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## Fitness-related parameters improve presence-only distribution modelling for conservation practice: The case of the red-backed shrike

Nicolas Titeux<sup>a,\*</sup>, Marc Dufrene<sup>b</sup>, Julien Radoux<sup>c</sup>, Alexandre H. Hirzel<sup>d</sup>, Pierre Defourny<sup>c</sup>

<sup>a</sup>Biodiversity Research Centre, Université catholique de Louvain, Croix du Sud 4-5, B-1348 Louvain-la-Neuve, Belgium

<sup>b</sup>Observatoire de la Faune, de la Flore et des Habitats, Ministère de la Région wallonne, Division Générale des Ressources Naturelles et de l'Environnement, Centre de Recherche de la Nature, des Forêts et du Bois, Avenue Maréchal Juin 23, B-5030 Gembloux, Belgium

<sup>c</sup>Department of Environmental Sciences and Land Use Planning, Université catholique de Louvain, Croix du Sud 2/16, B-1348 Louvain-la-Neuve, Belgium

<sup>d</sup>Department of Ecology and Evolution, University of Lausanne, Biophore, 1015 Lausanne, Switzerland

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### ABSTRACT

The red-backed shrike (*Lanius collurio* L.) is a bird living in human-altered agricultural areas that are managed by extensive farming techniques. This passerine species has declined significantly in Western Europe over the last 30–40 years. The development of efficient species-specific conservation strategies relies on fine-grained information about the ecological resources and environmental conditions that constitute its reproductive habitat in this agricultural landscape. Species distribution models are used increasingly in conservation biology to provide such information. Most studies investigate the environmental pattern of species distribution, assuming that species records are reliable indicators of habitat suitability. However, ecological theory on source-sink dynamics and ecological traps points out that some individuals may be located outside the environmental bounds of their species' reproductive niche. Those individuals could reduce model accuracy and limit model utility. Parameters related to the reproductive success of this shrike in Southern Belgium were integrated into a fine-scale presence-only modelling framework to demonstrate this problem and to address critical habitat requirements of this species relative to conservation management. Integrating reproductive parameters into the modelling framework showed that individuals occurred, but did not reproduce successfully, above a certain environmental threshold. This indicated that the reproductive niche of the shrike is ecologically narrower than standard practice in species distribution modelling would suggest. The major resources (nest sites availability, distance to human settlements, suitable perching sites, foraging areas and insect abundance) required for the reproduction of the red-backed shrike were quantified and ranked to offer concrete species-specific conservation management guidelines.

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\* Corresponding author: Tel.: +32 10 47 21 73; fax: +32 10 47 34 90.

E-mail addresses: [nicolas.titeux@uclouvain.be](mailto:nicolas.titeux@uclouvain.be) (N. Titeux), [M.dufrene@mrw.wallonie.be](mailto:M.dufrene@mrw.wallonie.be) (M. Dufrene), [radoux@mila.ucl.ac.be](mailto:radoux@mila.ucl.ac.be) (J. Radoux), [Alexandre.Hirzel@unil.ch](mailto:Alexandre.Hirzel@unil.ch) (A.H. Hirzel), [pierre.defourny@uclouvain.be](mailto:pierre.defourny@uclouvain.be) (P. Defourny).

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## 1. Introduction

The red-backed shrike (*Lanius collurio* L.) suffered a marked decline in Western and Northern Europe between 1970 and 1990 (Yosef, 1994). This decline continued less rapidly during the last decade (Lefranc and Worfolk, 1997; Lefranc, 2004). Although the causal factors remain unknown (Yosef, 1994), several reasons have been suggested, including reduction in suitable habitats, lack of food resources, climatic change and nest predation by corvids (Lefranc and Worfolk, 1997). Human development and agricultural intensification (e.g. intensive grazing or mowing, intensive monocultures, hedge removal, larger parcels or agrochemical use), as well as abandonment of agricultural activities in some areas (involving field encroachment, see Scozzafava and De Sanctis, 2006), lead to habitat loss, habitat deterioration and food shortage (Lefranc and Worfolk, 1997; Van Nieuwenhuysse, 1999). Therefore, the conservation of the red-backed shrike depends on European agricultural policy and how it is implemented regionally (Van Nieuwenhuysse, 1999).

Most Western European red-backed shrike populations breed in semi-open areas under a management regime of extensive farming (combination of livestock and hay production). The association between species presence and extensive farming in human-altered landscapes includes a range of occupied biotopes (Van Nieuwenhuysse and Vandekerckhove, 1992). Hence, one challenge is to detect the key environmental characteristics of shrike habitat-use. Breeding sites typically comprise scattered and thorny hedges and/or bushes (Van Nieuwenhuysse, 1998; Van Nieuwenhuysse et al., 1999; Lefranc, 2004) that are used as nest sites, vantage points for territory defence, perches on which the birds wait for the movement of prey (sit-and-wait strategy), or for storing prey items (mainly large insects). But there is a further need to collect and use accurate and fine-grained data about the ecological resources that make up the specific habitat of the red-backed shrike. Effective conservation strategies will likely benefit by incorporating data on breeding performance relative to habitat-use.

Species distribution models can provide useful information to assist shrike conservation. They relate species records to environmental descriptors through statistical functions (also called species response curves, Guisan and Zimmermann, 2000; Guisan et al., 2002; Rushton et al., 2004; Luoto et al., 2006). The projection of these functions into geographical space where environmental conditions are known, but where the species distribution is unknown, produces habitat suitability maps (Brotons et al., 2004; Rushton et al., 2004; Gibson et al., 2004a). The use of models to delineate suitable habitat of threatened species is of key significance for conservation biology (Seoane et al., 2006; Moisen et al., 2006), providing insights on species–environment relations and allowing the prioritization of management options amongst areas that vary in their contribution to regional species persistence (Araujo and Williams, 2000; Zaniwski et al., 2002; Guisan et al., 2006).

Most applications of species distribution models relate species records to coarse-scaled environmental descriptors like topography, climate or land-use variables (Engler et al., 2004; Brotons et al., 2004; Hirzel et al., 2004). Such approaches

are useful for describing large-scale distribution patterns, but they have also been criticized, especially for direct conservation implications (Guisan and Thuiller, 2005), transferability of models among areas (Guisan and Zimmermann, 2000; Vanreusel et al., 2007) and dubious (or at least unclear) ecological meaning in some cases (Austin, 2002; Heglund, 2002; Guisan and Thuiller, 2005). Only a few studies have focused on local and high-resolution applications of species distribution models (Seoane et al., 2006; Vanreusel and Van Dyck, 2007). A modelling focus on the ecological resources or environmental conditions that determine the functional interactions between organisms and their environment has recently been advocated (Dennis et al., 2003; Vanreusel and Van Dyck, 2007). This is of prime importance to address relevant local management strategies.

Besides selecting appropriate environmental descriptors, Austin (2002) stressed the importance of sound ecological theory when making and applying species distribution models. Guisan and Zimmermann (2000) argued that it is crucial to base the formulation of the model on an underlying conceptual framework backed by sound ecological knowledge about the focal species. In our case, the local pattern of settlement of a red-backed shrike population varies considerably between successive years, with not all suitable sites occupied each year (Van Nieuwenhuysse, 2000; Söderström, 2001). As a consequence, species absence data can give a confounding signal with no clear link to habitat suitability. Depending on species prevalence and tolerance (Hirzel et al., 2001; Brotons et al., 2004), this could entail severe limitations for building classical discrimination models that rely on presence–absence data, because these techniques assume that they indicate suitable and unsuitable environmental conditions, respectively (Guisan et al., 2002; Gu and Swihart, 2004; Engler et al., 2004; Guisan and Thuiller, 2005). Approaches based on presence-only data are in this case particularly advisable (Hirzel et al., 2001; Pearce and Boyce, 2005; Elith et al., 2006).

Based on Hutchinson's (1957) ecological niche paradigm, presence-only models delineate envelopes around species records in an environmental space (Pearce and Boyce, 2005), assuming that species records reflect suitable environmental conditions. However, ecological theory about source-sink dynamics (Pulliam and Danielson, 1991; Dunning et al., 1992) and ecological traps (Schlaepfer et al., 2002; Kristan, 2003) indicates that individuals may be located outside the bounds of the species niche (Pulliam, 2000). Beyond a certain environmental threshold, individuals may still be present but with insignificant reproductive success (Sarah et al., 2004; Guisan and Thuiller, 2005). Hence, such records could confuse the delineation of envelopes in the environmental space and should not be used to fit the models. This issue has often been ignored (but see Railsback et al., 2003; Olson et al., 2004) and most studies use indiscriminately all available species records (Guisan and Thuiller, 2005), without carefully testing what does and what does not constitute suitable habitat for the focal species (Pulliam, 2000).

Here we incorporate parameters related to the reproductive success of the red-backed shrike into a fine-scale presence-only modelling framework. First, we examine the main ecological resources and environmental conditions that make

up the shrike's reproductive niche. Second, we illustrate that failure to account for species records from habitat outside of the species niche may limit the utility of presence-only models in identifying suitable areas and species' critical habitat requirements. Finally, we discuss the implications of these findings for the conservation of the species in Western European agricultural areas.

