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Ecological niche shifts and environmental space anisotropy: a cautionary note

Desplazamientos en el nicho y la anisotropía del espacio ambiental: una nota precautoria

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Abstract. The anisotropic structure of climatic space may cause significant (and to a large extent unappreciated) non-evolutionary niche shifts. This can be seen mostly in the context of spatial transferability of ecological niche models. We explore this effect using a virtual species in the United States. We created a simple virtual species by postulating its fundamental niche as an ellipse in a two-dimensional realistic climatic space. The climatic combinations defined by the ellipse were projected in the geography of the United States and 2 regions of equal area were selected. The structure of niche in the 2 areas is compared. It is shown that the 2 regions have differently positioned subsets of the environmental space, which creates “shifts” in the realized niches despite the fact that no evolution and no biotic interactions are present. The most parsimonious hypothesis when ecological niche modeling reveals shifts in the realized niche is that environmental space is heterogeneous. Without considering differences in the structure of environmental space no speculation about niche evolution or the role of competitors should be attempted.

Key words: fundamental niche, realized niche, existing niche, ecological niche modeling, species distribution modeling, environmental space.

Resumen. La estructura anisotrópica del espacio climático puede causar desplazamientos significativos no evolutivos en los nichos de las especies. Este efecto poco apreciado en la literatura se manifiesta con gran claridad cuando se realizan transferencias espaciales de modelos de nicho ecológico. Se explora este efecto utilizando una especie virtual en los Estados Unidos. Se creó una especie virtual simplificada postulando su nicho fundamental en forma de una elipse en un espacio realista de 2 dimensiones. Las combinaciones climáticas definidas por la elipse se proyectaron en la geografía de los Estados Unidos y se seleccionaron 2 regiones de igual superficie espacial. Se compara la estructura del nicho en las 2 regiones, mostrando que estas 2 regiones espaciales presentan subconjuntos distintos del espacio de variables ambientales, lo cual induce “desplazamientos” en los nichos realizados, a despecho de que no existió evolución del nicho fundamental y de que no hay competidores ni otras interacciones bióticas presentes. Al modelar nichos ecológicos y transferirlos espacialmente, si se revelan desplazamientos en los nichos realizados, la hipótesis más parsimoniosa para explicar los desplazamientos es que el espacio ambiental tiene diferente estructura en las diferentes localidades. Sin considerar la estructura del espacio ambiental no debe especularse sobre evolución del nicho, ni sobre posibles efectos bióticos sobre él.

Palabras clave: nicho fundamental, nicho realizado, nicho existente, modelación de nichos ecológicos, modelación de distribuciones de especies, espacio medioambiental.

Introduction

Ecological niche modeling (ENM) is increasingly being used to predict potential ranges of invasive species (Soberón et al., 2001; Peterson, 2003; Thuiller et al., 2005; Ficetola et al., 2007). An important assumption in making such exercises feasible is that of conservatism in the ecological niche characteristics (Peterson et al., 1999; Ackerly, 2003; Wiens and Graham, 2005; Peterson, 2011): in essence, the

idea that the position and shape of the fundamental ecological niche evolve slowly relative to the invasion process. If the fundamental niche of a species is not conserved, a species would be able to invade novel regions of the world presenting environmental conditions very different from the original ones, and predictivity of the phenomenon would be nil. Similar reasoning applies to many other applications of the niche modeling idea: forecasting effects of global climate change (Thomas et al., 2004), hindcasting historical distributions (Waltari et al., 2007), etc.

Several recent studies have concluded that particular species invasions are associated with niche shifts

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(Broennimann et al., 2007; Fitzpatrick et al., 2007; Medley, 2010). These shifts are evidenced by displacements in the position of clouds of invaded-range occurrence points in environmental space relative to the environmental space of the native range. Niche shifts have been attributed to evolution of the fundamental niche, or to changes in its expression owing to presence of competitors, predators, or pathogens (Randin et al., 2006; Broennimann et al., 2007). However, another possible cause is simply that the structure of the environmental space differs between the 2 regions where the species is being studied (Elith and Graham, 2009). This last possibility is not always considered carefully, although the problem was recognized in the early niche measurement literature (Colwell and Futuyma, 1971; Green, 1971; Carnes and Slade, 1982). Nonetheless, this point has deep implications for niche modeling and for analysis of niche conservatism and shifts.

