specialisation (the amount of information, last column) explained by the factors.

the species' position within the global range of environmental conditions, the  $S_f/G_f$  distribution in the Swiss Alps was skewed towards high value classes, but both its median and maximum were situated within the investigated range (Fig. 3a). In the Black Forest area,  $S_f/G_f$  increased monotonically with increasing factor values suggesting that the species' optimum is situated at the extremum or even beyond the global range (Fig. 3b). In both regions, this bias applied only to the marginality factor. In the specialisation factors, the  $S_f/G_f$  distribution fitted more tightly to the  $S_f$  distribution (results not shown).

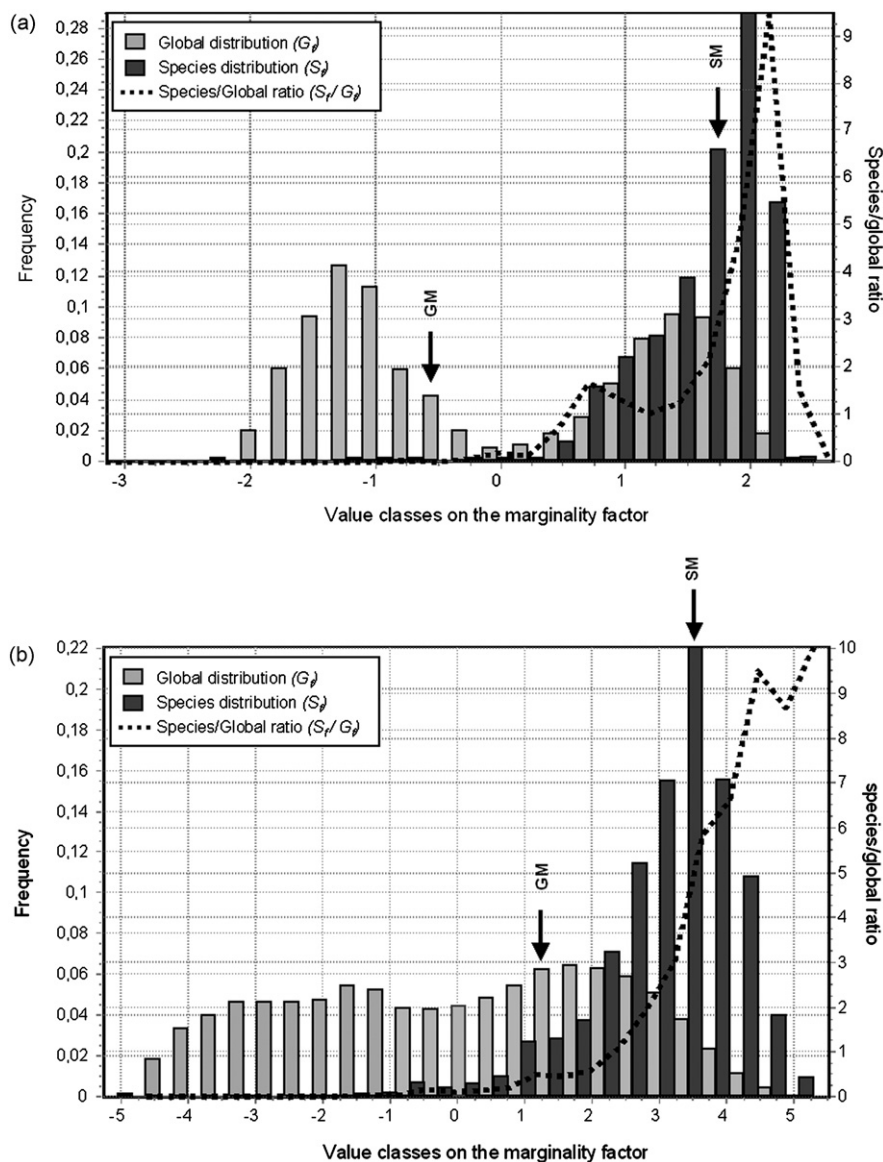
### 3.3. HS maps

The HS maps calculated with the four algorithms revealed different patterns (Fig. 4a–d). The M algorithm assigned the

highest scores to the margins of the habitat patches, while giving lower suitability to the core areas. By contrast,  $M_a$ ,  $M_e$  and  $M_{ae}$  increasingly dissolved this 'border effect' and assigned HSI scores that increased from habitat edges to core habitats. Similar results were found in the Swiss Alps study area (results not shown).

