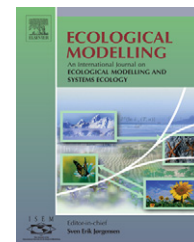


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/ecolmodel

Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis

Mathieu Basille^{a,*}, Clément Calenge^{a,b}, Éric Marboutin^c,
Reidar Andersen^d, Jean-Michel Gaillard^a

^a Université de Lyon, université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, 43 boulevard du 11 novembre 1918, Villeurbanne F-69 622, France

^b Office national de la chasse et de la faune sauvage, 95 rue Pierre Flourens, 34 000 Montpellier, France

^c Office national de la chasse et de la faune sauvage, Z.I. de Mayencin, 5 allée de Béthléem, 38 610 Gières, France

^d Museum of Natural History and Archaeology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

ARTICLE INFO

Article history:

Received 12 July 2006

Received in revised form

8 August 2007

Accepted 7 September 2007

Published on line 18 October 2007

Keywords:

Biplot

ENFA

Lynx

Lynx lynx

Marginality

Presence-only data

Specialization

Vosges mountains

ABSTRACT

We propose here some refinements of the ecological-niche factor analysis (ENFA) to describe precisely one organism's habitat selection. The ENFA is based on the concept of the ecological niche, and provides a measure of the realised niche within the available space from the computation of two parameters, the marginality and the specialization. By measuring the departure of the ecological niche from the average available habitat, the marginality identifies the preference of the individual, population, or species for specific conditions of the environment among the whole set of possibilities. The specialization appears as a consequence of the narrowness of the niche on some environmental variables. The ENFA is a factorial analysis that extracts one axis of marginality and several axes of specialization. We present here the use of biplots (i.e., the projection of both the pixels of the map and the environmental variables in the subspace extracted by the ENFA) as a way to identify the key-variables for management, assessing which habitat features are of prime importance and should be preserved or reinforced. With the help of this tool, we are now able to describe much more precisely the habitat selection of the organism under focus. In our application to the lynx in the Vosges mountains, based on sightings as well as other indices of lynx presence, we thus underlined a strong avoidance of agricultural areas by the lynx. We also highlighted the relative indifference of the lynx to the proximity of artificial areas and at the opposite, the sensitivity to the proximity of highways. The ENFA provides a suitable way to measure habitat use/selection under a large range of ecological contexts and should be used to define precisely the ecological niche and therefore identify the characteristics searched for by the organism under study.

© 2007 Elsevier B.V. All rights reserved.

1. Introduction

Assessing the relationships between individuals in a population and their environment is required in most ecological

studies, both from a theoretical and a management viewpoint. In particular the habitat use and the intensity of habitat selection displayed by individuals are likely to influence markedly the response of organisms to density dependence and envi-

* Corresponding author. Tel.: +33 472448437; fax: +33 478431388.

E-mail address: basille@biomserv.univ-lyon1.fr (M. Basille).

0304-3800/\$ – see front matter © 2007 Elsevier B.V. All rights reserved.

doi:10.1016/j.ecolmodel.2007.09.006

ronmental variation (Gilpin and Hanski, 1991; Tilman and Kareiva, 1997). The increasing availability of advanced tools such as geographic information system (GIS), and the ever increasing power of computers offer the possibility to include much more biological information in the analyses. This allows habitat use/selection to be assessed in a much more precise way (Guisan and Zimmermann, 2000). Consequently, work has been performed to develop new multivariate statistics in order to account for the complexity of the environment.

The lack of absence data in most sampling designs so far applied to study habitat use or selection, is one of the major problems ecologists have to solve (Hirzel et al., 2002a; Soberón and Peterson, 2005). While collecting reliable data on animal presence is straightforward in most case studies, it is difficult to assess the true absence of an animal in a given habitat. Are the animals really absent because the environment is not suitable for the species? Or because the animals did not yet colonize their whole suitable habitat (hunting, history of colonization, demographic stochasticity)? Or do we face an apparent absence because the animals are present, but not detected during the sampling, or temporarily absent (Martin et al., 2005)? For all these reasons, the absence of observation at a given location cannot be reliably interpreted as a true absence, thus we have to rely on the presence data only. The well-known concept of ecological niche (Hutchinson, 1957) provides a suitable way to analyse presence-only data. It is defined as the n -dimensional hypervolume, in which every point corresponds to a state of the environment which would permit the species to exist indefinitely. Each environmental variable then corresponds to a dimension in the so-called ecological space which defines the available habitat for the animals under study. The observed presences are used to assess the utilization of the space by the animals, i.e., the ecological niche (Fig. 1). Although originally developed to describe the ecological requirements of a species, the concept of ecological niche can easily be applied to other scales of biological organisation (community for larger scale, see e.g., Doleddec et al., 2000, individual for finer scale, see e.g., Calenge et al., 2005). Here, we will focus on the analyses of the distribution of populations of a given species, i.e., corresponding to a second-order selection