## 2. Materials and methods

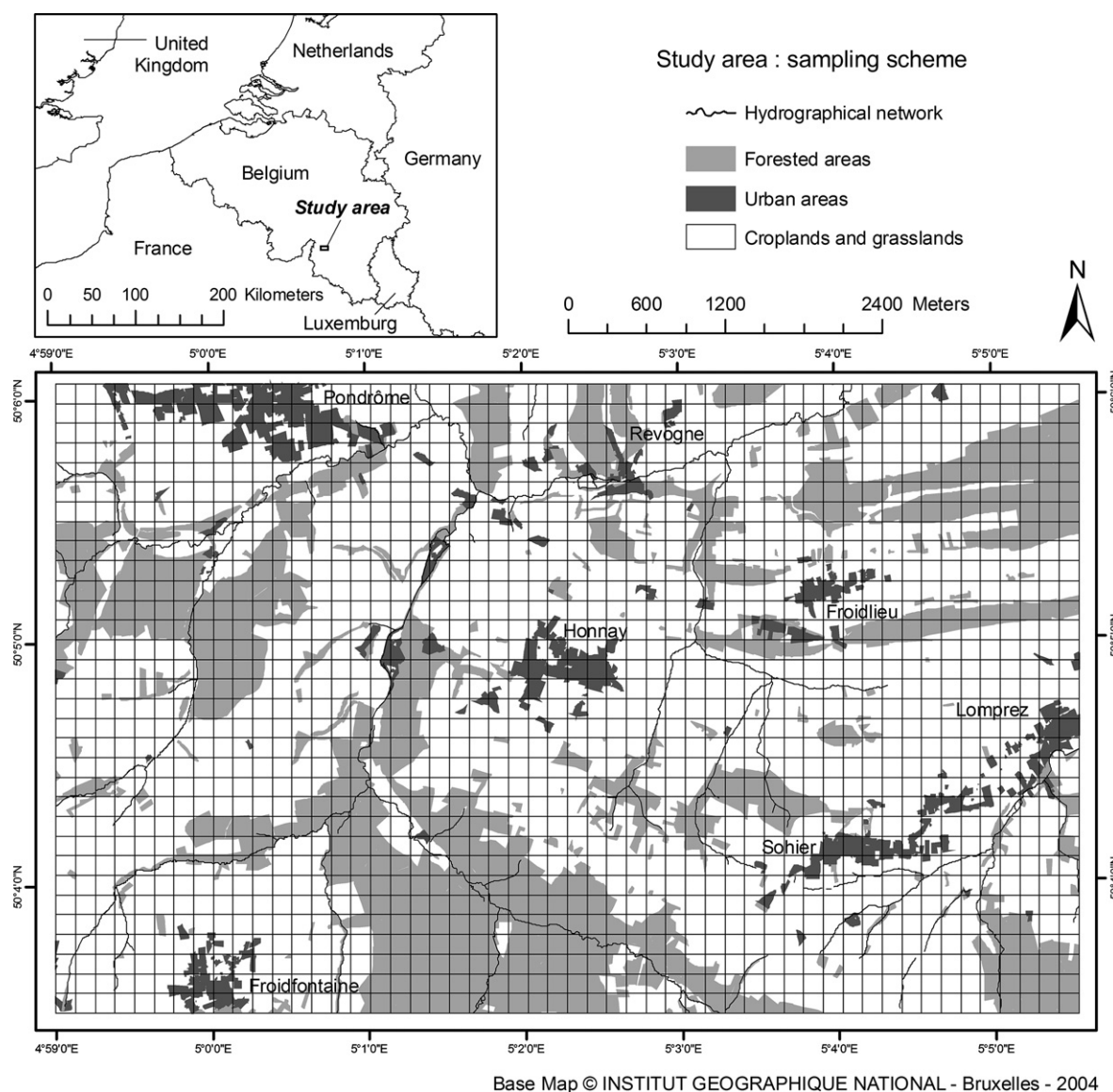
### 2.1. Study area

The study area (Fig. 1) covers about 38 km<sup>2</sup> in the Calestienne region (Southern Belgium). Calestienne is composed of numerous calcareous rocks forming a narrow west–east string of hills (altitude range: 170–300 m) interspersed with schistose areas. Hills are typically forested, while slopes and

depressions are pastured or cultivated depending on the soil. Small villages are scattered along the hydrographical network or between woodlands (Thill, 1964).

### 2.2. Species data

The study area was sampled according to a regular 150 m-resolution grid formed by 1664 square cells. Cell surface (2.25 ha) was close to the mean territory area of the red-backed shrike (about 1.5 ha, see Söderström, 2001; Karlsson, 2004; Lefranc, 2004). This sample unit size is a compromise between the spatial accuracy of the predictions, the scale on which key processes driving the local distribution pattern operate and the scale on which environmental data were collected. This match of scale is of key significance for understanding and quantifying species–environment relations (Van Horne, 2002; Wiens, 2002).



**Fig. 1** – Location of the study area, showing the 1664 150 m-resolution cells and the main villages. Croplands and grasslands are interspersed between forested and urban areas.

Territories of red-backed shrikes were surveyed during a comprehensive field survey in May–July 2005. All open areas were visited at least three times during the breeding season. Territory boundaries were delineated by connecting the outermost observations (15–20 per male) of territorial disputes or foraging during at least 20 min with sunshine and no wind. Territories were subsequently aggregated at the 150 m-resolution cell level. A value of 0 or 1 was assigned to each cell for absence or presence of the species, respectively. Depending on size and location, territories either covered up to three cells or were completely included within a single cell. In the first case, a value of 1 was assigned to cells when more than half of their surface was intersected by a territory. In the second case, a value of 1 was assigned to the cell whatever the territory size.

Various aspects of reproduction may serve as measures of breeding success, e.g. timing of breeding, clutch size, fledging success or fledgling weight (Leugger-Eggiman, 1997). While offspring production is an important component of breeding success, survival to their first breeding season is crucial for their contribution to future generations. Fledging success alone is not necessarily the best measure of parental fitness (Leugger-Eggiman, 1997), but it was assumed to be at least a relevant indicator of reproductive performance. Nesting pairs were considered successful if they produced at least one fledgling (Muller et al., 2005), because this information was relatively easy to collect accurately in the field.

Each record of an individual was allocated to (1) unpaired male, (2) unsuccessful pair (fledging failure) or (3) successful pair (fledging success). Replacement clutches following nesting failures and leading to fledging failure or success in the same cells were allocated to categories 2 or 3, respectively. Such pairs did not count twice.

### 2.3. Functional environmental descriptors

Fitting a distribution model relies on the existence of descriptors that define suitable environmental conditions for the species (Guisan and Zimmermann, 2000; Austin, 2002). Several existing environmental datasets were first combined using the GIS Software ArcGIS 8.3 (ESRI, 2002). A 30 m-resolution digital elevation model produced by the Belgian National Geographic Institute was used to describe the regional topography. A digital 1:20,000 vector soil map (I.R.S.I.A., 1966) allowed the derivation of soil descriptors. The 2004 edition of the 1:10,000 vector topographic map from the Belgian National Geographic Institute was used as a planimetric reference and for land use description.

In addition, data on a set of landscape elements were collected that may help to describe the species distribution. In particular, several types of point, linear and surface features were surveyed in the field during May–August 2004 and digitized from 40 cm-resolution aerial colour orthophotographs printed at 1:2500 edited by the Walloon Region in 1998. Landscape modifications between 2004 and 2005 were assumed negligible. Point and linear elements reported were trees and bushes on the one hand, and tree lines, hedges and fences on the other hand. Given their significance for the species' foraging and nesting ecology (Van Nieuwenhuysse, 1998; Karlsson, 2004; Lefranc, 2004), bushes and hedges were allo-

cated to (1) thorny or (2) others. The height of each point element, tree line and hedge fragment was recorded in the field.

Each homogeneous polygon of land was digitized in the field as a unique feature and classified into one of 31 vegetation types. EUNIS typology was followed for describing each feature. Some types were, however, subdivided according to the biological relevance in this specific context. In particular, the intensification of pastures was categorized into three classes according to the physiognomy and the floristic diversity of the grassland vegetation (Table 1).

Several functional environmental descriptors (Table 2) were computed and stored in GIS layers. They were designed on the basis of available ecological knowledge in order to integrate the major ecological resources (nest sites, food, foraging sites, predation pressure and anthropogenic disturbance) that determine the functional interactions between shrikes and their environment in the variety of biotopes they occupy (see functions and references in Table 2).

Most descriptors were calculated within the 150 m-resolution cells. Some of them needed finer spatial resolution since individuals may use resources that are restricted to some parts of their territories. These descriptors were computed using a 75 m-resolution grid. In contrast, to account for a wider neighbourhood, some descriptors were computed within 300 m-resolution cells. However, the descriptors were all brought to the same resolution (150 m), which was required for our modelling approach. Each 150 m-resolution cell was assigned the maximum value of descriptors computed for the 75 m-resolution cells it contained. For those descriptors computed at 300 m-resolution, overlapping moving windows centred on the 150 m-resolution cells were used.

### 2.4. Statistical methodology

A screening procedure excluded those cells that were completely wooded on the one hand or open land without bushes or hedges on the other, because both conditions are inappropriate for shrike settlement.

Descriptors were standardised (mean = 0 and variance = 1) and normalised using the Box-Cox algorithm (Sokal and Rohlf, 1998). Departure from normality after transformation was detected for some descriptors, but we considered our modelling approach to be insensitive to this assumption (Hirzel et al., 2002a).