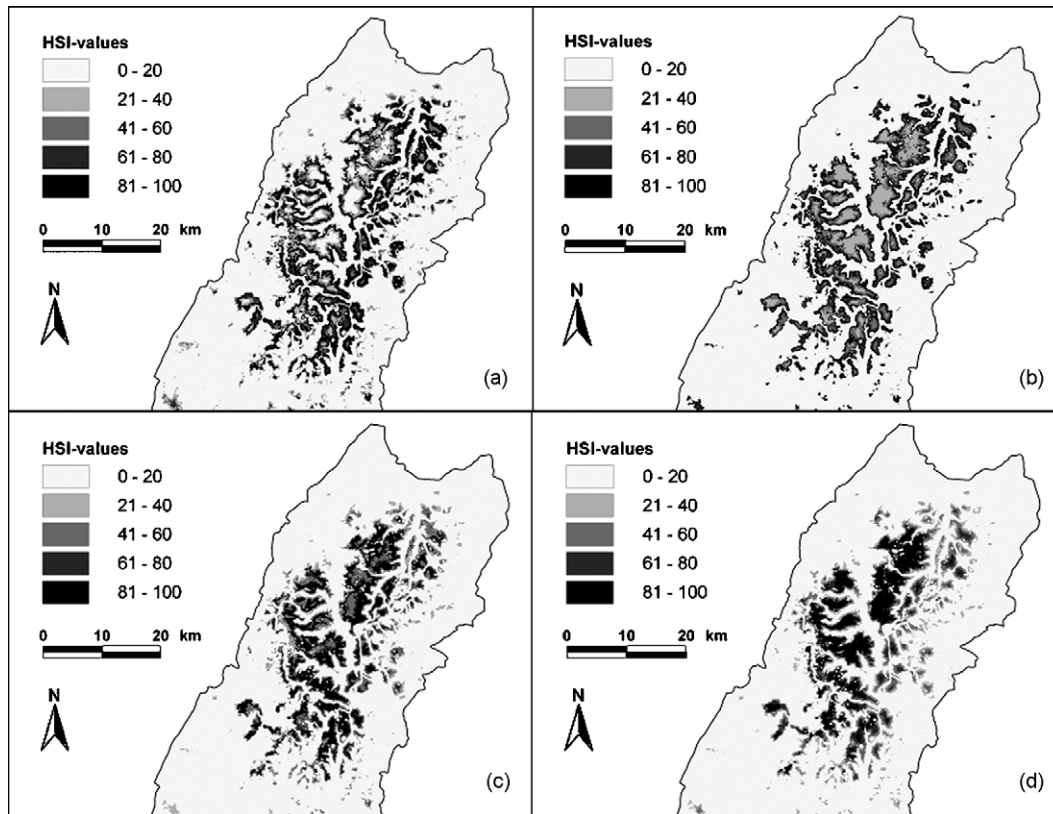
### 3.4. Cross-validation

According to the cross-validation results, all three new algorithms ( $M_a$ ,  $M_e$  and  $M_{ae}$ ) provided higher mean continuous Boyce indices than the median algorithm (Fig. 5a and b). This applied to both study areas, however, the differences were only significant for  $M/M_e$  and  $M/M_{ae}$  in the Swiss Alps. Moreover, the  $M_e$  performed better than  $M_a$  here. Whereas the model



**Fig. 3** – Frequency distribution of global and species cells on the marginality factor and ratio of species to global frequency in (a) the Swiss Alps and (b) the Black Forest. The medians of the global (GM) and species distribution (SM) are indicated. Both figures show that the species optimum, when defined by the median of the species distribution, diverges from the optimum that might be expected when comparing the selection of factor values relative to the abundance. This optimum is slightly shifted to the right in the Swiss Alps and the far right in the Black Forest.





**Fig. 4 – HSI maps resulting from the (a) median ( $M$ ), (b) area-adjusted median ( $M_a$ ), (c) median with extreme optimum ( $M_e$ ) and (d) area-adjusted median with extreme optimum ( $M_{ae}$ ) algorithms in the northern part of the Black Forest study area. The  $M$  algorithm assigns the highest scores to the margins of the habitat patches and a low suitability to the core areas. The new algorithms ( $M_a$ ,  $M_e$  and  $M_{ae}$ ) increasingly dissolve this 'border-effect'. HSI scores range from 0 to 100.**

quality increased from  $M$  over  $M_a$  and  $M_e$  to  $M_{ae}$  in the Swiss Alps, these differences were less pronounced in the Black Forest. Reducing the number of presence data led to a decrease in model quality irrespective of the algorithm (Fig. 6), the new algorithms were not more sensitive than the  $M$ . We concluded that  $M_e$  and  $M_{ae}$  tend to provide a higher predictive power than the median algorithm. The  $M_a$  also provides higher mean continuous Boyce indices, but suffers from a higher variance.

### 3.5. Model comparison using external data

The HSI scores of all four algorithms correlated significantly with the HSI obtained from field mappings and the expert

model (Table 3). Again, the new algorithms performed better than the regular median algorithm, with significantly higher correlation coefficients for  $M_e$  and the  $M_{ae}$ . In addition, the  $M_{ae}$  provided better results than the  $M_a$  and the  $M_e$ .