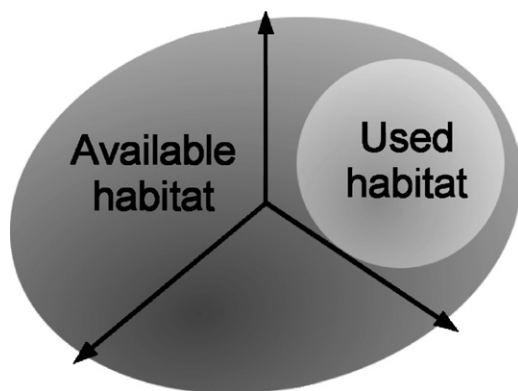


Fig. 1 – Representation of the ecological niche. The arrows identify the environmental variables defining the ecological space. The dark grey cloud stands for the available habitat and the light grey cloud stands for the used habitat, i.e., the ecological niche.

study according to Johnson's selection order (Johnson, 1980). However, the concept of ecological niche as defined above could be used for the study of habitat selection at all levels (e.g., the selection of the distribution range by a species, the selection of the home range of an animal within a region, the selection of patches within home range, etc.).

Several statistical analyses have been recently developed to assess habitat selection using presence-only data (Elith et al., 2006). These methods can be classified into two complementary approaches (see a review in Pearce and Boyce, 2006): exploratory analyses, which aim at extracting the characteristics of the environment used by a given organism (e.g., Calenge et al., 2005; Doleddec et al., 2000) and modelling analyses (Manly et al., 2002). Exploratory analyses can be seen as a required preliminary for modelling analyses as they lead to select the variables of interest to model the habitat. Among these, the ENFA (ecological-niche factor analysis, Hirzel et al., 2002a) searches for directions in the ecological space so that (i) the difference between the conditions used in average by the species and the conditions available on the study area (i.e., the marginality) is maximised, and (ii) the ratio between the variance of available conditions on the variance of conditions used by the species (specialisation) is maximised. According to the structure of Austin (2007), the ENFA belongs to the theory of the ecological niche, relies on presence-only data and takes place in the well-studied family of multivariate analyses. Up to now, biologists have used the ENFA in order to build habitat suitability maps. Such maps rely on the assumption that habitat suitability in a given pixel of a map can be estimated by the probability of presence of the individual, population, or species under study. Several algorithms have been proposed and compared to assess the reliability of the maps (Hirzel and Arlettaz, 2003b, a). The ENFA has then been used to predict the potential habitat in a large range of animal taxons (insects: e.g., Gallego et al., 2004; cetaceans: e.g., Compton, 2004; birds: e.g., Hirzel et al., 2004; mammals: e.g., Dettki et al., 2003; Zimmermann, 2004), in some plants (e.g., Zaniewski et al., 2002) and rare or endangered species (e.g., Reutter et al., 2003).

However, the usefulness of the ENFA in other ecological contexts have been overlooked. In addition of providing an answer to the where-question ("Where can the organisms establish?"), the ENFA can be used to answer the what-question ("What do the organisms search for?").

The ENFA is indeed suitable to assess the habitat features that are preferred by the individual, population or species under study. Therefore, while valuable, the construction of habitat suitability maps appears to us as a secondary task after having identified the processes behind the habitat use or selection by a given individual, population, or species.

In this paper, we develop the required refinements of the ENFA to reach such a goal, and we show how the use of biplots (i.e., the projection of both the ecological niche and the environmental variables on the subspace defined by the axes of the ENFA) is an essential step in that direction. As an illustration of the usefulness of our approach, we use these extensions of the ENFA in the study of the habitat selection by the lynx (*Lynx lynx*) in the Vosges mountains (France). The data used corresponds to sightings as well as other indices (scats, hairs, carcasses, etc.) of lynx presence, the kind of presence-only

data that perfectly fulfills the requirements of the ENFA. All the statistical procedures are implemented in the R-software (R Development Core Team, 2005) within the R-package “ade-habitat” (Calenge, 2006).

2. The ecological-niche factor analysis

2.1. Description of the design

The available habitat is described by a set of raster maps of the study area, giving the values of P environmental variables in N pixels. Let Z be the $N \times P$ matrix with the values of the P variables in the N pixels; Z defines a cloud of points (the available space) in the P -dimensional ecological space (Fig. 2A). The Z matrix is column-centered and scaled so that its variance is equal to 1 and the centroid (barycenter) of the scatterpoint corresponds to the origin O of the ecological space and represents the average available habitat. To each available pixel is associated an “availability weight” describing the availability of the pixel to the species, population or individual (with weights summing to 1; defaulting to $1/N$ for all pixels). Let D be the $N \times N$ matrix containing these weights on the diagonal (defaulting to $D = \text{Diag}(1/N)$).