#### 2.4.1. Ecological niche factor analysis

As some red-backed shrike absences may provide confounding information about habitat suitability, the species niche was described using a presence-only approach, the ecological niche factor analysis (ENFA, Hirzel et al., 2002a). ENFA uses the distribution of species records to summarise descriptors into independent components that are related to the species ecological niche. The first component (called 'marginality factor') explains the marginality of the species regarding the set of descriptors, describing how far the species optimum is from the average environmental conditions (hereafter called 'global data') defined by all the cells that were not previously excluded. Subsequent factors (called 'specialization factors') are then extracted orthogonally to explain the specialization of the species, describing the narrowness of its niche (Hirzel

**Table 1 – List of land use types adapted from EUNIS typology**

Type	Land use
Aquatic habitats	Permanent oligotrophic ponds Hydrographical network
Shrub-covered habitats	Scrubs Densely shrub-covered area Sparsely shrub-covered area
Cultivated habitats	Arable land (1) Recently unmanaged arable land* (1.5)
Forested habitats	Broadleaved deciduous woodland Mixed woodlands Coniferous woodland Low-stem tree orchards
Grazed/mowed habitats	Permanent extensive mesotrophic pastures* (2) (containing patches of ungrazed and diversified vegetation) Permanent intensive mesotrophic pastures* (1) (short but quite diversified and heterogeneous vegetation) Permanent very intensive mesotrophic pastures* (0.5) (overgrazed and homogeneous vegetation) Hay meadows* (3) Aftermath grazed meadows* (2.5)
(Temporarily) unimproved habitats	Wet grasslands* Dry grasslands* Grassy fallow* Wet fallow* Dry heath* Dry heath with scattered trees Dry heath with numerous bushes Wet heaths* Wet heaths with numerous bushes
Anthropogenic habitats	Rail networks Road networks ( if secondary roads or pathways) Agricultural constructions Buildings of cities, towns and villages Domestic gardens of villages and urban peripheries Artificial and sterile habitats

Each land use type was assigned to one of seven groups. The vast majority of hay meadows in Calesstienne are in fact aftermath grazed meadows, but were classified as such only if they were grazed during the breeding season of the red-backed shrike. Unmanaged habitats are patches not used for cultivation or rearing and were classified according to (1) herbaceous composition and structure and (2) ligneous density and composition. Parenthetically mentioned weighting coefficients were adapted from Kruess and Tscharncke (2002a,b) to quantify the relative abundance of main prey (Coleoptera, Hymenoptera and Orthoptera, see Tryjanowski et al. (2003) and Karlsson (2004)) according to the intensity level of several types of pastured or cultivated patches.

\* Suitable land use for foraging.

2.4.2. *Habitat suitability*

The first few factors of the ENFA, gathering the majority of the information according to Mac-Arthur's broken-stick advice (Jackson, 1993; Hirzel et al., 2002a), were used to compute habitat suitability values between 0 and 1 for any site within the study area. Several algorithms are available for habitat suitability computation (Hirzel et al., 2002b). The distance geometric-mean algorithm was used, as it has been shown to provide a good trade-off between the opposing constraints of precision and generality (Hirzel and Arlettaz, 2003). While making no assumption on the shape of the species distribution along the different factors, this algorithm takes into account the density of species records in the ENFA space to increase the influence of those that are close to each other. Thus, the distance geometric-mean algorithm relies on the assumption that the higher the density of records in ENFA space, the higher the suitability of the corresponding environmental conditions (Hirzel et al., 2002b; Hirzel and Arlettaz, 2003). Several envelopes can then be delineated within the modelled habitat suitability field, enclosing various proportions of species records, from the central part to the marginal part of the records distribution in the ENFA space. A core envelope, for example, comprised 50% of the innermost records; the next envelope, somewhat broader, encloses 60% and so forth until even marginal records were included (100%). Finally, a habitat suitability value is assigned to each envelope by counting the proportion of species records they encompass (Hirzel et al., 2002b). Habitat suitability values were calculated according to both the standard-ENFA space and the breeding-ENFA space.

2.4.3. *Model evaluation*

The performance of the models was evaluated by means of a cross-validation procedure (Manly, 1997; Fielding and Bell, 1997; Sokal and Rohlf, 1998; Hirzel and Arlettaz, 2003). The dataset was partitioned into 20 subsets. In turn, 19 of these were used for model calibration and the remaining one for model evaluation.

Three evaluation indices were computed for each turn of the cross-validation procedure to provide mean and standard deviation for these indices. First, the Absolute Validation Index was the proportion of species records among the evaluation dataset that were assigned a habitat suitability value higher than 0.5, i.e. that were enclosed in the envelope circumscribing 50% of species records with the highest habitat suitability values (hereafter called the core area) among the calibration dataset. The second index,  $A_g$ , served to identify the proportion of species records in the evaluation dataset that might have been included in the core area by chance alone. It was computed as the proportion of all evaluation data points (both occupied and unoccupied cells) that were assigned a habitat suitability value higher than 0.5. Third, Absolute Validation Index and  $A_g$  were compared by calculating their difference, yielding the Contrast Validation Index, which ranges from 0 to  $1 - A_g$ . This index reflects model accuracy (Hirzel et al., 2004), with values near 0 indicating that the model does not outperform a random one (Hirzel and Arlettaz, 2003).

et al., 2002a for technical considerations). ENFA was applied with BIOMAPPER 3.1 (Hirzel et al., 2002b) using (1) all species records indiscriminately (standard-ENFA) and next (2) for successful pairs only (breeding-ENFA).

**Table 2 – List of functional environmental descriptors calculated for each cell, with their spatial scale of computation, their functional significance, a brief description and selected references related to the red-backed shrike or its main preys**

Descriptor	Resolution (m)			Functional significance	Unit	Description	References
	75	150	300				
Nest		×		Nesting	–	Abundance of bushes and/or hedges (transformed to points separated by 5 m- intervals) suitable for carrying a nest (thorny/height 1–6 m/ length < 50 m/not completely inside a very intensive pasture/distance to forest > 25 m)	Van Nieuwenhuysse and Vandekerckhove (1992), Tryjanowski et al. (2000), Lefranc (2004)
NestDist		×		Nesting	m	=Nest, where each bush and/or hedge is positively weighted by its distance to urban area	Söderström et al. (1998), Söderström (2001), Horvath et al. (1998), Roos and Part (2004), Muller et al. (2005)
NestStd		×		Nesting	m	Standard deviation of the heights of bushes and/or hedges suitable for nest installation	Van Nieuwenhuysse (1998)
Arable		×	×	Food – predation pressure	m <sup>2</sup>	Area of arable lands	Söderström (2001), Lefranc (2004)
IntPast			×	Food	m <sup>2</sup>	Area of very intensive pastures	Morris (2000), O' Neill et al. (2003)
SemiNat			×	Food	m <sup>2</sup>	Area of (temporarily) unmanaged land uses (Table 1) and/or hay meadows (considered as a 'semi-natural' land use)	Stoner and Joern (2004), Pywell et al. (2005)
SemiNatWe		×	×	Food	m <sup>2</sup>	=SemiNat, where area of each patch is weighted by the area of other 'semi-natural' patches within a radius of 250 m	Stoner and Joern (2004), Pywell et al. (2005)
Extensive		×	×	Food	–	Extensification level computed by weighting the area of each pastured and cultivated patch by the relative prey density (Table 1)	Kruess and Tschardt (2002a,b)
SoilDry				Food	m	Euclidean distance between the centre of the cell and the nearest point where phreatic table depth is less than 15 cm	Couvreur and Godeau (2000), Holland (2002)
SoilDepth			×	Food	cm	Mean phreatic table depth	Couvreur and Godeau (2000), Holland (2002)
DiForest				Food – predation pressure	m	Euclidean distance between the centre of the cell and the nearest forest	Magura et al. (2001), Söderström et al. (1998)
DiUrban				Predation pressure Anthropogenic disturbance	m	Euclidean distance between the centre of the cell and the nearest urban area (building)	Horvath et al. (1998), Roos and Part (2004), Muller et al. (2005)
Forage	×	×		Foraging	m <sup>2</sup>	Accessible area for foraging defined by a 20 m buffer around each suitable perch for foraging (height 1–4 m/bush, hedge or fence/distance to suitable nest site < 40 m) and intersecting suitable patches for foraging (* in Table 1)	Van Nieuwenhuysse (1998), Van Nieuwenhuysse et al. (1999), Karlsson (2004), Lefranc (2004)

Table 2 – continued

Descriptor	Resolution (m)			Functional significance	Unit	Description	References
	75	150	300				
ForageVg	×	×		Foraging	m <sup>2</sup>	=Forage, where the area of each intersected patch is negatively weighted by the vegetation height of this patch type	Van Nieuwenhuysse and Vandekerkhove (1992), Van Nieuwenhuysse et al. (1999), Lefranc (2004)
NbForage		×		Food – Foraging	–	Number of patches intersecting the accessible area for foraging	Lefranc (2004)
Interface		×	×	Food – Foraging	m	Length of all interfaces between the different open-vegetation patches	Van Nieuwenhuysse et al. (1999), Meek et al. (2002), Backman and Tiainen (2002), Holland (2002)
Contrast		×	×	Food – Foraging	m	=Interface, where each Interface type is positively weighted by the difference of vegetation height between both patch types	Van Nieuwenhuysse (1998), Van Nieuwenhuysse et al. (1999), Lefranc (2004)

It is noteworthy to indicate that forests and urban areas outside the study area were taken into account for distances computations (external buffer of 1 km).

#### 2.4.4. Euclidian distance

To support the discussion about the discrepancies between the standard-ENFA and the breeding-ENFA, the species–environment relationship was additionally evaluated in a different but complementary environmental space. The Euclidian distance ( $D_E$ ) between each species record and the average environmental conditions from all species records (hereafter called ‘species average conditions’) was computed in a  $p$ -dimensional environmental space where each dimension corresponded to a descriptor ( $p = 24$ ). As the descriptors were standardised and normalised, their relative contributions to  $D_E$  values were comparable (Legendre and Legendre, 1998).  $D_E$  reflected how the environmental conditions of an occupied cell departed from the species average conditions, but unlike the distance geometric-mean algorithm this multidimensional distance coefficient is sensitive to one-dimensional departure from the species average conditions. Cells for which one or a few descriptors departed from the species average conditions were allocated to high  $D_E$  values, while cells characterized by descriptors that were all close to the species average conditions were allocated to low  $D_E$  values. A parallel will be drawn between ENFA-independent  $D_E$  values and ENFA-based habitat suitability values.