To clarify the issue, we begin by establishing some terminology. Using terminology and symbols may appear unnecessary, if not downright pedantic, but in the end it helps significantly to prevent confusion when referring to complex relationships between concepts. Ecological niche modeling moves in a duality (Colwell and Rangel, 2009) of a geographic space (\mathbf{G}) and the space (\mathbf{E}) of environmental combinations of scenopoetic variables (Hutchinson, 1978), as illustrated in Figure 1. \mathbf{G} , the geographic region relevant to the problem at hand is divided into a grid, and for every cell g in \mathbf{G} , we have a vector $\vec{e}(g)$ of environmental variables. Geographic information systems allow mapping from portions of \mathbf{G} to \mathbf{E} and *vice versa* (Guisan and Zimmermann, 2000). Typically, E-spaces are anisotropic (in the sense that its aspect changes with direction: see scatterplot in Fig. 1) and very irregular in shape, mostly at large geographic

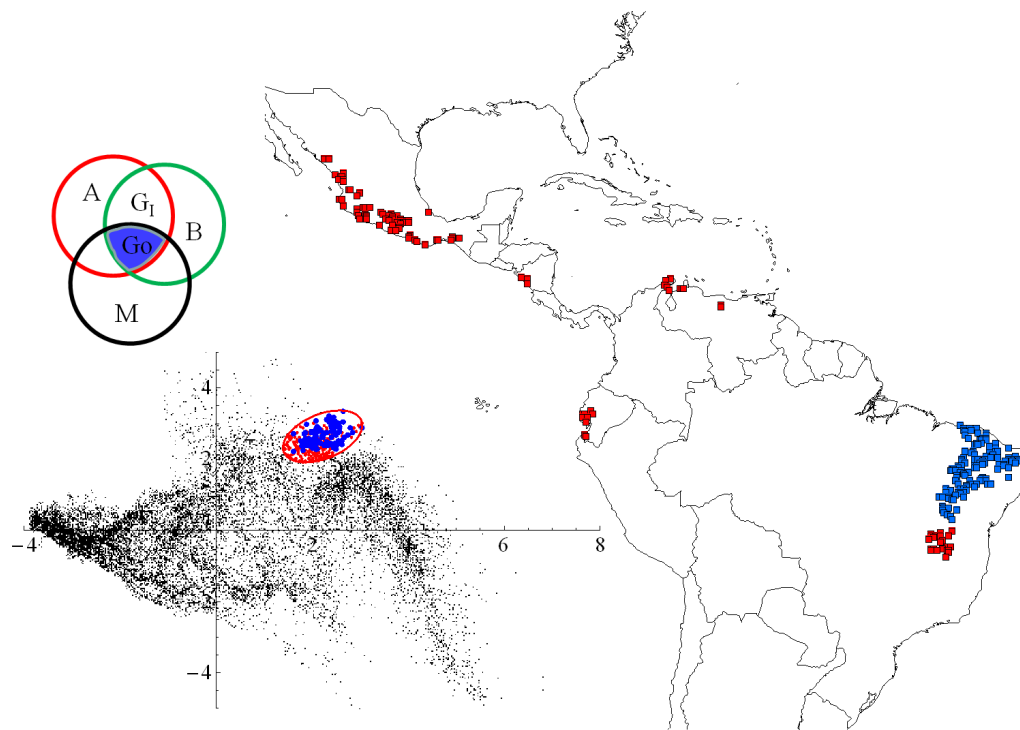


Figure 1. Major symbols used in the paper and their correspondence in geographic and environmental spaces. The first 2 principal components of the environmental space \mathbf{E} of the Americas are represented. The Venn diagram is an abstract representation of the geographic space \mathbf{G} . The green circle (B) represent the regions of the planet that are biologically favorable to the species and the black (M) circle the regions that have been accessible to the species over an appropriate period of time. The red circle, in the Venn diagram, symbolized with an A, represents regions with environments within the fundamental niche (the red points inside the ellipse). In the map these correspond to the red and the blue points. In environmental space the existing points inside \mathbf{N}_f constitute the existing fundamental niche. The blue points in the map represent those areas that are: i) environmentally favorable, ii) accessible, and iii) biologically suitable. This is the occupied area G_o . Finally, depending on biological suitability, all (or none) of the remaining, unoccupied red points represents a potentially invadable region (G_i).