The locations of the individual, population, or species sampled define the used habitat. The vector p of length N provides the proportion of locations in each pixel and defines the utilization weights (with weights summing to 1). Let D_p be the $N \times N$ matrix containing these utilisation weights p on the diagonal: $D_p = \text{Diag}(p)$.

The points in the available space for which the corresponding utilization weights are upper than zero define the used

space, i.e., the ecological niche. Therefore the centroid G of the niche corresponds to the average used habitat (Fig. 2A).

2.2. Concept of marginality

The marginality is measured as the squared distance from the mean available space to the mean used space. It is geometrically defined as the squared norm of the vector from the origin O of the ecological space to the centroid G of the niche (Fig. 2A). Let m be this vector:

$$m = Z^t D_p 1_N \quad (1)$$

where Z^t is the transpose of Z , 1_N is a N -vector of 1.

The marginality is then the squared norm of the vector m :

$$M = m^t m \quad (2)$$

The vector of marginality is normed for further analyses:

$$q = \frac{m}{\sqrt{m^t m}} \quad (3)$$

The marginality measures a position and expresses the magnitude of the deviation of the niche relative to the available space (Fig. 2A). The higher the marginality, the more the niche deviates from the average conditions of the available habitat. When marginality is high, the individual, population, or species are present in areas displaying quite different habitat features compared to what is available.

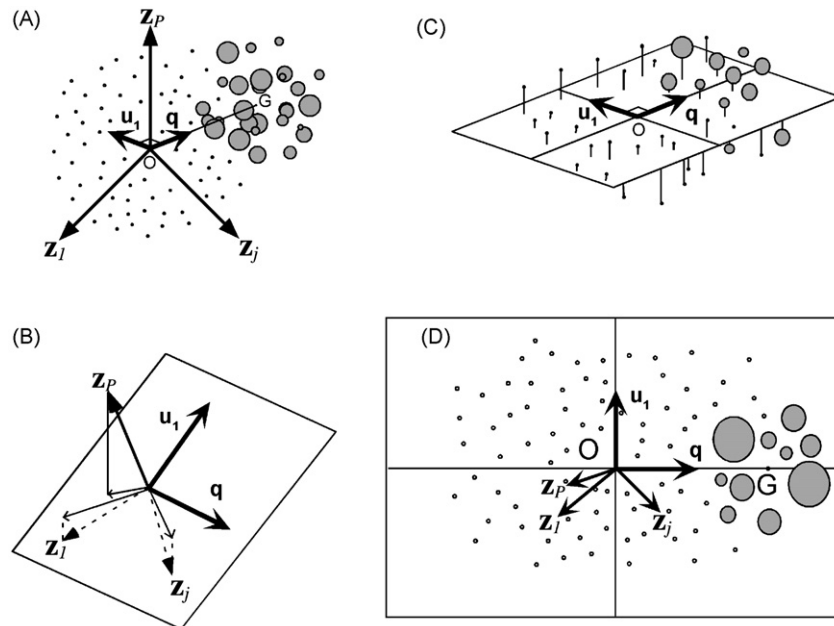


Fig. 2 – Construction of the biplot built from the ENFA. (A) The ecological space is defined here by three environmental variables z_1 , z_j and z_p . The marginality vector m connects the centroid of the available space O to the centroid of the used space G . The vector q corresponds to the marginality vector normed to 1. The vector u_1 corresponds to the first vector of specialization. **(B)** The vectors q and u_1 are orthogonal and define the plane on which the points are projected. **(C)** The variables are projected in the same plane. **(D)** The simultaneous representation of coordinates of the points and the variables on the same plot leads to the best representation of the ecological niche, and an easy interpretation of it.

2.3. Concept of specialization

The specialization measures the narrowness of the niche. The specialization corresponds to the axes on which the ratio of variance of the available habitat to the used habitat is the highest. We are thus looking for the $P - 1$ vectors orthogonal to the vector of marginality that lead to extract most of the specialization. Such a procedure is equivalent to find a vector \mathbf{u} matching the following conditions:

$$\mathbf{u}^t \mathbf{u} = 1 \quad (4)$$

$$\mathbf{u}^t \mathbf{m} = 0 \quad (5)$$

$$R = \frac{\mathbf{y}^t \mathbf{D}_p \mathbf{y}}{\mathbf{y}^t \mathbf{D}_p \mathbf{y}} \quad \text{Max} \quad (6)$$

where $\mathbf{Z}\mathbf{u} = \mathbf{y}$.