## 4. Discussion

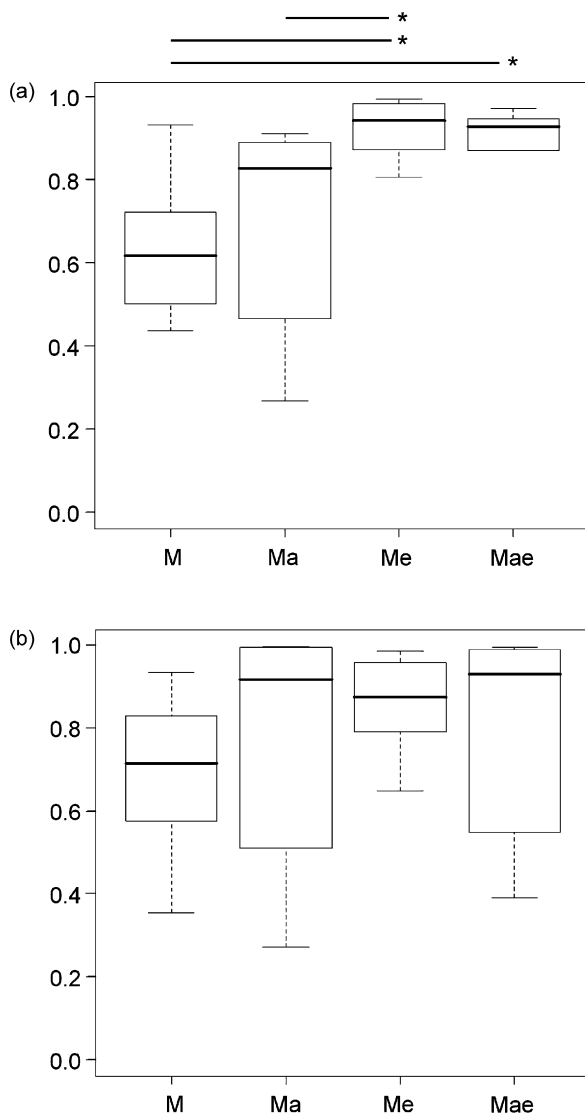
### 4.1. Algorithm performance with respect to the model species

Environmental envelope-based algorithms, which directly transform the absolute density of species records in the envi-

**Table 3 – Correlations between habitat suitability indices (HSI) obtained by the four algorithms (HSI  $M$ , HSI  $M_a$ , HSI  $M_e$ , HSI  $M_{ae}$ ) and HSI obtained by the expert model (HSI<sub>year</sub>) (a) and the pairwise differences between the correlation coefficients tested by using the two-sided test for correlation coefficients (STATISTICA, StatSoft 1999) (b)**

Pearson's R, level of significance (a)		Level of significance (b)		
		R (HSI $M$ –HSI year)	R (HSI $M_a$ –HSI year)	R (HSI $M_e$ –HSI year)
R (HSI $M$ –HSI year):	0.37***	–	–	–
R (HSI $M_a$ –HSI year):	0.41***	n.s.	–	–
R (HSI $M_e$ –HSI year):	0.43***	*	n.s.	–
R (HSI $M_{ae}$ –HSI year):	0.48***	***	**	*

(\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , n.s. not significant).



**Fig. 5 – Box plots of the 10 replicates of the continuous Boyce indices stemming from the cross-validation, computed for the four algorithms (M: median,  $M_a$ : area-adjusted median,  $M_e$ : median with extreme optimum,  $M_{ae}$ : area-adjusted median with extreme optimum). (a) Swiss Alps, (b) Black Forest. The bold line indicates the median, the box encompasses the interquartile range (IQ) and the whiskers the last data point within 1.5 times the IQ range. Significant differences (bootstraps, 1000 replicates, significance level:  $p < 0.05$ ) are indicated.**

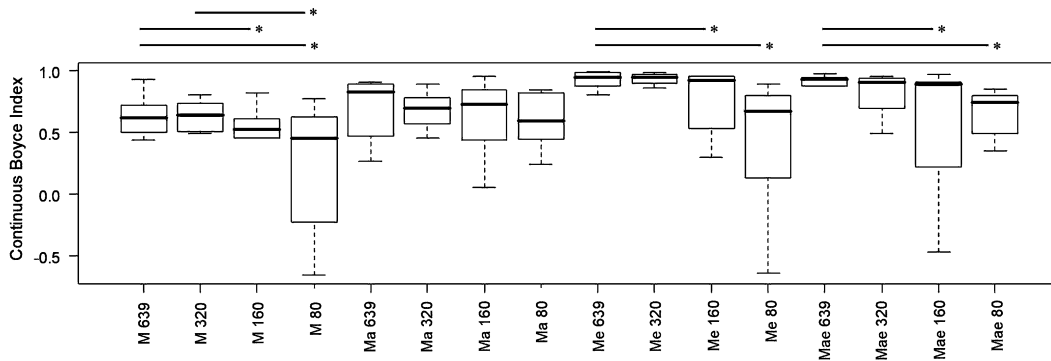
ronmental hyperspace into HS indices, tend to overestimate suboptimal and underestimate optimal habitats, when the species distribution is skewed towards suboptimal conditions. Using the example of capercaillie, this was demonstrated for the median algorithm here, but also applied to the other available algorithms such as the geometric mean, harmonic mean and minimum distance algorithm (cf. Hirzel and Arlettaz, 2003a,b) (results not shown).