#### 2.4.5. Importance of predation

The proximity of potential predators’ nesting sites was quantified by DiForest for the eurasian jay (*Garrulus glandarius*) or the carrion crow (*Corvus corone*) and by DiUrban for the black-billed magpie (*Pica pica*) or the domestic cats. In addition, corvids like the carrion crow typically forage in arable lands, thus the descriptor Arable quantified the proximity of potential predators’ foraging sites. Logistic regression models (with logit link) were used to evaluate the

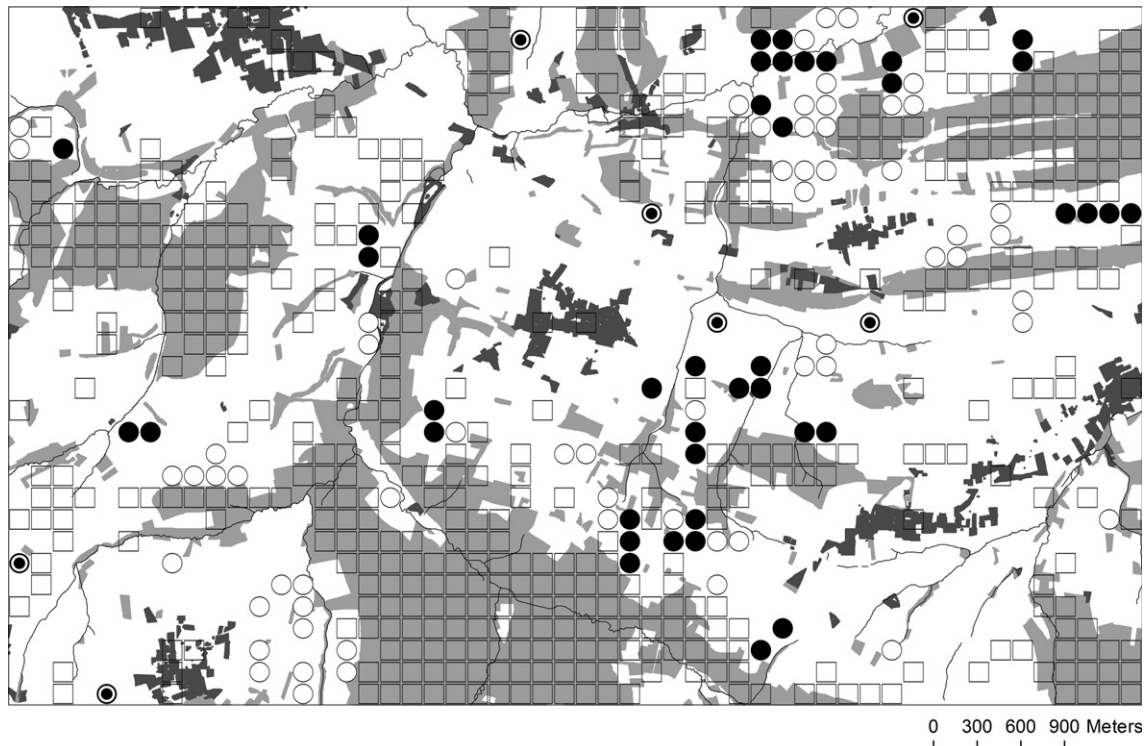
importance of these descriptors (i.e. indirectly of the predation pressure) in discriminating between successful ( $n = 44$ ) and unsuccessful ( $n = 23$ ) pairs. For territories covering adjacent cells, the mean values of these descriptors were used in the analyses.

### 3. Results

The initial screening of grid cells for land-use types that were incompatible with habitat-use by the shrike excluded 480 cells (Fig. 2). The remaining 1184 were used for subsequent analyses. No strong correlation was detected between descriptors of different functional significance (spearman  $|\rho| < 0.7$ ), but a few were quite correlated ( $|\rho| > 0.7$ ) within functional types (especially among Foraging descriptors, see Table 2) or between spatial scales for multi-scale descriptors (Extensive, Arable, Forage). This is not problematic as ENFA deals with multicollinearity in the descriptors (Hirzel et al., 2002a).

#### 3.1. Standard-ENFA

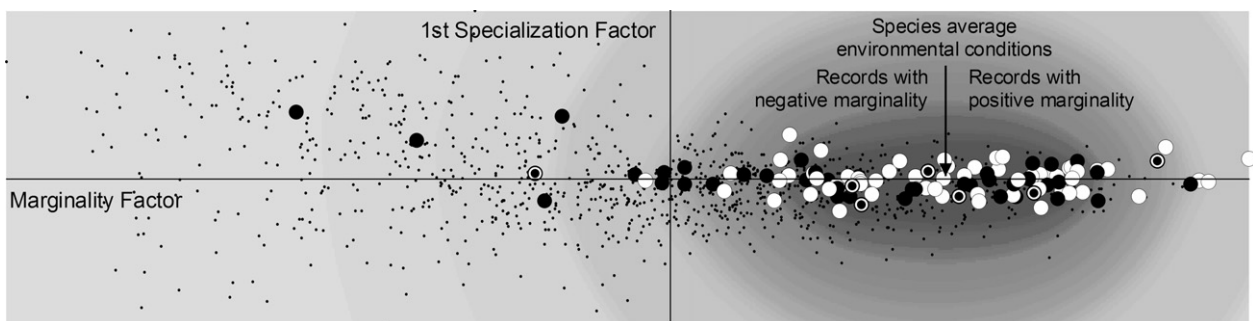
In 2005, 74 males settled in the study area, of which 67 were paired with females. Territories were aggregated at the cell level, leading to a total of 110 occupied cells because some territories covered more than 1 cell (Fig. 2). Marginality and tolerance coefficients based on standard-ENFA were 1.32 and 0.72, respectively. These values indicate that the red-backed shrike settled in environmental conditions departing from the average (corresponding to null marginality) but with a rather large niche breadth (tolerance ranges from 0 to 1 for highly specialized to ubiquitous species, respectively). By



**Fig. 2** – Location of species records within the study area. Successful and unsuccessful pairs are represented by white and black dots, respectively. Unpaired males ( $n = 7$ ) are depicted by encircled black points. Squares represent screened-out cells ( $n = 480$ ), where land use is incompatible with the red-backed shrike settlement. For background features, see Fig. 1.

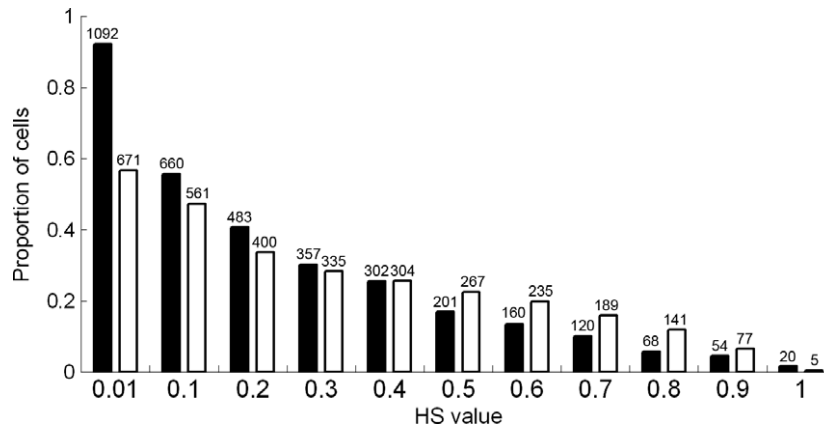
comparing the eigenvalues to Mac-Arthur's broken-stick distribution (Jackson, 1993; Hirzel et al., 2002a), four significant factors of the standard-ENFA were retained for habitat suitability computation. Together they explained about 72% of the information (100% of the marginality and 44% of the specialization). This means that four factors were sufficient to describe the shrike niche when using all species records indiscriminately. The projection of the 1184 cells on the first two factors is shown in Fig. 3. Besides marginality, the first factor explained only 8% of specialization. This low fraction indicates that the combination of descriptors that explained shrike marginality did not explain its specialization adequately.

The cross-validation procedure provided mean Absolute and Contrast Validation Indices of 0.53 (SD = 0.20) and 0.35 (SD = 0.20), respectively. The Absolute Validation Index value indicates that the model predictions were very consistent with the evaluation datasets since on average ~50% of evaluation species records were enclosed in the core area. The difference between Absolute and Contrast Validation Indices shows that part of model performance might be attributable to randomness. When both calibration and evaluation datasets were combined, 201 cells were enclosed in the core area (averaged from the 20 cross-validation runs), of which 148 (74%) were unoccupied in 2005. Fig. 4 shows the proportions of cells enclosed in several envelopes within the habitat suitability field.



**Fig. 3** – Red-backed shrike records (Fig. 2 for symbols) and habitat suitability field (the darker, the higher the habitat suitability value) represented in the first two dimensions of the standard-ENFA space. Unoccupied cells of the global data are depicted by little black spots.





**Fig. 4 – Proportions of cells (among the global data) enclosed in several envelopes (averaged from the 20 cross-validation runs), from marginal (low habitat suitability (HS) values) to inner areas (high habitat suitability values), following the standard-ENFA (black bars) and breeding-ENFA (white bars). The number of cells is indicated above each bar. Envelopes circumscribing all shrike records (standard-ENFA) or all successful pairs (breeding-ENFA) correspond to a habitat suitability value of 0.01, according to the distance geometric-mean algorithm and habitat suitability isopleths scaling. The envelopes circumscribing 50% of shrike records (standard-ENFA) or of successful pairs (breeding-ENFA) (i.e. core areas) correspond to a habitat suitability value of 0.5.**

Coefficients on the marginality factor were positive for most descriptors (Table 3), showing that the shrike was found in areas where these descriptors were higher than average. These descriptors were – by decreasing order of importance

– related to nest sites abundance, distance to urban areas, suitability for foraging (prey detectability) and prey density. Negative coefficients revealed that the species settled in areas where soil dryness and the amount of very intensive pastures