In other words, the vector \mathbf{u} is of length 1, and is orthogonal to the marginality vector \mathbf{m} . Because the vector \mathbf{u} is normed, the vector \mathbf{y} is the projection of the rows of \mathbf{Z} on the vector \mathbf{u} . The vector \mathbf{y} contains the scores of the pixels projected on \mathbf{u} . The condition (6) therefore implies that the specialization is maximized on the vector \mathbf{u} .

We compute the covariance matrices $\mathbf{S} = \mathbf{Z}^t \mathbf{D}_p \mathbf{Z}$ and $\mathbf{G} = \mathbf{Z}^t \mathbf{D} \mathbf{Z}$ and define $\mathbf{x} = \mathbf{S}^{-1/2} \mathbf{m}$, $\mathbf{b} = \mathbf{x} / \sqrt{\mathbf{x}^t \mathbf{x}}$ and $\mathbf{W} = \mathbf{S}^{-1/2} \mathbf{G} \mathbf{S}^{-1/2}$. Let the matrix \mathbf{H} :

$$\mathbf{H} = (\mathbf{I}_v - \mathbf{b}\mathbf{b}^t) \mathbf{W} (\mathbf{I}_v - \mathbf{b}\mathbf{b}^t) \quad (7)$$

If \mathbf{H} is of rank v , then this matrix has v non-null eigenvalues, associated to v eigenvectors \mathbf{v}_i . Hirzel et al. (2002a) have shown that the eigenvectors \mathbf{v}_i of the matrix \mathbf{H} are related to the vectors \mathbf{u}_i by the equation:

$$\mathbf{u}_i = \frac{\mathbf{S}^{-1/2} \mathbf{v}_i}{\sqrt{\mathbf{v}_i^t \mathbf{S}^{-1} \mathbf{v}_i}} \quad (8)$$

The vector \mathbf{u}_i is the i th vector of the analysis. The eigenvalues λ_i are the values of the specialization on the vectors \mathbf{u}_i .

Note that:

$$\mathbf{u}_i^t \mathbf{u}_j = \frac{\mathbf{v}_i^t \mathbf{S}^{-1} \mathbf{v}_j}{\sqrt{\mathbf{v}_i^t \mathbf{S}^{-1} \mathbf{v}_i} \cdot \sqrt{\mathbf{v}_j^t \mathbf{S}^{-1} \mathbf{v}_j}} \neq 0 \quad (9)$$

The axes of specialization are therefore not orthogonal.

The specialization measures the dispersion of the ecological niche and expresses the restriction of the ecological niche on some particular directions (Fig. 2A). The higher the specialization, the more restricted is the niche in that dimension. A high specialization on a given dimension indicates that the individual, population, or species does not tolerate large variation of the habitat features that mostly determine that dimension.

2.4. Identifying the ecological niche

The vectors \mathbf{q} and \mathbf{u}_i provide the scores of the environmental variables on, respectively, the marginality axis and the special-

ization axes (Fig. 2B). The coordinates of the pixels are defined with $\mathbf{f} = \mathbf{Z}\mathbf{q}$ on the marginality axis, and $\mathbf{y}_i = \mathbf{Z}\mathbf{u}_i$ on the specialization axes since the vectors \mathbf{q} and \mathbf{u}_i are of length 1. Since the vectors of specialization \mathbf{u}_i are orthogonal to the vector of marginality \mathbf{m} (or \mathbf{q}), the plot of \mathbf{f} and \mathbf{y}_i displays the projection of the rows of \mathbf{Z} on the plane $\mathbf{q} - \mathbf{u}_i$, which exactly (i.e., not altered, Fig. 2C) corresponds to the best possible 'photograph' of the ecological niche *sensu* Hutchinson (1957).

We can project the used and available points in the ecological space on the plane defined by the marginality axis and one specialisation axis to obtain a biplot (Fig. 2D) in the sense of Gabriel (1971). This biplot is of primary help to assess the habitat selection, with respect to the marginality and the specialization. On the biplot, the environmental variables are represented by an arrow with two components of importance: the length and the direction. The length of the arrow identifies the contribution of a given environmental variable to the definition of the axes of the ENFA, i.e., their influence on the position and volume of the ecological niche within the available habitat. The direction measures how this contribution is decomposed on the marginality or specialization axes. The first step is then to identify the variables which correspond to the longest arrows. These are the critical variables in terms of habitat selection. In the second place, the relative contribution of the marginality or specialization is assessed by the coordinates of the arrow on the corresponding axis.