The capercaillie is a relict species in Central Europe. Here, its distribution reaches its southern limit. Correspondingly,

most capercaillie habitats show characteristics of an edge situation with regard to the environmental niche of the species, which is mainly characterised by large, continuous conifer forests in cold winter climates with a low degree of human disturbance (Klaus et al., 1989, this study). Consequently, the availability of suitable conditions in Central Europe is a priori restricted to montaneous regions and limited by topographic constraints. Both investigated populations are geographically isolated at the continental scale (Segelbacher, 2002). Thus, habitat selection in these relict populations is entirely restricted to the conditions available within the study area and a shift to other areas is impossible. Ongoing habitat loss and fragmentation continues to cause population declines in both areas (Mollet et al., 2003; Braunisch and Suchant, 2006). As the investigated populations are not at equilibrium with their environment, it is likely that several species records represent inhabited suboptimal habitats. Moreover, there is strong evidence that both metapopulations consist of few large, self-sustaining source populations and several small, dependent sink populations (Segelbacher and Storch, 2002; Segelbacher et al., 2003; Segelbacher, in review), which contribute to a considerable proportion of the inhabited area—and species records. Although this study does not explicitly address skews of species–habitat interrelations due to source–sink dynamics, such processes are expected to increase such skews by supporting the persistence of capercaillie presence in suboptimal habitat conditions.

The marginal position of the study area in relation to the species' fundamental niche becomes particularly obvious in the Black Forest, where suitable habitats are mainly limited by the climatic–altitudinal gradient, which is also most correlated with the marginality factor. In the Swiss Alps an intermediary position is occupied with respect to this environmental dimension. Considering both these ecological considerations and the shape of the ( $S_f/G_f$ ) distribution on the marginality factor (skewed in the Swiss Alps and monotonically increasing in the Black Forest, Fig. 3), we expected that the  $M_a$  would perform best in the Swiss Alps study area, whereas an extremum-based algorithm ( $M_e$  or  $M_{ae}$ ) would provide better results for the Black Forest. Instead we obtained the best results from  $M_{ae}$  in both cases. However, in the Swiss Alps the marginality factor was most highly correlated with the variable 'forest abundance' (coefficient value  $f_1$ : 0.772). This variable can be regarded as a limiting resource in the Swiss Alps, where suitable forests are restricted to a comparatively narrow band along the mountain slopes. As habitat suitability increases monotonically along the 'forest availability' gradient, the 'true optimum' on the marginality factor may actually be located at the extremum, or even outside of the investigated range, although no species records were available in the extreme factor value class.

This highlights another potential application of the extremum-based algorithms. In the case of many variables (e.g., variables that quantify the availability of a resource or the distance to a source of disturbance), habitat suitability increases monotonically along a gradient. The same can apply to factors that are mainly correlated with such variables, especially the marginality factor which, by maximising the difference between global mean and species mean, expresses preferences for extreme conditions. In such situations the



**Fig. 6 – Box plots of the 10 replicates of the continuous Boyce indices stemming from the cross-validation, computed for the four algorithms (M: median,  $M_a$ : area-adjusted median,  $M_e$ : median with extreme optimum,  $M_{ae}$ : area-adjusted median with extreme optimum), comparing models based on different numbers of species records (639, 320, 160 and 80) in the Swiss Alps. The bold line indicates the median, the box encompasses the interquartile range (IQ) and the whiskers the last data point within 1.5 times the IQ range. Significant differences (bootstraps, 1000 replicates, significance level:  $p < 0.05$ ) are indicated.**

extremum-based algorithms ( $M_e$  and  $M_{ae}$ ) can improve the model results, as they differentiate between marginality and specialisation, when defining the species' optimum. This has been demonstrated for *Rhinolophus hipposideros*, an endangered bat species that is highly specialised on woodland habitats (Bontadina, Sattler and Braunisch, unpublished data) and *Lanius collurio* a bird species living in extensive farming landscapes (Titeux, Braunisch and Hirzel, unpublished data).

**4.2. Species optimum: median vs. maximum**

The  $S_f/G_f$  distributions and the respective HSI results (Fig. 2) suggest that it would have been sufficient to generate one single algorithm assuming the maximum of the species to global ratio  $\text{Max}(S_f/G_f)$  as optimum, instead of the median  $\text{Med}(S_f/G_f)$ . This could have superseded a differentiation between marginality factor and specialisation factors in the extremum-based algorithms. However,  $\text{Max}(S_f/G_f)$  turned out to be very sensitive to stochastic events, especially when the model was based on few presence data (results not presented). The  $\text{Med}(S_f/G_f)$  provided a more stable indicator of the species' optimum, which is comparable to the  $\text{Med}(S_f)$ . When reducing the number of presence data in the Swiss Alps, the cross-validation results for the area-adjusted algorithms ( $M_a$  and  $M_{ae}$ ) did not reveal a greater increase in variance than the algorithms based on the absolute frequency of species presence (M and  $M_e$ ). In fact, while a significant decrease in model performance was recorded for M,  $M_e$  and  $M_{ae}$  when using 160 presence points and less, no such effect was recorded for  $M_a$ . In addition,  $\text{Max}(S_f/G_f)$  closely coincides with  $\text{Med}(S_f/G_f)$  when the  $S_f/G_f$  distribution in the study area is bell-shaped.