extents, a quality not frequently mentioned in the niche modeling literature.

The fundamental niche, \mathbf{N}_F (Hutchinson, 1957), is the multivariate range of physiological tolerances to variables like temperature, water availability, etc., within which a species will have positive intrinsic population growth rates (Birch, 1953; Hooper et al., 2008). It is feasible to transform such biophysical, microclimatic ranges into broader climatic terms (Kearney and Porter, 2009), allowing one to express niches in terms of coarse-grained environmental variables. Jackson and Overpeck (2000) identified the idea of a “potential niche”, which we denote by \mathbf{N}_F^* . This is the intersection of the fundamental niche with the available environmental space (Green, 1971): $\mathbf{N}_F^* = \mathbf{N}_F \cap \mathbf{E}$. In other words, \mathbf{N}_F^* is the set of climatic features actually existing on the relevant landscape and time, that coincides with the physiological requirements of the species. Notice that \mathbf{E} and therefore \mathbf{N}_F^* depend on the focal region under study: the same fundamental niche in a changed reference region may produce a different \mathbf{N}_F^* . As illustrated in Figure 1, geographically, the environments in \mathbf{N}_F^* are found in the actual occupied range (blue regions denoted by \mathbf{G}_O), and also in the remaining regions in \mathbf{G} that potentially could be invaded because they are also suitable (denoted by \mathbf{G}_I) but still inaccessible. The realized niche, \mathbf{N}_R , is the subset of \mathbf{E} in the occupied area (\mathbf{G}_O) of the species. In symbols

$$\mathbf{N}_R = \eta(\mathbf{G}_O) \subseteq \mathbf{N}_F^* \subseteq \mathbf{N}_F \quad (1)$$

Where the symbol $\eta(\mathbf{G}_O)$ represents the environments in \mathbf{G}_O . This simple set relation expresses that the environments constituting the realized niche are equal to the environments in the actual, occupied area of distribution, and in turn these are a subset of those existing environments in the area of reference that intersect with the fundamental niche. This is a very important equation that may be regarded as the fundamental hypothesis of niche modeling, and verbally it has been known since Hutchinson (1957). He proposed that \mathbf{N}_R would be smaller than \mathbf{N}_F owing only to the effect of negative biotic interactions (Colwell and Futuyma, 1971; Austin, 1999). More recent authors have stressed that \mathbf{N}_R should be a subset of \mathbf{N}_F , because, first, what has geographic existence is \mathbf{N}_F^* , which almost certainly is smaller than \mathbf{N}_F , and second, because \mathbf{N}_F^* can be reduced by interactions like competition, or not expressed fully by lack of dispersal capacities of the species (Jackson and Overpeck, 2000; Pulliam, 2000; Svenning and Skov, 2004; Soberón and Peterson, 2005; Pearson, 2007; Colwell and Rangel, 2009). Operationally, \mathbf{N}_F may only be measured experimentally, or based on first principles of physiology and biophysics (Kearney and Porter, 2009), taking into

account the fact that adaptation to local conditions may create subpopulations with slightly different ranges of tolerances (Labra et al., 2009), and that strictly speaking, one cannot ever measure the fundamental niche, but only assess the probability that an environment is part of it (Godsoe, 2009). On the other hand, \mathbf{N}_R can only be estimated from unbiased observations of both presences and absences, since the results of interactions are difficult to anticipate. The difference between \mathbf{N}_F and \mathbf{N}_R , taking into account the actual structure of \mathbf{E} , is major, so failing to consider it confuses interpretation considerably.