2.5. The relationship between the marginality axis and the specialization axis

It is noteworthy that the specialization is constrained by the marginality: all the specialization axes are orthogonal to the marginality axis, but not to each other. To conserve the distances and angles of the projection of both variables and pixels in the biplot, the use of an orthogonal base is required. Therefore, we can only use the plan formed by the marginality axis and any specialization axis to compute the biplot with a representation of the niche not altered, i.e., the distances and angles between points are exact. Conversely, the specialization axes are not necessarily orthogonal so that the projection of the niche in the plan formed by two specialization axes will be twisted because of the straightening of the specialization axes in the biplot. Note that the marginality axis in itself expresses some specialization (the higher the marginality, the higher is the specialization, due to the departure of the ecological niche from the centroid of the ecological space). If the ecological niche is most narrow in the dimension of the marginality axis, the main part of the specialization will already be taken on this axis. The first axis of specialization which is next extracted is constrained to be orthogonal to the marginality axis and will not explain the main part of specialization but the remaining part of it, thus resulting in a meaningless analysis of specialization. However, it is possible to estimate the specialization accounted for in the dimension of the marginality axis: it is given by the ratio of variances projected on the marginality axis of the available habitat to the used habitat. This ratio is computed in the same way as the eigenvalues of specialization and can be compared to them.

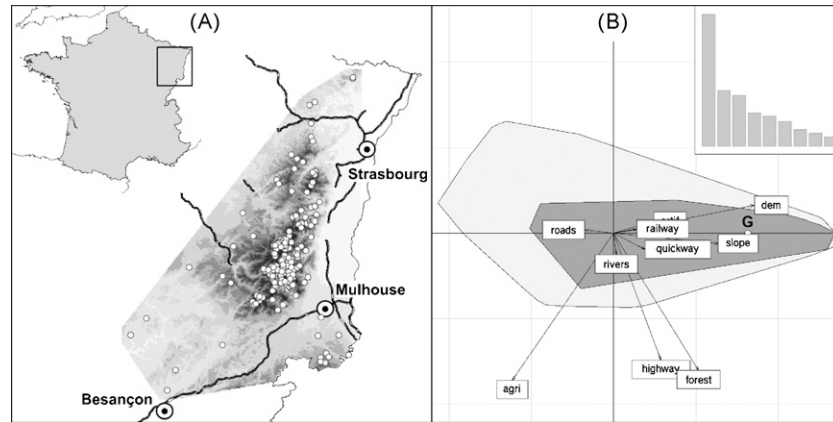


Fig. 3 – Results of the illustration. (A) The study area is situated in the eastern part of France, in the southern part of the Vosges mountains. The lines represent the highways and the dots are the locations of lynx used in the analysis. The elevation is represented in the background. (B) Biplot of the ENFA, in the plane formed by the marginality axis (X-axis) and the first specialization axis (Y-axis). The light and dark areas correspond to the minimum convex polygon enclosing all the projections of the available and used points, respectively. The white dot G corresponds to the centroid of the used habitat. The arrows are the projections of the environmental variables. The insert gives the eigenvalues of specialization. One axis of specialization explains most of the specialization and is kept for the analysis.

3. Application to a case study: the lynx in the Vosges mountains (France)

3.1. Study area

From 1983 to 1993, 21 lynx have been reintroduced to the Vosges mountains (Vandel et al., 2006). The issuing population later colonized the whole southern part of the massif. The study area is about 16,500 km²(Fig. 3A) and is bordered by an intensive human-used area on the eastern part (along the Strasbourg–Mulhouse connection) connected by highways to the northern and southern directions. The lynx mainly colonized the central part of the area that includes a large patch of high-elevation deciduous forests (from 500 to 1 400 m a.s.l.), with almost no agriculture and urbanized areas. The surrounding area has lower elevation (less than 500 m a.s.l.) and is more used for agriculture and human activities.

3.2. Data

The French Lynx network organised the collection of all signs of presence of the lynx, including sightings, carcasses (of both lynx and preys), hairs, tracks, and scats (Vandel and Stahl, 2005). During the study period (1998–2002), 292 indices were collected. A minimum convex polygon was drawn from these locations, and a buffer of 5 km was added to define the available habitat for the lynx. The choice of a 5 km buffer corresponded to the average radius of a female lynx home-range in the area (around 80 km², see Vandel et al., 2006). We selected some environmental variables that could a priori affect the use of space by the lynx within the available habitat. We included characteristics of the physical environment and the vegetation, as well as the influence of humans (Table 1).

3.3. Assessing the ecological niche of the lynx: results and interpretation

We first normalized through a square root transformation all the environmental variables that deviated from normality. Indeed, although the ENFA is quite robust to departure from normality, it is optimal when the environmental variables are unimodal and roughly symmetric. We then performed the first step of the ENFA that involves the selection of the number of specialization axes to retain. The diagram of the eigenvalues clearly indicated that only one axis accounted for the main part of specialization (Fig. 3B). Thus, in the present case, only two axes (i.e., the axis of marginality and the first axis of specialization) accounted for most of the information.