**4.3. Evaluation by comparison with an expert model**

When employing data from other data sources, like vegetation mappings, there is always the risk that new uncertainties are introduced into the evaluation procedure (Guisan and Zimmermann, 2000; Zimmermann and Kienast, 1999). In our

study, these may include the following. First, the expert model quantifies habitat suitability based solely on topography and vegetation structure. Other influences, such as forest availability, forest fragmentation and human disturbance are not considered in the model of Storch (2002) and therefore could not be included. Second, the relationship between landscape scale variables and local scale forest structure is often overruled by human impacts (forestry) or stochastic events (windthrow, calamities), which can lead to great variance of forest structures in similar landscape conditions. Third, the variables included in the expert model were mapped for forest stand units whereas the EV included in the ENFA models referred to grid cells. We reduced the potential bias arising from different mapping resolutions by averaging the modelled HS values for each forest stand unit. Finally, the evaluation was conducted for a relatively small part of the study area.

Therefore, correlation coefficients between predicted and expert-based HSI scores were comparatively low, but nevertheless supported the cross-validation results and the visual pattern of the habitat suitability maps (Fig. 4a–d) by showing a significant improvement in model performance for the two extremum-based algorithms ( $M_e$  and  $M_{ae}$ ) and a slight, non-significant improvement for the  $M_a$ .

**4.4. Algorithm evaluation: limitations and future perspectives**

Algorithm performance was evaluated using cross-validation and the results of an expert model based on independent field data. In doing so the new algorithms were compared against each other and with the original median algorithm, providing an estimate of their relative performance. This relative estimate is expected to be valid, as the results of both evaluation steps corresponded, and as the algorithms revealed similar, sometimes even more pronounced results when applied to other conservation-relevant species in 'edge of niche' situations (e.g., *R. hipposideros*, *L. collurio*, *Gypaetus barbatus*, *Alauda arvensis*) (results not presented). However, as we do not know the 'truth', neither with regard to the actual spatial pattern of

habitat suitability in the study area nor to the validity of the expert model of Storch (2002), we were not able to determine the absolute effectiveness of the algorithms. Although the factors determining habitat suitability for capercaillie have been well studied (Storch, 1993a,b, 1995; Sachot, 2002; Graf et al., 2005; Braunisch and Suchant, 2007), Storch's expert model has been evaluated with data on capercaillie abundance and their changes in different Central European populations (Storch, 2002, Storch personal communication) and several other studies support the variable rating (Ménoni, 1994; Schroth, 1994; Suchant and Braunisch, 2004), it cannot be stated conclusively that the model is error free, particularly as some important habitat factors are not included.

Given the inherent problems of assessing the 'truth' for real species under field conditions, a quantitative determination of the absolute performance of the new algorithms might be achieved by testing them on a set of virtual species (e.g., Hirzel et al., 2001; Hirzel and Guisan, 2002) creating different patterns of species and habitat distributions and simulating different situations regarding the species' positions on the environmental gradient. This approach could also be used to compare the new algorithms to the other existing algorithms (e.g., geometric mean, harmonic mean, minimum distance algorithm) and will be an important issue of further investigation.

#### 4.5. Application

Restricting the range of environmental conditions over which niche-based models are calibrated to a small subset of the species' full environmental niche can strongly influence the estimation of the species' response curves, particularly at their outermost edges (e.g., Austin et al., 1990, 1994; Thuiller et al., 2004). This may reduce the models' applicability for extrapolation purposes; for instance, for predicting species-habitat interactions for other areas, times or climates (Austin and Meyers, 1996; Pearson and Dawson, 2003). For such objectives it would therefore be preferable to include most of the species' environmental gradient (Pearson et al., 2002), in order to obtain the best possible approximation of the modelled realised niche to the fundamental niche conditions, for example, by extending the study area to a large part of the entire species range (Beerling et al., 1995). This, however, often implies a reduced availability of data of adequate quality or spatial resolution and, consequently, a trade-off with model precision (e.g., Thuiller et al., 2003). In addition to data constraints, other practical or ecological reasons can cause restrictions of the considered environmental range. Many applied studies that address habitat selection patterns in order to delineate priority areas for species conservation are restricted to administrative units. Moreover, conservation-relevant species frequently occur in isolated habitats without spatial or functional connectivity to the core areas of the species distribution range. The aim of this study was, therefore, to provide cues for the identification of potential skews in species-habitat relations and to offer a method that allows the assignment of relative scores of habitat suitability within a study area, applicable without having information about the entire species range. As the HS scores within a study area always range between 0 and 100, the best habitat conditions in marginal areas would achieve the same absolute values as the best conditions in

study areas that cover the full range of suitable conditions. As this might be misinterpreted as an overestimation of habitat suitability in marginal conditions, we stress that the presented algorithms do not provide absolute measures of habitat suitability but rather relative scores valid for the extent of the study area, and not directly comparable with the HS scores of other areas.

Although developed specifically for 'edge of niche' situations, the new algorithms may also be advantageous in areas covering the full range of niche conditions. Problems with Gaussian response curves have been recorded for other modelling approaches as well, particularly in situations when habitat suitability is a linear or truncated linear function of the most relevant variables (cf. Hirzel et al., 2001), or when the species' true optimum is located at or near an extremum of the environmental gradient (e.g., Austin et al., 1990, 1994; Rydgren et al., 2003; Coudun and Gégout, 2006). As Biomapper provides a graphic representation of the species frequency distribution on the significant ENFA factors indicating the habitat selection pattern relative to global conditions in the study area, skews in species-habitat interrelations or non-Gaussian species response curves can be easily detected and the choice of the algorithm can be adjusted accordingly.