**Table 3 – Correlation between the retained standard-ENFA factors and the descriptors**

	Factor 1 (8%)	Factor 2 (16%)	Factor 3 (11%)	Factor 4 (9%)	M <sub>STANDARD</sub>	SD <sub>STANDARD</sub>	M <sub>GLOBAL</sub>	SD <sub>GLOBAL</sub>
Nest-150	+++	****	0	****	22.427	14.031	10.766	11.688
NestDist-150	++++	*****	**	*****	13,182	9572.6	4481	6701.8
NestStd-150	+++	0	0	*	1.1594	0.67725	0.69039	0.73007
Arable-150	0	*	**	*	2394.8	4154.6	3166.9	5415.8
Arable-300	0	0	0	*	10,420	13,588	12,928	16,916
IntPast-300	–	*	0	0	4313.9	13,065	6207.9	13,698
SemiNat-300	++	0	*	*	15,961	13,860	10,227	12,007
SemiNatWe-150	++	0	0	0	2241	2865.4	1301	2239.1
SemiNatWe-300	+	0	*	**	3928.5	4228.5	2820.9	3508.4
Extensive-150	++	0	*	**	1.7645	0.56769	1.5057	0.58654
Extensive-300	++	*	*	*	1.7202	0.44046	1.5038	0.44145
SoilDry	–	*	*	0	163.76	151.88	190.41	159.61
SoilDepth-300	–	**	*	*	76.337	21.717	86.358	22.166
DiForest	0	**	***	0	99.018	54.481	115.07	103.66
DiUrban	++	****	**	**	596.38	249.45	416.08	303.04
Forage-75	+++	*	**	***	3626.1	1123.7	2447.2	1557
Forage-150	+++	0	*****	*	8977.4	4004.5	5302.3	4358.4
ForageVg-75	+	0	**	0	296.45	182.56	246.66	200.75
ForageVg-150	++	0	*	*	640.68	428.54	485.05	457.47
NbForage-150	++	0	*	0	6.0273	3.0195	4.5169	3.2023
Interface-150	++	*	***	*	414.35	209.88	305.03	210.15
Interface-300	++	**	****	0	1399	506.41	1169.6	576.93
Contrast-150	++	*	0	*	16,238	13,650	9868.7	10,656
Contrast-300	++	*	***	*	53,433	30,292	37,516	27,876

Percentages indicate the proportion of specialization explained by each factor (100% of the marginality is accounted for by the first factor). Summary statistics (means M and standard deviations SD) are provided for species (all species records indiscriminately, M<sub>STANDARD</sub> and SD<sub>STANDARD</sub>) and global (M<sub>GLOBAL</sub> and SD<sub>GLOBAL</sub>) distribution along all descriptors (see units in Table 2).

For the first factor (marginality factor), the symbols + and – mean the red-backed shrike settled in areas with higher and lower values than average, respectively (0 indicates a very weak or no correlation). The number of symbols is proportional to the strength of the correlation.

For subsequent factors (specialization factors), the symbol \* indicates that the red-backed shrike occupies a narrower range of values than available (0 indicates a very low specialization). The number of symbols is proportional to this narrowness.

were slightly lower than average. Table 3 provides the summary statistics for the species (all species records) and global distribution along all descriptors.

Niche breadth was mainly restricted by nest sites abundance and distance to human settlements, and to a lesser extent by distance to forest, suitable and accessible areas for foraging and field margin abundance. Amount of arable lands was weakly correlated with the retained factors. Marginality and specialization coefficients were quite insensitive to the scale of computation.

### 3.2. Breeding-ENFA

Of the 74 territories (67 pairs and seven unpaired males) found in 2005, 44 pairs bred successfully at the first ( $n = 36$ ) or second (replacement clutch,  $n = 8$ ) attempt (63 cells in total). The logistic models showed that the proximity of potential predators did not significantly explain the differences between successful and unsuccessful pairs (log-likelihood ratio tests:  $p = 0.75, 0.71, 0.89$  and  $0.44$  for DiForest, DiUrban, Arable-150 and Arable-300 respectively,  $p = 0.55$  for the full model including these four descriptors). In addition, the breeding-ENFA and standard-ENFA revealed that the marginality of successful pairs only and of all shrike records were related to the same descriptors (see correlation between

all descriptors and the first ENFA factors in Tables 3 and 4).

On the other hand, based on these successful records, the marginality coefficient was higher in comparison to the standard-ENFA (1.52 vs. 1.32). This indicates that the red-backed shrike bred successfully in environmental conditions that depart more strongly from average, as compared with mere species presence. Moreover, the global tolerance decreased (0.41 vs. 0.72) showing that the niche modelled with these successful pairs was more restricted compared with all shrike records (Fig. 3). Only two significant factors of the breeding-ENFA were retained for habitat suitability computation. Together they accounted for 84% of the information (100% of the marginality and 68% of the specialization). In contrast with the standard-ENFA, the breeding-ENFA marginality factor explained nearly half (47%) the specialization, indicating that the reproductive niche breadth and marginality were mainly defined by the same combination of descriptors, mostly nest sites abundance, distance to human settlements and suitability for foraging. Table 4 provides summary statistics for the species (successful species records only) and global distribution along all descriptors.

The cross-validation procedure provided mean Absolute and Contrast Validation Indices of 0.58 (SD = 0.33) and 0.35 (SD = 0.32), respectively. These values did not differ signifi-

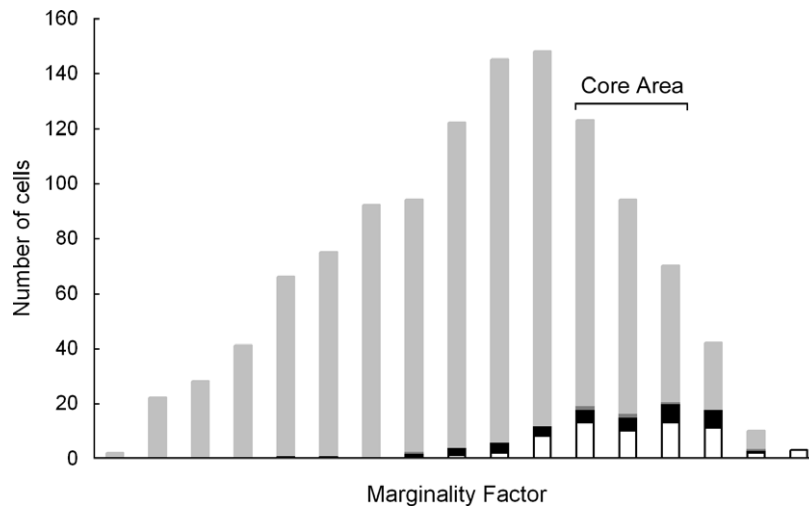
**Table 4 – Correlation between the retained breeding-ENFA factors and the descriptors**

	Factor 1 (47%)	Factor 2 (21%)	$M_{\text{BREEDING}}$	$SD_{\text{BREEDING}}$	$M_{\text{GLOBAL}}$	$SD_{\text{GLOBAL}}$
Nest-150	+++	****	24.492	14.343	10.766	11.688
NestDist-150	++++	*****	14,496	10,140	4481	6701.8
NestStd-150	+++	0	1.2178	0.54923	0.69039	0.73007
Arable-150	0	0	2321.9	4051.7	3166.9	5415.8
Arable-300	0	0	10,120	13,066	12,928	16,916
IntPast-300	–	0	2318.7	6907.4	6207.9	13,698
SemiNat-300	++	0	16,851	14,523	10,227	12,007
SemiNatWe-150	++	0	2267.9	3114.5	1301	2239.1
SemiNatWe-300	++	0	4110.5	4765.9	2820.9	3508.4
Extensive-150	++	0	1.8844	0.55242	1.5057	0.58654
Extensive-300	++	*	1.8279	0.37776	1.5038	0.44145
SoilDry	–	0	172.2	167.91	190.41	159.61
SoilDepth-300	–	0	73.448	24.244	86.358	22.166
DiForest	0	0	93.143	53.945	115.07	103.66
DiUrban	++	****	594.24	244.2	416.08	303.04
Forage-75	+++	*	3751.3	1029.2	2447.2	1557
Forage-150	+++	*	9588.6	3968.6	5302.3	4358.4
ForageVg-75	+	*	277.15	152.84	246.66	200.75
ForageVg-150	++	*	617.51	375.77	485.05	457.47
NbForage-150	++	0	6.1905	3.1666	4.5169	3.2023
Interface-150	++	0	430.74	223.15	305.03	210.15
Interface-300	+	0	1424.4	543.26	1169.6	576.93
Contrast-150	++	0	17,113	13,755	9868.7	10,656
Contrast-300	++	0	57,774	32,530	37,516	27,876

Percentages indicate the proportion of specialization explained by each factor (100% of the marginality is accounted for by the first factor). Summary statistics (means  $M$  and standard deviations  $SD$ ) are provided for species (successful species records only,  $M_{\text{BREEDING}}$  and  $SD_{\text{BREEDING}}$ ) and global ( $M_{\text{GLOBAL}}$  and  $SD_{\text{GLOBAL}}$ ) distribution along all descriptors (see units in Table 2). For each descriptor, the most suitable conditions lie above (respectively below) the  $M_{\text{BREEDING}}$  when the corresponding marginality coefficient is positive (respectively negative).

For the first factor (marginality factor), the symbols + and – mean the red-backed shrike settled in areas with higher and lower values than average, respectively (0 indicates a very weak or no correlation). The number of symbols is proportional to the strength of the correlation.

For subsequent factors (specialization factors), the symbol \* indicates that the red-backed shrike occupies a narrower range of values than available (0 indicates a very low specialization). The number of symbols is proportional to this narrowness.