The biplot of the ENFA provided us much information. The distance between the centroid of the ecological niche and the centroid of the available habitat was quite high, resulting in a pronounced marginality (X-axis, Fig. 3B), i.e., the optimum of the species was rather different from the mean available conditions. On the other hand the specialization (Y-axis, Fig. 3B)

Table 1 – Environmental variables used in the analysis

Name	Description
agri	Proportion of agricultural areas within a radius of 5 km
artif	Distance to artificial areas
dem	Digital Elevation Model: altitude
forest	Proportion of forests within a radius of 5 km
highway	Distance to highways
quickway	Distance to main roads (without highways)
railway	Distance to railways
rivers	Distance to rivers
roads	Density of all kind of roads within a radius of 5 km
slope	Slope

corresponded to an eigenvalue of 8, which means that the variance of the available habitat was eight times higher than the variance of the ecological niche in this dimension, thus the ecological niche was much narrower than the available habitat. The significance of both the marginality and the first eigenvalue of specialization was assessed with a Monte–Carlo test. One thousand sets of 292 localizations were randomly distributed over the area. For each one, the marginality and the specialization were computed, and the actual values were compared with these random distributions. Both statistics were highly significant ($P < 0.001$). The most relevant information was provided by the projection of the environmental variables in this new space (Fig. 3B). Five variables were of prime importance for the analysis: the elevation, the slope, the proportion of deciduous forest, the distance to highways and the proportion of agricultural areas. The elevation and the slope contributed the most to the marginality, followed by the proportion of agricultural areas, the proportion of deciduous forest, and to a lesser extent the distance to highways. The lynx searched for high values of both elevation and slope, for low use of agricultural area, for high proportions of forest, and avoided highways. The proportion of deciduous forest, the distance to highways and the proportion of agricultural areas contributed the most to the specialization axis. However, the proportions of deciduous forest and agricultural areas were strongly negatively correlated (correlation of -0.95) so that their contribution at the same level on the specialization axis vanishes. The lynx was thus not tolerant to the variation of distance to highways (i.e., the lynx was restricted on a limited range on this variable), with a mean shifted toward high distances.

The lynx was reintroduced to the central part of the study area characterized by a high elevation, a dense forest cover, and a low human use, however, later colonizing the whole central part, but avoiding the proximity of the surrounding area and particularly the eastern part, characterized by the Strasbourg–Mulhouse highway. Based on the interpretation of the marginality using the biplot, we can assess that the lynx was actually searching for a high elevation (and therefore high slopes), a dense forest cover and was avoiding highways and high agricultural use. Even more interestingly, the ENFA allowed us to assess the high specialization (i.e., low tolerance of variations) on the distance from highways. We thus found that the lynx was restricted to areas with low values of agricultural use, far from highways, and with a high proportion of forest, and was really sensitive to departure from a high distance to highways.

Another important result highlighted by the ENFA was the weak influence of artificial areas on lynx habitat use. While apparently counter-intuitive, such a result is actually not really surprising. The lynx can be seen really close to houses (Bunnefeld et al., 2006); additionally, Sunde et al. (1998) already showed that the lynx could endure a high human activity, provided that there is a high density of forested plots. From a human point of view, the lynx was just restricted to low agricultural-use areas far from the highways, thus, the eastern part was avoided due to a high proportion of agricultural areas and the presence of a highway, but not because of the presence of two big cities. Finally, the critical habitat features for the lynx included the proportion of forest and

agricultural areas, and the distance from highways. The apparent selection for a high elevation and steep slopes could just be a byproduct of the proportion of forest, agricultural areas, and highways in the area. High elevation and steep slopes indeed occur in areas which are not suitable for agriculture and highways.

4. Discussion

In habitat selection studies, the where-question (“Where can the organisms establish?”) has been under focus for many years. With the assumption that this probability of occurrence is proportional to the quality of habitat, many methods have been developed to compute habitat suitability maps (Clark et al., 1993; Guisan and Zimmermann, 2000). Computing habitat suitability maps allows the identification of suitable areas not yet, or not anymore colonized, and critical areas that need to be preserved, such as faunistic corridors (Gibson et al., 2004; Chefaoui et al., 2005). It can also be used to assess the habitat loss and fragmentation (Ciarniello et al., 2003), to estimate the population size, and to simulate spatial population dynamics (Mladenoff et al., 1995; Fielding and Bell, 1997).

Although answering the where-question is of first importance, Rushton et al. (2004) pointed out the need to understand the factors determining the distribution of the population or species. This answer to the what-question (“What do the organisms search for?”) is needed to know as well as possible the ecology of the individual, population or species under study. Before a conservation plan is set, any decision should be taken with a lot of care, based on the knowledge of the processes that drive the species distribution. Soberón and Peterson (2005) underlined the lack of effective tools for exploring, analyzing, and visualizing ecological niches in many-dimensional environmental space. We present here such a tool with a new development of the ENFA (ecological-niche factor analysis).