For the sake of simplicity and illustration, we assume that \mathbf{N}_F can be represented using convex shapes that contain environments favorable for the species (Maguire, 1973). Notice, however, that neither \mathbf{N}_F^* nor \mathbf{N}_R should be expected to be convex in shape, since \mathbf{N}_F^* might have been distorted by the shape of \mathbf{E} , and \mathbf{N}_R by movement limitations or biological interactions. The 3 sets \mathbf{N}_F , \mathbf{N}_F^* and \mathbf{N}_R can be measured in terms of their position, shape and size (Jackson and Overpeck, 2000; Pearman et al., 2007; Rangel et al., 2007); what matters most from the perspective of niche conservatism is whether the position of \mathbf{N}_F within \mathbf{E} is changing, and at what speed (Soberón and Nakamura, 2009).

However, as we said before, measuring the \mathbf{N}_F can only be done, generally speaking, mechanistically or experimentally (Kearney, 2006; Soberón, 2007; Kearney and Porter, 2009). The widely used correlative methods estimate vaguely defined objects: an area of distribution somewhere between the actual and the potential (Jiménez-Valverde et al., 2008), and thus the corresponding environmental subsets lie between \mathbf{N}_F^* and \mathbf{N}_R , as expressed in equation (1). Unfortunately when presence-only data is used, without extra information it is impossible to assess where exactly the position of the estimate lies (Soberón, 2010). If, however, distributions are modeled using correlative methods that include unbiased data documenting absences, most likely one gets an estimation of the actual occupied area of the species, \mathbf{G}_O , with associated $\mathbf{N}_R = \eta(\mathbf{G}_O)$. At the other extreme, lacking data on absences and resorting only to envelope methods, it is likely that estimates shift towards the potential area of distribution ($\mathbf{G}_O \cup \mathbf{G}_I$), and therefore the environmental space associated with $\eta(\mathbf{G}_O \cup \mathbf{G}_I)$ shifts more towards \mathbf{N}_F^* (Jiménez-Valverde et al., 2008). In any case, correlative methods clearly do not provide immediate evidence about shifts in the \mathbf{N}_F , but only, indirectly, about \mathbf{N}_F^* and \mathbf{N}_R .

Observing displacements in \mathbf{N}_R estimates for the native and invaded ranges of *Centaurea maculosa*, Broennimann et al. (2007) suggested 2 explanations: (i) genuine evolutionary change in \mathbf{N}_F , or (ii) actions of ecological factors like lack of suitable habitat or presence

of competitors are modifying the N_R . In a paper discussing transferability of predictions of species distributions, Randin et al. (2006) also explained niche shifts by differences in land-use history, phenotypic plasticity, and the ranges of environmental predictors being different. Dormann et al. (2010), studying climatic niche conservation in European mammals, were also aware of the possibility that differences in niche space may affect results, and developed a test to check whether “climate niches” (without specification of whether it is the fundamental, the realized or an intermediate) of sister species are affected by the underlying structure of E-space. Their test appears to be valid as regards to realized niches, but perhaps not so if used as evidence of fundamental niche conservatism.

Finally, in a very recent paper, Godsoe (2010) used virtual species with identical environmental requirements (i.e., fundamental niches) to explore how gradients and dispersal limitations affect the capacity of different methods to detect differences in both fundamental and realized niches. His results further illustrate the difficulties of making inferences about the fundamental niches on the basis of observed distributional data.

These results are very recent, and the implications of anisotropy of E-space for studying fundamental niche conservatism have not been appreciated widely. The structure of existing environmental combinations may vary radically from 1 region of G to another, and through time as well, so species with conserved N_F may have N_R significantly shifted in different regions, just because the environmental combinations available in 2 regions of the planet are different. This point is key in interpreting niche conservatism, as we will show below.