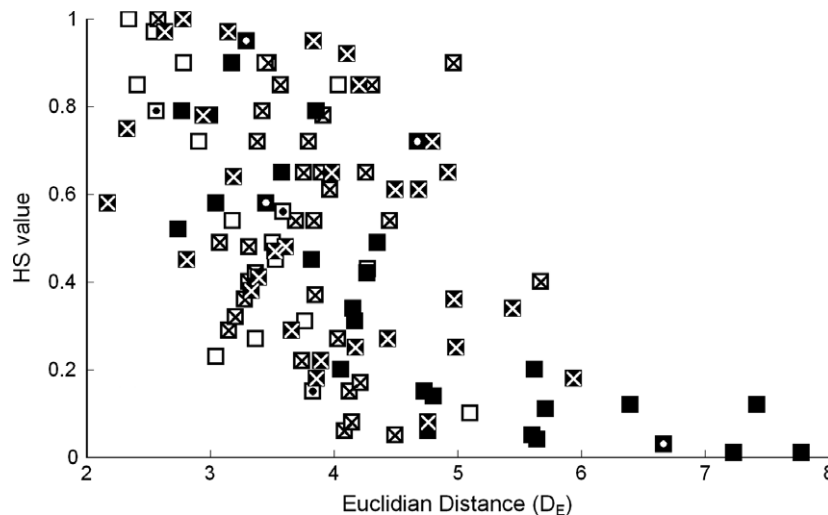
**Fig. 5 – Distribution of occupied (white, black and dark grey bars, for successful pairs, unsuccessful pairs and unpaired males, respectively) and unoccupied (light grey bars) cells along the marginality factor of the standard-ENFA.**

cantly from their counterpart for the standard-ENFA (Student's tests,  $df = 38$ ,  $p = 0.59$  and  $0.96$ , respectively –  $p$ -values are given as an indication only because tests were not fully valid due to redundancy in breeding-ENFA and standard-ENFA data). While a bit wider according to the breeding-ENFA (leading to a larger mean difference between Absolute and Contrast Validation Indices), the core areas defined by both procedures were fairly similar. In contrast, the proportions of cells enclosed in the marginal envelopes (lowest habitat suitability values) differed considerably (Fig. 4). This was due to the loosely scattered shrike records which did not exhibit successful reproduction towards the negative end of the standard-ENFA marginality factor (Figs. 3 and 5). When they

were removed from the species records for computing the breeding-ENFA, the remaining successfully reproductive shrike records ended up more restricted in the space.

### 3.3. Outlying species records

In the standard-ENFA space, some shrike records appeared to be off-centre relative to the average environmental conditions used by the species. Both ends of the marginality factor proved to be affected by this issue. However, despite similarities in the habitat suitability values assigned to both subsets of outlying records (positive and negative), they differed considerably regarding four aspects.



**Fig. 6 – Two-dimensional scatter plot of shrike records defined by  $D_E$  and habitat suitability (HS) values. White and black squares represent records with positive and negative marginality, respectively, compared with the species average environmental conditions (Fig. 3). Crossed squares represent successful pairs. Punctuated squares represent unpaired males. Outlying shrike records in the standard-ENFA space are situated at the bottom of the scatter plot (low habitat suitability values).**

- (1) Outlying records on the positive end of the marginality factor were found in uncommon environmental conditions, while outlying records towards the negative end were located in common conditions (Figs. 3 and 5).
- (2) The environmental conditions occupied by the outlying records were highly prized on the positive end of the marginality factor, while those towards the negative end were sporadically used (Fig. 5).
- (3) The Euclidian distance to species average environmental conditions ( $D_E$ ) was shorter for outlying records on the positive end of the marginality factor than for those towards the negative end (Fig. 6), indicating that one or a few descriptors for the latter were considerably farther from the species average conditions.
- (4) The pattern in the breeding success was diametrically opposed on both ends of the marginality factor (Fig. 5), indicating that environmental conditions with positive marginality appeared to be highly suitable for the reproduction of the red-backed shrike.

All these elements converge to indicate that outlying records towards the negative end of the marginality factor were pairs located under unsuitable environmental conditions, while those on the positive end were most probably an artefact of the model.

## 4. Discussion

### 4.1. Relationship between red-backed shrike niche and distribution

Nest predation – mainly by corvids (Söderström et al., 1998; Horvath et al., 1998; Roos and Part, 2004) – accounts for a significant part of the breeding failures in the red-backed shrike (Söderström, 2001; Muller et al., 2005). However, our results indicated that the environmental distinction between breeding success and failure was not closely related to the proximity of predators' nesting or foraging sites. This does not weaken the assumption of a globally strong selective pressure of predation and its importance in shaping the habitat selection pattern of the red-backed shrike (Söderström, 2001; Roos, 2002; Roos and Part, 2004), but the risk of nest predation alone did not explain the dramatic decrease in breeding success towards the negative end of the marginality factor (Figs. 3 and 5). Instead, these unsuccessful records lacked one or few other essential resources for the reproduction of the shrike, as revealed by  $D_E$  (Fig. 6). From farthest to nearest outlying records with negative marginality in the standard-ENFA space, these missing resources were accessible foraging areas, nest sites and prey density. Since these resources were probably non-substitutable for shrike reproduction (see functional significance in Table 2), shortage in one or few of them might explain the failure of reproduction, maybe in addition to predation events. Conversely,  $D_E$  values of the outlying records with positive marginality were more comparable with those of the rest of shrike records (Fig. 6). This pattern suggested that none of the descriptors characterizing these outlying records excessively departed from the species average

conditions. These sites were actually better than the species average conditions and hence than the global average conditions, which explained their outlying position in the ENFA space.

Furthermore, despite their similar habitat suitability values, both kinds of outlying records differed largely with regard to breeding success. On the one hand, those with negative marginality were pairs that attempted to breed under unsuitable conditions but failed. On the other hand, those territories with positive marginality were clearly located under highly prized conditions and were rewarded by successful reproduction (Fig. 5), indicating a high suitability.

Because of a low availability of the most suitable conditions within the study area (Fig. 5), some off-centre shrike records with positive marginality were assigned aberrantly low habitat suitability values when assuming that the absolute record frequency in the environmental space was a direct indicator of habitat suitability. Such biased availability of environmental conditions is often encountered when modelling species distributions (Kadmon et al., 2003; Thuiller et al., 2004) and affects other modelling approaches (comparative studies are currently lacking) by yielding skewed predictions on the tails of the species response curves (Austin et al., 1994; Rydgren et al., 2003; Coudun and Gegout, 2006). This obviously hampers the precise delineation of trustable habitat suitability maps. This issue especially arises when using restricted data that prevent the correct capture of the entire environmental range of the species (Thuiller et al., 2004), when the true optimum of the species lies near or even beyond an extreme of the investigated environmental gradient (Rydgren et al., 2003; Coudun and Gegout, 2006) or when habitat suitability monotonically increases/decreases along this gradient. This was clearly the case for the shrike and the restriction to successful records did not help to improve this model shortcoming. Comparative studies should be carried out to evaluate the relative ability of several modelling approaches to face up to biased availability of environmental conditions. Within a presence-only modelling framework, further developments of the envelope-based algorithms should tackle this issue.

Despite this technical issue, the incorporation of fitness-related parameters into the modelling framework allowed the environmental bounds of the red-backed shrike's niche to be defined more exactly than indiscriminate use of all species records. Although standard-ENFA and breeding-ENFA provided very similar models regarding the descriptor coefficients, the latter had a higher marginality, a lower tolerance and a higher percentage of information explained with fewer factors. This revealed that reproducing individuals were more selective when choosing their nest site. In other words, the reproductive niche of the red-backed shrike was environmentally narrower than ordinary practice in presence-only modelling would have suggested. Similarities of Absolute and Contrast Validation Indices for standard-ENFA and breeding-ENFA were due to the main discrepancies not lying in the core areas but in the margins of the space (Fig. 4). This breeding success pattern in the red-backed shrike illustrates the need for identifying and discarding confounding species records before circumscribing the species niche in the environmental

space (Pulliam, 2000; Guisan and Thuiller, 2005). In light of the distribution of shrike records in the standard-ENFA space (Fig. 3), we argue that about 10% of the most outlying records with negative marginality should be regarded as confounding indicators of habitat suitability. Ignoring this issue when drawing habitat suitability maps by means of presence-only techniques would result in overestimating the amount of suitable areas, which may have significant conservation consequences (Loiselle et al., 2003).

The existence and the number of confounding records most probably depend on the ecology of species (e.g. mobile vs. sessile species or response to conspecifics, McPherson and Jetz, 2007), and on the scale or location of the study area relative to the species geographical or environmental range. Moreover, different modelling approaches are probably unequally affected by the presence of confounding records. Therefore, we encourage researchers to be aware of marginal records in their data. Outlying records should not be considered as insignificant species presences without further consideration. Analyzing the factors that incite individuals to occupy unsuitable conditions could improve understanding of the environmental boundaries of the species niche. Furthermore, the location of non-breeding individuals is still important for the overall distribution pattern of the species. When developing conservation strategies, maintaining these marginal habitats may be important for the persistence of the species (Sarah et al., 2004). Accordingly, deciding on whether or not species records should be excluded from the analysis will ultimately depend on the purpose of the study.

#### 4.2. Implications for shrike conservation

Every species responds to different combinations of environmental forces in different parts of its distribution range (Osborne and Suarez-Seoane, 2002; Gibson et al., 2004b; Whittingham et al., 2007). As a consequence, transferring the model outcomes to other areas must be undertaken with caution (Fielding and Haworth, 1995; Whittingham et al., 2003). While the issue of model transferability is still under debate (Seoane et al., 2005; Ozesmi et al., 2006; Randin et al., 2006), focusing on the ecological resources that determine the functional interactions between the organisms and their environment should allow the application of our findings to populations established in similar Western European agricultural areas with some confidence (Guisan and Zimmermann, 2000; Vanreusel et al., 2007).