The ENFA is based on the concept of the ecological niche, and provides a measure of the realised niche within the available space from the computation of two parameters with a clear biological meaning, as first described by Perrin (1984). By measuring the departure of the ecological niche from the average available habitat, the marginality identifies the preference of the individual, population, or species for specific conditions of the environment (e.g., high proportion of forests, high altitude, etc. in our case study) among the whole set of possibilities. When the niche is unimodal, the position of the centroid of the niche defines the optimum of the individual, population, or species, i.e., the conditions of the environment associated to the highest probability of presence. The specialization appears as a consequence of the narrowness of the ecological niche that involves the restriction of the occurrence on some environmental variables. It can also be interpreted as the sensitivity of the individual, population or species to variations around its optimum, highlighting limiting factors for the use of the space.

The ENFA presents several advantages. First, being fundamentally a descriptive analysis, it does not rely on any underlying hypothesis for the data, in particular autocorre-

lation is not a problem as such. However, for the sake of interpretation, the niche is supposed to be normal multivariate. Second, the ENFA relies on the concept of ecological niche and is therefore especially suited to a presence-only design (Hirzel et al., 2002a). The ENFA was first implemented in the Biomapper software (Hirzel et al., 2002b) which is aimed at computing habitat suitability maps, i.e., answering the where-question. The widespread use of this software resulted in biologists computing such maps, without looking carefully at the factors that are responsible for this map. Moreover, the accuracy of such maps has been questioned (Calenge et al., in press) and as it depends on the ad hoc algorithm used (Hirzel and Arlettaz, 2003b, a), it can be less accurate than classical linear modelling techniques in some cases (see Olivier and Wotherspoon, 2006, for an example). The ENFA, however, provides a way to identify precisely the ecological niche and therefore to answer the what-question. For this task the biplot we proposed here is probably one of the best tools (Gabriel, 1971). Marginality and specialization can be used to identify key-variables for management, assessing which habitat features are of prime importance and should be preserved or reinforced. In our application to the lynx in the Vosges mountains, we thus underlined the importance of the proportion of agricultural areas, on which the lynx had a clear preference for low values. Highlighting the relative indifference of the lynx to the proximity of artificial areas and at the opposite, the sensitivity to the proximity of highways, we got a precise picture of the influence of the human use of land for the ecology of the lynx. Thus, balancing the development of human activities and the conservation of viable lynx populations, such information will be crucial.

The ENFA provides a suitable way to measure habitat use/selection under a large range of ecological contexts. The ENFA allows us to compute uncorrelated axes from correlated variables. The method presented here uses the same core procedure as in Hirzel et al. (2002a) but we incorporated the utilization weights so that the method can handle the case where several occurrences of the species fall in the same pixel. Additionally, although we only used quantitative variables as an illustration, Calenge (2005) generalized the theory to show that qualitative variables can be included in the analysis as well. Consequently, the ENFA is probably the only analysis based on the concept of ecological niche that describes precisely the specialization, in addition to the marginality. As the marginality and the specialization are two complementary measures of the niche with different status, future work would need to tease apart the analyses of marginality and specialization. By proceeding step by step we could have a proper representation of the specialization of the organism under study, in addition to its marginality.

Software availability

The ENFA is implemented in the R-package “adehabitat” (Calenge, 2006), which collects many tools for the analysis of habitat selection by animals and trajectories of individuals. The R-software itself (R Development Core Team, 2005) is freely available on the Internet at the URL <http://www.r-project.org/>.

Acknowledgments

We warmly thank everyone involved in the French lynx network in countless hours of data collection. The French Ministry of Research, the University of Lyon and the Office National de la Chasse et de la Faune Sauvage (ONCFS) provided financial support of this work. We are indebted to Alexandre Hirzel for constructive comments on earlier drafts of the manuscript.