#### 4.6. Algorithm selection

As skewed  $S_f/G_f$  distributions and extreme optima may not only be due to the location of the study area but can also depend on the variables included in the model, different algorithms may provide the best results for the same species investigated in different situations. Therefore, we suggest that the distributions of  $S_f$  and  $S_f/G_f$  be compared. If  $\text{Med}(S_f)$  diverges from  $\text{Med}(S_f/G_f)$  (Fig. 2a), an area-adjusted algorithm is likely to improve the results of the model. The same applies for a bimodal distribution of  $S_f$  (Fig. 2c). If  $S_f/G_f$  either increases or decreases monotonically and  $\text{Max}(S_f/G_f)$  is located at one of the two extrema (Fig. 2b), an extremum-based algorithm is expected to perform best. This may not only happen in 'edge of niche situations' but also in situations where HS increases/decreases monotonically for the EVs that are most correlated with the marginality factor.

#### 4.7. Conclusions

Predictive species distribution models based on empirical data generally model the 'realised ecological niche' of a species relative to the environmental conditions within a predefined study area (Guisan and Zimmermann, 2000). If this area represents only an edge of a species' ecological niche and the species distribution is skewed towards suboptimal habitats (Hirzel and Arlettaz, 2003a), HS calculation techniques that refer to the absolute frequency of species presence can bias model results. Employing such results for decision-making in conservation management can even entail inadequate management implications, as discussed by Sachot (2002). In the case of capercaillie, as indicated by the HS map for the Black Forest, this would lead to a prioritisation of conservation activities in small forest patches and at the margins of suitable habitat, while disregarding the large unfragmented forest

patches with optimal climate conditions. The algorithms presented here relate the frequency of species presence to the availability of environmental conditions and thus evaluate species' habitat selection. This allows a relative gradation of habitat suitability that is at least valid within the study area. The shape of the species/global ratio distribution provides an important cue for the choice of the most appropriate algorithm. By improving HS modelling for species in marginal habitats, the new algorithms can expand the applicability of environmental envelope models such as ENFA models in conservation management.

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## REFERENCES

- Aldinger, E., Hübner, W., Michiels, H.G., Mühlhäußer, G., Schreiner, M., Wiebel, M., 1998. Überarbeitung der standortkundlichen regionalen Gliederung im südwestdeutschen Standortkundlichen Verfahren. *Mitteilungen des Vereins für Forstliche Standortserkundung und Forstpflanzenzüchtung* 39, 5–72 (in German).
- Austin, M.P., Smith, T.M., 1989. A new model for the continuum concept. *Vegetatio* 83, 35–47.
- Austin, M.P., Nicholls, A.O., Margules, C.R., 1990. Measurement of the realized qualitative niche: environmental niches of five eucalyptus species. *Ecol. Monogr.* 60/2, 161–177.
- Austin, M.P., Nicholls, A.O., Doherty, M.D., Meyers, J.A., 1994. Determining species response functions to an environmental gradient by means of a beta-function. *J. Veg. Sci.* 5, 215–228.
- Austin, M.P., Meyers, J.A., 1996. Current approaches to modelling the environmental niche of eucalypts: implications for management of forest biodiversity. *Forest Ecol. Manage.* 85, 95–106.
- Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Modell.* 157, 101–118.
- Beerling, D.J., Huntley, B., Bailey, J.P., 1995. Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surface. *J. Veg. Sci.* 6, 269–282.
- Boag, D.A., Rolstad, J., 1991. Aims and methods of managing forests for the conservation of tetraonids. *Ornis Scand.* 22, 225–226.
- Bollmann, K., Weibel, P., Graf, R.F., 2005. An analysis of central Alpine capercaillie spring habitat at the forest stand scale. *Forest Ecol. Manage.* 215, 307–318.
- Box, G.E.P., Cox, D.R., 1964. An analysis of transformation. *Roy. Stat. Soc. Ser. B* 26, 211–243.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecol. Modell.* 157, 281–300.
- Braunschweig, V., Suchant, R., 2006. Das Raufußhühner—Monitoring der FVA. In: *Berichte Freiburger Forstliche Forschung* 64, pp. 47–65 (in German).
- Braunschweig, V., Suchant, R., 2007. A model for evaluating the 'habitat potential' of a landscape for capercaillie (*Tetrao urogallus*): a tool for conservation planning. *Wildlife Biol.* 13/1, 21–33.
- Busby, J.R., 1991. BIOCLIM—a bioclimate analysis and prediction system. In: Margules, C.R., Austin, M.P. (Eds.), *Nature Conservation: cost Effective Biological Surveys and Data Analysis*. CSIRO, Melbourne (Chapter 10).
- Carpenter, G., Gillison, A.N., Winter, J., 1993. DOMAIN: a flexible modelling procedure for mapping potential distribution of plants, animals. *Biodiv. Conserv.* 2, 667–680.
- Cas, J., Adamic, M., 1998. The influence of forest alteration on the distribution of capercaillie leks in the Eastern Alps. *Zbornik* 57, 5–57.
- Coudun, C., Gégout, J.C., 2006. The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. *Ecol. Modell.* 199 (3), 164–175.
- Eastman, J.R., 1990. IDRISI—A grid-based geographic analysis system (User's Manual). Clark University, Worcester.
- ESRI, 1996. *Using ArcView GIS: User manual*. Environmental Systems Research Institute, Redlands, California, pp. 350.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Gjerde, I., Rolstad, J., Wegge, P., Larsen, B.B., 1989. Capercaillie leks in fragmented forests: a 10-year study of the Torstima population, Varaldskogen. In: *Transactions Congress International Union Game Biologist Trondheim*, vol. 19, Norway, pp. 454–459.
- Gonseth, Y., Wohlgemuth, T., Sansonnens, B., Buttler, A., 2001. Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. In: *Bundesamt für Umwelt, Wald und Landschaft (Eds.): Umwelt Materialien 137*, Bern 48 pp. (in German).
- Graf, R.F., Bollmann, K., Suter, W., Bugmann, H., 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. *Landscape Ecol.* 20, 703–717.
- Graf, R.F., Bollmann, K., Sachot, S., Suter, W., Bugmann, H., 2006. On the generality of habitat distribution models: a case study with capercaillie in three Swiss regions. *Ecography* 29, 319–328.
- Grinnell, J., 1917. The niche-relationships of the California Thrasher. *Auk* 34, 427–433.
- Guisan, A., Weiss, S.B., Weiss, A.D., 1999. GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology* 143, 107–122.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecological Modell.* 135, 147–186.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009.
- Helle, P., Jokimäki, J., Lindén, H., 1990. Habitat selection of the male capercaillie in northern Finland: a study based on radiotelemetry. *Suomen Riista* 36, 72–81.
- Hirzel, A.H., Helfer, V., Métral, F., 2001. Assessing habitat-suitability models with a virtual species. *Ecol. Modell.* 145/2, 111–121.
- Hirzel, A.H., Guisan, A., 2002. Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling* 157/2-3, 331–341.

- Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83, 2027–2036.
- Hirzel, A.H., Arlettaz, R., 2003a. Environmental-envelope based habitat-suitability models. In: Manly, B.F.J. (Ed.), 1st Conference on Resource Selection by Animals. Omnipress, Laramie, USA.
- Hirzel, A.H., Arlettaz, R., 2003b. Modelling habitat suitability for complex species distributions by the environmental-distance geometric mean. *Environ. Manage.* 32, 614–623.
- Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Modell.* 199, 142–152.
- Hirzel, A.H., Hausser, J., Perrin, N., 2007. Biomapper1.0–4.0. Lab. of Conservation Biology. Department of Ecology and Evolution, University of Lausanne, Switzerland (URL: <http://www.unil.ch/biomapper>).
- Holt, R.D., Keitt, T.H., 2000. Alternative causes for range limits: a metapopulation perspective. *Ecol. Lett.* 3, 41–47.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22, pp. 415–427.
- Jackson, D.A., 1993. Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology* 74, 2204–2214.
- James, F.C., Johnston, R.F., Wamer, N.O., Niemi, G.J., Boecklen, W.J., 1984. The Grinnellian niche of the Wood Thrush. *Am. Nat.* 124, 17–47.
- Klaus, S., Andreev, V., Bergmann, H.H., Müller, F., Porkert, J., Wiesner, J., 1989. Die Auerhühner—Die Neue Brehm-Bücherei, vol. 86. Westarp Wissenschaften, Magdeburg, 276 pp. (in German).
- Klaus, S., Bergmann, H.H., 1994. Distribution, status and limiting factors of capercaillie (*Tetrao urogallus*) in Central Europe, particularly in Germany, including an evaluation or reintroduction. *Gibier Faune Sauvage* 11/2, 99–124.
- Manel, S., Dias, J.M., Ormerod, S.J., 1999. Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. *Ecol. Modell.* 120, 337–347.
- Ménoni, E., 1994. Statut, évolution et facteurs limitants des populations françaises de grand tétras *Tetrao urogallus*: synthèse bibliographique. *Gibier Faune Sauvage Game and Wildlife* 11/1, 97–158 (in French with an English summary).
- Mladenoff, D.J., Sickley, T.A., 1998. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favourable habitat and potential population levels. *J. Wildlife Manage.* 62, 1–10.
- Mollet, P., Badilatti, B., Bollmann, K., Graf, R.F., Hess, R., Jenny, H., Mulhauser, B., Perrenoud, A., Rudmann, F., Sachont, S., Studer, J., 2003. Verbreitung und Bestand des Auerhuhns *Tetrao urogallus* in der Schweiz 2001 und ihre Veränderungen im 19. und 20. Jahrhundert. *Der Ornithologische Beobachter* 100, 67–86 (in German).
- Olivier, F., Wotherspoon, S.J., 2006. Modelling habitat selection using presence-only data: case study of a colonial hollow nesting bird, the snow petrel. *Ecol. Modell.* 195, 195–204.
- Ottaviani, D., Lasinio, G.J., Boitani, L., 2004. Two statistical methods to validate habitat suitability models using presence-only data. *Ecol. Modell.* 179, 417–443.
- Pearson, R.G., Dawson, T.P., Berry, P.M., Harrison, P.A., 2002. SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecol. Modell.* 154, 289–300.
- Pearson, R.G., Dawson, T.E., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeogr.* 12, 361–372.
- Pulliam, H.R., 1988. Sources, sinks and population regulation. *Am. Nat.* 137, 652–661.
- Pulliam, H.R., 2000. On the relationships between niche and distribution. *Ecol. Lett.* 3, 349–361.
- Rydgren, K., Økland, R.H., Økland, T., 2003. Species response curves along environmental gradients. A case study from SE Norwegian swamp forests. *J. Veg. Sci.* 14, 869–880.
- Sachot, S., 2002. Viability and management of an endangered capercaillie (*Tetrao urogallus*) metapopulation. These de doctorat, Faculté des Sciences de l'Université de Lausanne, Lausanne, 117 pp.
- Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczenski, P., Breitenmoser, U., Bufka, L., Cervený, J., Koubek, P., Huber, T., Stanisa, C., Trepl, L., 2002. Assessing the suitability of central European landscapes for the reintroduction of the Eurasian lynx. *J. Appl. Ecol.* 39/2, 189–203.
- Scherzinger, W., 1989. Biotopansprüche bedrohter Waldvogelarten und ihre Eingliederung in die Waldsukzession. *Stapfia/Linz* 20, 81–100 (in German).
- Scherzinger, W., 1991. Das Mosaik-Zyklus-Konzept aus der Sicht des zoologischen Artenschutzes. In: Bayerische Akademie für Naturschutz und Landschaftspflege (Ed.); Das Mosaik-Zyklus-Konzept und seine Bedeutung für den Naturschutz. *Laufener Seminarbeiträge* 5/91, pp. 30–42 (in German).
- Schneider, C., Schönbein, J., 2003. Klimatologische Analyse der Schneesicherheit und Beschneibarkeit von Wintersportgebieten in deutschen Mittelgebirgen. Gutachten für die Stiftung Sicherheit im Skisport des Deutschen Skiverbandes, 97 pp. (in German).
- Schroth, K.E., 1994. Zum Lebensraum des Auerhuhns (*Tetrao urogallus* L.) im Nordschwarzwald. *Mitteilungen der FVA Baden-Württemberg* 178, 133 (in German).
- Segelbacher, G., 2002. Genetic structure of capercaillie populations: a non-invasive approach at multiple spatial scales. Dissertation an der Technischen Universität München, 91 pp.
- Segelbacher, G., Storch, I., 2002. Capercaillie in the Alps: genetic evidence of metapopulation structure and population decline. *Mol. Ecol.* 11, 1669–1677.
- Segelbacher, G., Storch, I., Tomiuk, J., 2003. Genetic evidence of capercaillie *Tetrao urogallus* dispersal sources and sinks in the Alps. *Wildlife Biol.* 9, 267–272.
- Segelbacher, G., Sex specific fine scale genetic structure in a rapidly declining population of capercaillie. *Conservation Genetics* (in review).
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman and Co., New York, 887 pp.
- StatSoft Inc., 1999. *STATISTICA for Windows*. Edition '99. StatSoft Inc., OK, USA, 321 pp.
- Storch, I., 1993a. Habitat use and spacing of capercaillie in relation to forest fragmentation patterns. Dissertation, Universität München Fakultät für Biologie, 97 p.
- Storch, I., 1993b. Habitat selection by capercaillie in summer and autumn—is bilberry important? *Oecologia* 95, 257–265.
- Storch, I., 1995. Habitat requirements of capercaillie. In: *Proceedings of the 6th International Grouse Symposium*, pp. 151–154.
- Storch, I., 2000. Status survey and Conservation Action Plan 2000–2004: Grouse. WPA/BirdLife/SSC Grouse Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK and World Pheasant Association, Reading, UK, 112 pp.
- Storch, I., 2002. On spatial regulation in habitat models: can small-scale forest structure explain capercaillie numbers? *Conserv. Ecol.* 6 (online URL: <http://www.consecol.org/vol6/iss1/art6>).