Materials and methods

We illustrate the effect of differences in existing conditions on N_R by constructing a virtual species with a known hypothetical fundamental niche, in a world with no biotic interactions, and unlimited ability to expand within a given region. To construct the E space, we start with the 19 bioclimatic variables in WorldClim (Hijmans et al., 2005) for the Western Hemisphere, at a spatial resolution of 5° . To reduce dimensionality and standardize variables, we performed a z-transformation of the data and then a PCA analysis. The first 5 components explain almost 98% of the variance, but we used just the first 2 axes (which explain around 90%) in order to simplify the figures. We assumed a 2-dimensional ellipsoid as the fundamental niche for the hypothetical species using the following equation:

$$(\mathbf{x} - \boldsymbol{\mu}) \boldsymbol{\Sigma}^{-1} (\mathbf{x} - \boldsymbol{\mu})' = 1$$

where \mathbf{x} are vectors of 2 coordinates, $\boldsymbol{\mu} = (-0.295, 0.4407)$ is the centroid of N_F and

$$\boldsymbol{\Sigma} = \begin{bmatrix} 0.0147 & -0.0135 \\ -0.0135 & 0.0540 \end{bmatrix}$$

is a covariance matrix with eigenvectors and eigenvalues determining the directions of the axes of the N_F and its area (Legendre and Legendre, 1998). The above parameters define the ellipse illustrated in Figures 2 and 3. Its intersection with the 2-dimensional E space (N_F^*) is projected to geographic space as a potential distributional area. For the sake of illustration, we selected 2 equal-sized regions in the United States (Figs. 3A, B), each containing environments within N_F .

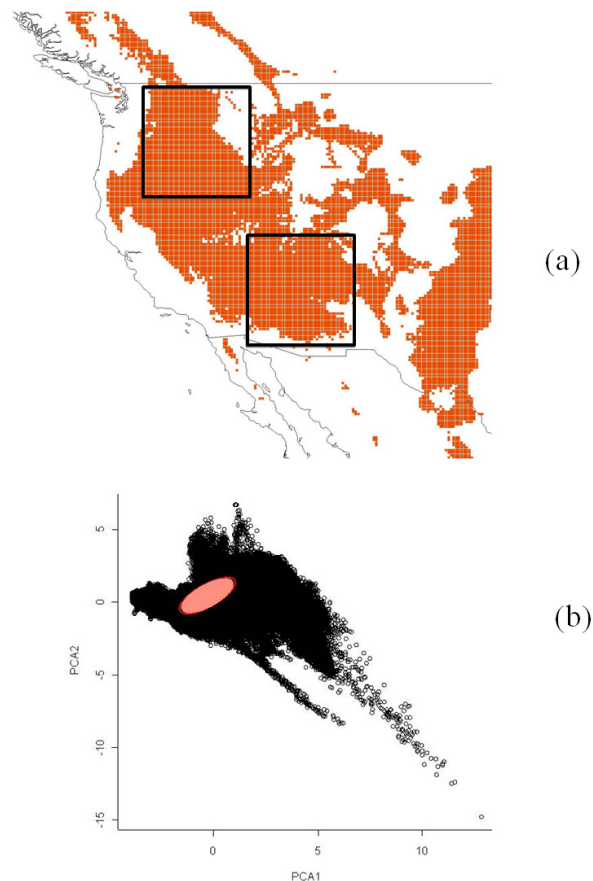


Figure 2. Representation of the distributional area of the virtual species. Western North America showing a distributional area (A) corresponding to the climates within the ellipse contained in the bottom panel. The niche space (B) is illustrated with the first 2 principal components of the bioclimatic variables described in the text. The ellipse represents the fundamental niche of a hypothetical species.