REFERENCES

- Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol. Model.* 200, 1–19.
- Bunnefeld, N., Linnell, J.D.C., Odden, J., van Duijn, M.A.J., Andersen, R., 2006. Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. *J. Zool.* 270, 31–39.
- Calenge, C., 2005. Des outils statistiques pour l'analyse des semis de points dans l'espace écologique. Ph.D. Thesis. Université Claude Bernard Lyon 1.
- Calenge, C., 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519.
- Calenge, C., Darmon, G., Basille, M., Loison, A., Jullien, J.-M., in press. The factorial decomposition of the mahalanobis distances in habitat selection studies. *Ecology*.
- Calenge, C., Dufour, A., Maillard, D., 2005. K-select analysis: a new method to analyse habitat selection in radio-tracking studies. *Ecol. Model.* 186, 143–153.
- Chefaoui, R.M., Hortal, J., Lobo, J.M., 2005. Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian Copris species. *Biol. Conserv.* 122, 327–338.
- Ciarniello, L.M., Boyce, M.S., Beyer, H., 2003. Resource selection function for the plateau landscape of the Parsnip grizzly bear project (an update for 2003). Tech. Rep., British Columbia Ministry of Forests.
- Clark, J.D., Dunn, J.E., Smith, K.G., 1993. A multivariate model of female black bear habitat use for a geographic information system. *J. Wildl. Manage.* 57, 519–526.
- Compton, R.C., 2004. Predicting Key Habitat and Potential Distribution of Northern Bottlenose Whales (*Hyperoodon ampullatus*) in the Northwest Atlantic Ocean. Master's Thesis. University of Plymouth.
- Dettki, H., Lofstrand, R., Edenius, L., 2003. Modeling habitat suitability for moose in coastal northern Sweden: empirical vs. process-oriented approaches. *Ambio* 32, 549–556.
- Doledec, S., Chessel, D., Gimaret Carpentier, C., 2000. Niche separation in community analysis: a new method. *Ecology* 81, 2914–2927.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, 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., Peterson, A.T., Phillips, S.J., Richardson, K., 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.
- Fielding, A., Bell, J., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.

- Gabriel, K., 1971. The biplot graphic display of matrices with application to principal component analysis. *Biometrika* 58, 453–467.
- Gallego, D., Canovas, F., Esteve, M.A., Galián, J., 2004. Descriptive biogeography of *Tomicus* (Coleoptera: Scolytidae) species in Spain. *J. Biogeogr.* 31, 2011–2024.
- Gibson, L.A., Wilson, B.A., Cahill, D.M., Hill, J., 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *J. Appl. Ecol.* 41, 213–223.
- Gilpin, M., Hanski, I. (Eds.), 1991. *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London, 336 pp.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186.
- Hirzel, A.H., Arlettaz, R., 2003a. Environmental-envelope based habitat-suitability models. In: Manly, B.F.J. (Ed.), *Proceedings of the First Conference on Resource Selection by Animals*. Omnipress, Laramie, USA, pp. 67–76.
- Hirzel, A.H., Arlettaz, R., 2003b. Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. *Environ. Manage.* 32, 614–623.
- 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*. Lab. for Conservation Biology. Department of Ecology and Evolution, University of Lausanne. <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. *J. Appl. Ecol.* 41, 1103–1116.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbour Symp. Quant. Biol.* 22, 415–427.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. *Resource Selection by Animals. Statistical Design and Analysis for Field Studies*, 2nd ed. Kluwer Academic, Dordrecht, The Netherlands.
- Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J., Possingham, H.P., 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecol. Lett.* 8, 1235–1246.
- Mladenoff, D.J., Sickley, T.A., Haight, R.G., Wydeven, A.P., 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conserv. Biol.* 9, 279–294.
- 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. Model.* 195, 187–204.
- Pearce, J.L., Boyce, M.S., 2006. Modelling distribution and abundance with presence-only data. *J. Appl. Ecol.* 43, 405–412.
- Perrin, N., 1984. Contribution à l'écologie du genre *Cepaea* (Gastropoda): approche descriptive et expérimentale de l'habitat et de la niche écologique. Ph.D. Thesis. Faculté des Sciences de l'Université de Lausanne.
- R Development Core Team, 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. <http://www.R-project.org>.
- Reutter, B.A., Helfer, V., Hirzel, A.H., Vogel, P., 2003. Modelling habitat-suitability using museum collections: an example with three sympatric *Apodemus* species from the Alps. *J. Biogeogr.* 30, 581–590.
- Rushton, S.P., Ormerod, S.J., Kerby, G., 2004. New paradigms for modelling species distributions? *J. Appl. Ecol.* 41, 193–200.
- Soberón, J., Peterson, A.T., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Infor.* 2, 1–10.
- Sunde, P., Stener, S.Ø., Kvam, T., 1998. Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. *Wildl. Biol.* 4, 177–183.
- Tilman, D., Kareiva, P. (Eds.), 1997. *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, 368 pp.
- Vandel, J.-M., Stahl, P., 2005. Distribution trend of the Eurasian lynx (*Lynx lynx*) populations in France. *Mammalia* 69, 145–158.
- Vandel, J.-M., Stahl, P., Herrenscheidt, V., Marboutin, E., 2006. Reintroduction of the lynx into the Vosges mountain massif: from animal survival and movements to population development. *Biol. Conserv.* 131, 370–385.
- Zaniewski, A.E., Lehmann, A., Overton, J.M., 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecol. Model.* 157, 261–280.
- Zimmermann, F., 2004. Conservation of the Eurasian lynx (*Lynx lynx*) in a Fragmented Landscape—Habitat Models, Dispersal and Potential Distribution. Ph.D. Thesis. Faculté de biologie et de médecine de l'Université de Lausanne, Département d'Ecologie et Evolution, Lausanne.