- Suchant, R., Braunisch, V., 2004. Multidimensional habitat modelling in forest management—a case study using capercaillie in the Black Forest, Germany. *Ecol. Bull.* 51, 455–649.
- Suter, W., Graf, R.F., Hess, R., 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conserv. Biol.* 16, 778–788.
- Thuiller, W., Vayreda, J., Pino, J., Sabate, S., Lavorel, S., Gracia, C., 2003. Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). *Global Ecol. Biogeogr.* 12, 313–325.
- Thuiller, W., Brotons, L., Araújo, M.B., Lavorel, S., 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27, 165–172.
- Titeux, N., 2006. Modelling species distribution when habitat occupancy departs from suitability: application to birds in a landscape context. PhD Thesis. Université Catholique de Louvain, Belgique, 256 p.
- Tole, L., 2006. Choosing reserve sites probabilistically: a Colombian Amazon case study. *Ecol. Modell.* 194, 344–356.
- Walker, P.A., Cocks, K.D., 1991. HABITAT—a procedure for modeling a disjoint environmental envelope for a plant or animal species. *Global Ecol. Biogeogr.* 1, 108–118.
- Zaniewski, A.E., Lehmann, A., Overton, J.M.C., 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecol. Modell.* 157, 261–280.
- Zimmermann, N.E., Kienast, F., 1999. Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *J. Veg. Sci.* 10, 469–482.