Below, we propose six recommendations for the conservation of the red-backed shrike. The correlation between the environmental descriptors and the breeding-ENFA factors (Table 4) allowed ranking the shrike's reproductive habitat requirements and presenting them by decreasing order of importance. To circumvent model artefacts caused by the rarity of best conditions, we considered the sign of the marginality coefficients for the different descriptors on the one hand and the mean positions of the successful species records along these descriptors (Table 4) on the other hand. Hence, we ensure that the most suitable conditions lie above (respectively below) these positions when marginality coefficients are positive (respectively negative), even if such places are scarce. The following recommendations thus represent

**Table 5 – Recommendation list for the conservation of the red-backed shrike in Western European agricultural areas (sorted by decreasing order of importance, Table 4)**

Resource	Quantitative guidelines	Qualitative guidelines
1 Nest sites	Maintaining at least 10 suitable nest sites per ha Height 1–6 m/length < 50 m Distance to forest > 25 m	Thorny hedge fragments or bushes Mixing high and low bushes and hedges
2 Distance to urban areas	Focusing management on sites > 600 m away from urban areas	Reducing human settlement in or close to suitable rural areas
3 Suitable perches and foraging areas	Arranging perches and open patches to make at least ~40% of the total area simultaneously suitable and accessible (less than 20 m distant from adequate perches) for foraging Height of foraging perches: 1–4 m Maximal distance between foraging perches and suitable nest sites: 40 m	Foraging perches: bushes, hedges or fences Foraging areas: see * in Table 1
4 Field margins	Maintaining at least 200 m of field margins per ha of farming areas	Favouring the alternation of tight, tiny and imbricated patches of contrasted open-vegetation heights
5 Prey abundance		Maintaining the amount and spatial cohesion of unimproved patches Promoting non-intensive farming techniques Mixing extensive pastures, aftermath grazed meadows and hay meadows Alleviating grazing pressure and fertilizer application
6 Soil moisture		Avoiding field drainage and filling of ditches

These measures are to be viewed by managers as minimalist and to be implemented on 2-ha areas as a strict minimum.

minimum requirements for the shrike. Their significance is discussed below and Table 5 summarises them in a quantitative way.

First, the red-backed shrike showed a marked association with, and selection for, areas where suitable nest sites were abundant. Previous studies (Van Nieuwenhuysse, 1998; Tryjanowski et al., 2000; Muller et al., 2005) indicated that nest site selection and structural characteristics of the immediate environment surrounding the nest have a strong effect on a shrike's breeding performance; the probability of finding a suitable breeding site is positively correlated with the amount of thorny bushes or hedge fragments.

Second, shrikes did not nest close to urban areas (Nest-Dist and DiUrban, see also Kuzniak and Tryjanowski, 2000). This may be caused, at least to some extent, by direct human disturbance and higher predation pressure by anthropophilic species, like black-billed magpies or domestic cats (Muller et al., 2005). The ongoing expansion of human settlement in rural areas is thus likely to negatively affect the species.

Third, the red-backed shrike was highly associated with sites where foraging perches were scattered providing a maximal foraging area on a minimal total surface (Forage), which is essential for its sit-and-wait foraging strategy. We found that, on average, cells occupied by successful pairs had 43% (9588 m<sup>2</sup> per 2.25 ha-cell, see Forage-150 in Table 4) of their surface accessible for foraging, while the global average was only 23%. Van Nieuwenhuysse et al. (1999) suggested that a distance of about 15–20 m between suitable foraging perches would increase the accessible foraging area and, hence, the foraging efficiency. Accessible foraging area has also been shown to be a key habitat factor for the Great Grey Shrike (Rothhaupt and Klein, 1998).

Fourth, although the red-backed shrike forages preferentially on low vegetation or bare soils (Van Nieuwenhuysse and Vandekerckhove, 1992; Lefranc, 2004), inversely weighting the accessible foraging area by the mean vegetation height of each intersecting patch type (ForageVg) failed to provide significant information. This most probably relates to the fact that (1) the relationship between preferences for foraging and vegetation height is not straightforward and (2) the foraging process happens at a finer spatial scale, involving unmapped landscape or vegetation features like path side slopes or rocky outcrops. Nonetheless, the species was associated with high density field margins (Interface) and contrasts of high and low vegetation (Contrast). High level of vegetation heterogeneity with differently sized open meadows and borders of rough grassy vegetation of different height, some bare ground, and scattered shrubs and hedges enhances (1) prey abundance (Meek et al., 2002; Holland, 2002; Backman and Tiainen, 2002; Pywell et al., 2005) and (2) prey accessibility (Van Nieuwenhuysse, 1998; Van Nieuwenhuysse et al., 1999; Lefranc, 2004).

Fifth, beside the spatial configuration of vegetation features, the composition of the agricultural landscape is also significant to this insectivorous species, as it was associated with areas harbouring considerable amounts of extensively managed pastures or hay meadows (Extensive), or unimproved patches (SemiNat). This pattern most likely relates to the reduction in physiognomic heterogeneity and floristic

diversity of the herbaceous vegetation (therefore in invertebrate density and biomass) in intensively managed agricultural areas (Morris, 2000; O' Neill et al., 2003; Stoner and Joern, 2004; Pywell et al., 2005). This was shown to be detrimental to the red-backed shrike because of increasing the parental-expenditure in intensive farming areas (Leugger-Eggiman, 1997; Karlsson, 2004). However, no precise management recommendations (e.g. in terms of grazing pressure or fertilizer application threshold) can be provided from the current model results. This aspect clearly needs further research.

Finally, soil moisture was on average slightly higher in occupied sites than in available ones, probably because poorly drained soils enhance prey biomass or density, especially for large species of Orthoptera (Couvreur and Godeau, 2000) and Carabidae (Holland, 2002). This suggests that field drainage and filling of ditches may negatively affect the abundance of these insect prey taxa.

Many (but not all) descriptors (e.g. nest availability, food density and availability, shelters from predation) were related to the reproductive niche of the red-backed shrike. As we did not find strong correlations between the functional groups of descriptors, it indicates that they are to large extent additive factors. In other words, species-specific habitat management or restoration has to take into account jointly all of these resources and environmental conditions.

Our habitat modelling results illustrate that particular attention has to be paid to the wider environment for such a species living in human-altered, agricultural landscapes. Vulnerable or even threatened species like shrikes are not the only factor involved in the conservation management of such areas. Moreover, as we are dealing with agricultural land, conservation measures should be integrated into the socio-economic context focusing on the multiple services and functions provided by agricultural areas and including financial returns from agriculture and nature conservation (Groot et al., 2007). The complexity of the multiple factors involved in these human-wildlife relations has led to the development of comprehensive tools for decision makers to evaluate the effect of several management alternative in terms of services and functions (Le Lay et al., 2001; Groot et al., 2007). The concrete conservation suggestions arising from fine-scale habitat suitability models like ours (Table 5) constitute valuable inputs for those integrative tools.

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## REFERENCES

- Araujo, M.B., Williams, P.H., 2000. Selecting areas for species persistence using occurrence data. *Biological Conservation* 96, 331–345.
- Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157, 101–118.
- 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. *Journal of Vegetation Science* 5, 215–228.
- Backman, J.P.C., Tiainen, J., 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). *Agriculture Ecosystems & Environment* 89, 53–68.
- Brotons, L., Thuiller, W., Araujo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27, 437–448.
- Coudun, C., Gegout, J.-C., 2006. The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. *Ecological Modelling* 199, 164–175.
- Couvreux, J.M., Godeau, J.F., 2000. Atlas des Orthoptères de la Famenne (Criquets, sauterelles et grillons). *Jeunes & Nature a.s.b.l., Centre de Recherche de la Nature, des Forêts et du Bois*.
- Dennis, R.L.H., Shreeve, T.G., Van Dyck, H., 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos* 102, 417–426.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* 41, 263–274.
- ESRI, 2002. Arcmap version 8.3. Environment Research System Inc, Redlands, CA, USA.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24, 38–49.
- Fielding, A.H., Haworth, P.F., 1995. Testing the generality of bird-habitat models. *Conservation Biology* 9, 1466–1481.
- Gibson, L.A., Wilson, B.A., Cahill, D.M., Hill, J., 2004a. Modelling habitat suitability of the swamp antechinus (*Antechinus minimus maritimus*) in the coastal heathlands of southern Victoria, Australia. *Biological Conservation* 117, 143–150.
- Gibson, L.A., Wilson, B.A., Cahill, D.M., Hill, J., 2004b. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *Journal of Applied Ecology* 41, 213–223.
- Groot, J.C.J., Rossing, W.A.H., Jellema, A., Stobbelaar, D.J., Renting, H., Van Ittersum, M.K., 2007. Exploring multi-scale trade-offs between nature conservation, agricultural profits and landscape quality – a methodology to support discussions on land-use perspectives. *Agriculture, Ecosystems & Environment* 120, 58–69.
- Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* 116, 195–203.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8, 993–1009.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135, 147–186.
- Guisan, A., Edwards, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157, 89–100.
- Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A., Zimmermann, N.E., 2006. Using niche-based models to improve the sampling of rare species. *Conservation Biology* 20, 501–511.
- Heglund, P.J., 2002. Foundations of species–environment relations. In: Scott, J.M. et al. (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Coleto, WA, pp. 35–41.
- Hirzel, A.H., Arlettaz, R., 2003. Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. *Environmental Management* 32, 614–623.
- Hirzel, A.H., Helfer, V., Metral, F., 2001. Assessing habitat-suitability models with a virtual species. *Ecological Modelling* 145, 111–121.
- Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002a. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83, 2027–2036.
- Hirzel, A.H., Hausser, J., Perrin, N., 2002b. Biomapper 3.1, Division of Conservation Biology, University of Bern. Available from: <<http://www.unil.ch/biomapper>>.
- Hirzel, A.H., Posse, B., Oggier, P.A., Crettenand, Y., Glenz, C., Arlettaz, R., 2004. Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *Journal of Applied Ecology* 41, 1103–1116.
- Holland, J.M., 2002. *The Agroecology of Carabid Beetles*. The Game Conservancy Trust, Fordingbridge, Hampshire, UK.
- Horvath, R., Kovacs, K., Farkas, R., 1998. Reproductive biology of the Red-Backed Shrike (*Lanius collurio*) in the Aggteleki Nemzeti Park, Hungary. In: Yosef, R., Lohrer, F.E. (Eds.), *Shrikes of the World - II: Conservation Implementation*. Proceedings of the Second International Shrike Symposium, 17–23 March 1996, International Birdwatching Center in Eilat, Israel, pp. 49–50.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22, 415–427.
- I.R.S.I.A., 1966. Carte des sols de la Belgique. Laboratoire de Géopédologie, Faculté universitaire des Sciences agronomiques, Gembloux, Belgique.
- Jackson, D.A., 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. *Ecology* 74, 2204–2214.
- Kadmon, R., Farber, O., Danin, A., 2003. A systematic analysis of factors affecting the performance of climatic envelope models. *Ecological Applications* 13, 853–867.
- Karlsson, S., 2004. Season-dependent diet composition and habitat use of red-backed shrikes *Lanius collurio* in SW Finland. *Ornis Fennica* 81, 97–108.
- Kristan, W.B., 2003. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos* 103, 457–468.
- Kruess, A., Tschardt, T., 2002a. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106, 293–302.

- Kruess, A., Tscharntke, T., 2002b. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology* 16, 1570–1580.
- Kuzniak, S., Tryjanowski, P., 2000. Distribution and breeding habitat of the red-backed shrike (*Lanius collurio*) in an intensively used farmland. *Ring* 22, 89–93.
- Lefranc, N., 2004. La pie-grièche écorcheur. *Éveil Nature, Approche*.
- Lefranc, N., Worfolk, T., 1997. *Shrikes: A Guide to the Shrikes of the World*. Pica Press, Sussex, England.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier Health Sciences B.V., Amsterdam.
- Le Lay, G., Clergeau, P., Hubert-Moy, L., 2001. Computerized map of risk to manage wildlife species in urban areas. *Environmental Management* 27, 451–461.
- Leugger-Eggiman, U., 1997. Parental expenditure of Red-backed Shrike in habitats of varying farming intensity. Ph.D. Thesis, Université de Bâle, Allschwill.
- Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G., Williams, P.H., 2003. Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology* 17, 1591–1600.
- Luoto, M., Heikkinen, R.K., Poyry, J., Saarinen, K., 2006. Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography* 33, 1764–1778.
- Magura, T., Tothmeresz, B., Molnar, T., 2001. Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity and Conservation* 10, 287–300.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- McPherson, J.M., Jetz, W., 2007. Effects of species' ecology on the accuracy of distribution models. *Ecography* 30, 135–151.
- Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation* 106, 259–271.
- Moisen, G.G., Edwards, J., Osborne, P.E., 2006. Further advances in predicting species distributions. *Ecological Modelling* 199, 129–131.
- Morris, M.G., 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation* 95, 129–142.
- Muller, M., Pasinelli, G., Schiegg, K., Spaar, R., Jenni, L., 2005. Ecological and social effects on reproduction and local recruitment in the red-backed shrike. *Oecologia* 143, 37–50.
- Neill, K.M., Olson, B.E., Rolston, M.G., Wallander, R., Larson, D.P., Seibert, C.E., 2003. Effects of livestock grazing on rangeland grasshopper (Orthoptera: Acrididae) abundance. *Agriculture Ecosystems & Environment* 97, 51–64.
- Olson, G.S., Glenn, E.M., Anthony, R.G., Forsman, E.D., Reid, J.A., Loschl, P.J., Ripple, W.J., 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. *Journal of Wildlife Management* 68, 1039–1053.
- Osborne, P.E., Suarez-Seoane, S., 2002. Should data be partitioned spatially before building large-scale distribution models? *Ecological Modelling* 157, 249–259.
- Ozesmi, U., Tan, C.O., Ozesmi, S.L., Robertson, R.J., 2006. Generalizability of artificial neural network models in ecological applications: predicting nest occurrence and breeding success of the red-winged blackbird *Agelaius phoeniceus*. *Ecological Modelling* 195, 94–104.
- Pearce, J.L., Boyce, M.S., 2005. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology* 43, 405–412.
- Pulliam, H.R., 2000. On the relationship between niche and distribution. *Ecology Letters* 3, 349–361.
- Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks, and habitat selection – a landscape perspective on population-dynamics. *American Naturalist* 137, S50–S66.
- Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121, 479–494.
- Railsback, S.F., Stauffer, H.B., Harvey, B.C., 2003. What can habitat preference models tell us? Tests using a virtual trout population. *Ecological Applications* 13, 1580–1594.
- Randin, C.F., Dirnbock, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? *Journal of Biogeography* 33, 1689–1703.
- Roos, S., 2002. Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* 133, 608–615.
- Roos, S., Part, T., 2004. Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology* 73, 117–127.
- Rothhaupt, G., Klein, H., 1998. Usable area as a key factor for habitat occupancy in the Great Grey Shrike. In: Yosef, R., Lohrer, F.E. (Eds.), *Shrikes of the World - II: Conservation Implementation. Proceedings of the Second International Shrike Symposium, 17–23 March 1996*, International Birdwatching Center in Eilat, Israel, pp. 64–67.
- Rushton, S.P., Ormerod, S.J., Kerby, G., 2004. New paradigms for modelling species distributions? *Journal of Applied Ecology* 41, 193–200.
- Rydgen, K., Okland, R.H., Okland, T., 2003. Species response curves along environmental gradients. A case study from SE Norwegian swamp forests. *Journal of Vegetation Science* 14, 869–880.
- Sarah, E.A., dit Durell, L.V., Clarke, R.T., 2004. The buffer effect of non-breeding birds and the timing of farmland bird declines. *Biological Conservation* 120, 375–382.
- Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution* 17, 474–480.
- Scozzafava, S., De Sanctis, A., 2006. Exploring the effects of land abandonment on habitat structures and on habitat suitability for three passerine species in a highland area of Central Italy. *Landscape and Urban Planning* 75, 23–33.
- Seoane, J., Bustamante, J., Diaz-Delgado, R., 2005. Effect of expert opinion on the predictive ability of environmental models of bird distribution. *Conservation Biology* 19, 512–522.
- Seoane, J., Justribo, J.H., Garcia, F., Retamar, J., Rabadan, C., Atienza, J.C., 2006. Habitat-suitability modelling to assess the effects of land-use changes on Dupont's lark *Chersophilus duponti*: a case study in the Layna Important Bird Area. *Biological Conservation* 128, 241–252.
- Söderström, B., 2001. Seasonal change in red-backed shrike *Lanius collurio* territory quality – the role of nest predation. *Ibis* 143, 561–571.
- Söderström, B., Part, T., Erikson, S., Kavanagh, R.P., 1998. The effect of breeding habitat and nest site choice on Red-Backed Shrike (*Lanius collurio*) reproductive success: a comparison of clearcuts and grasslands. In: Yosef, R., Lohrer, F.E. (Eds.), *Shrikes of the World - II: Conservation Implementation. Proceedings of the Second International Shrike Symposium, 17–23 March 1996*, International Birdwatching Center in Eilat, Israel, pp. 74–78.
- Sokal, R.R., Rohlf, F.J., 1998. *Biometry: The Principles and Practice of Statistics in Biological Research*, third ed. W.H. Freeman, New York.
- Stoner, K.J.L., Joern, A., 2004. Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. *Ecological Applications* 14, 1306–1320.



- Thill, A., 1964. La Flore et la Végétation du Parc National de Lesse et Lomme. Ardenne et Gaume, Monographie 5.
- Thuiller, W., Brotons, L., Araujo, M.B., Lavorel, S., 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27, 165–172.
- Tryjanowski, P., Kuzniak, S., Diehl, B., 2000. Does breeding performance of red-backed shrike *Lanius collurio* depend on nest site selection? *Ornis Fennica* 77, 137–141.
- Tryjanowski, P., Karg, M.K., Karg, J., 2003. Diet composition and prey choice by the red-backed shrike *Lanius collurio* in western Poland. *Belgian Journal of Zoology* 133, 157–162.
- Van Horne, B., 2002. Approaches to habitat modelling: the tensions between pattern and processes and between specificity and generality. In: Scott, J.M. et al. (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Colelo, WA, pp. 7–21.
- Van Nieuwenhuysse, D., 1998. Conservation opportunities for the Red-Backed Shrike (*Lanius collurio*). In: Yosef, R., Lohrer, F.E. (Eds.), *Shrikes of the World - II: Conservation Implementation*. Proceedings of the Second International Shrike Symposium, 17–23 March 1996, International Birdwatching Center in Eilat, Israel, pp. 79–82.
- Van Nieuwenhuysse, D., 1999. Global Shrike Conservation: problems, methods and opportunities. *Aves* 36, 193–204.
- Van Nieuwenhuysse, D., 2000. Dispersal patterns of the Red-backed Shrike (*Lanius collurio*) in Gaume, Belgium. *Ring* 22, 65–78.
- Van Nieuwenhuysse, D., Vandekerckhove, K., 1992. Caractéristiques et typologie des territoires de la pie-grièche écorcheur (*Lanius collurio*) en Lorraine belge. *Aves* 29, 137–154.
- Van Nieuwenhuysse, D., Nollet, F., Evans, A.D., 1999. The ecology and conservation of the Red-backed Shrike *Lanius collurio* breeding in Europe. *Aves* 36, 179–192.
- Vanreusel, W., Van Dyck, H., 2007. When functional habitat does not match vegetation types: a resource-based approach to map butterfly habitat. *Biological Conservation* 135, 202–211.
- Vanreusel, W., Maes, D., Van Dyck, H., 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation Biology* 21, 201–212.
- Whittingham, M.J., Wilson, J.D., Donald, P.F., 2003. Do habitat association models have any generality? Predicting skylark *Alauda arvensis* abundance in different regions of southern England. *Ecography* 26, 521–531.
- Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D., Freckleton, R.P., 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecology Letters* 10, 25–35.
- Wiens, J.A., 2002. Predicting species occurrences: progress, problems, and prospects. In: Scott, J.M. et al. (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Colelo, WA, pp. 739–749.
- Yosef, R., 1994. Evaluation of the global decline in the true shrikes (Family Laniidae). *Auk* 111, 228–233.
- 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. *Ecological Modelling* 157, 261–280.