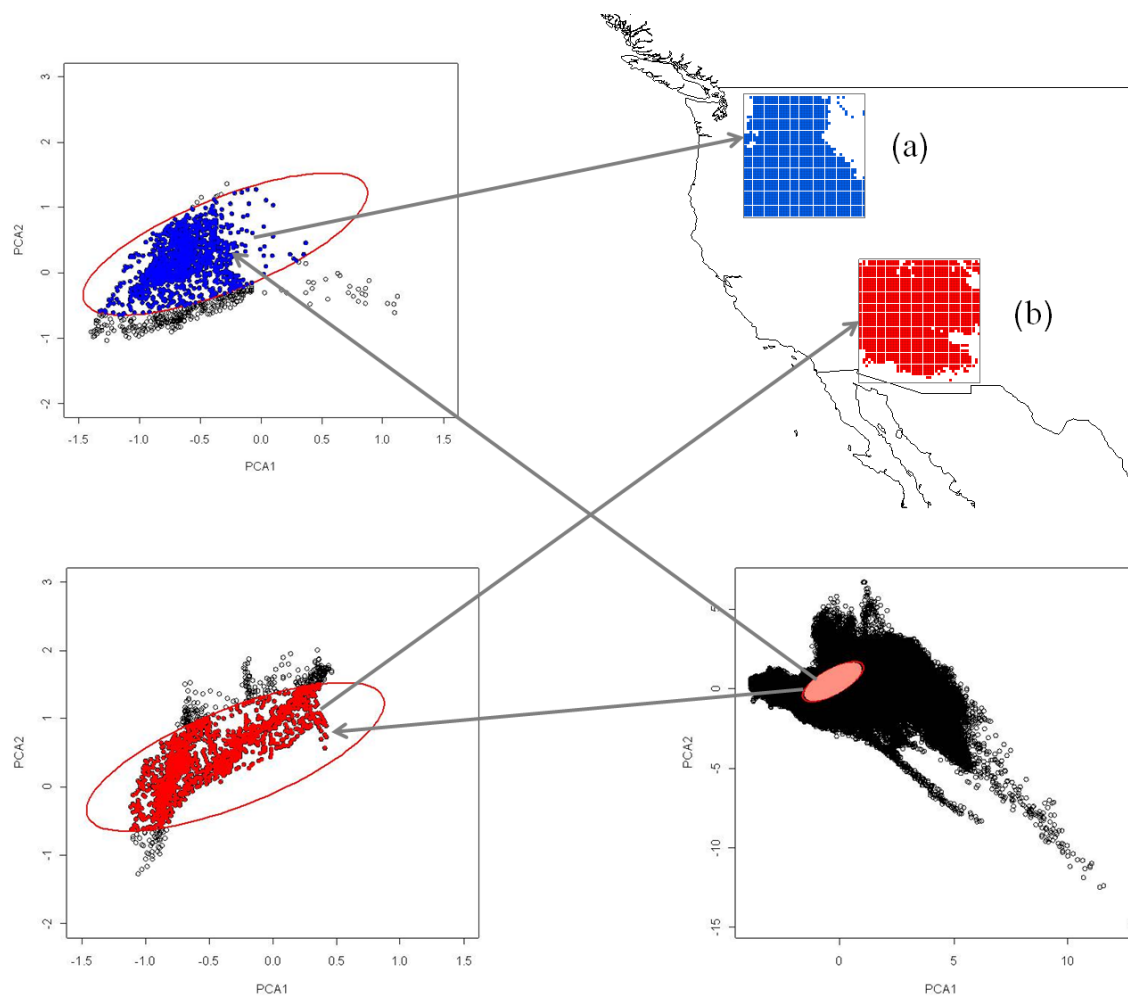


Figure 3. Anisotropic structure of the E -space in 2 different regions of the USA. The cloud of points in the lower right represents the combinations of the first 2 principal components of the climates in the Americas. A hypothetical N_F of a species is represented by the red ellipse. The structure of climatic variables is very different in the northern (A) and southern (B) regions. Despite the assumptions of total fundamental niche conservatism, no competitors, and full dispersion equilibrium within the regions enclosed in the squares in the map, obvious shifts in the composition of $N_R = N_F$ in the North and South are displayed. This effect is entirely due to the anisotropies in E .

To compare results we followed Broennimann et al. (2007) and analyzed the data using between-classes inertia analysis (Doledec et al., 2000) with the `ade4` package of R which gave an inter-inertia ratio of 0.273, with a $p < 10^{-5}$, obtained by Monte Carlo simulation with 10 000 replicates. Inertia analysis explores the position and shape of clouds of points in environmental space by studying their distance to the centroid of the entire available space, and the degree of scatter on a vector linking the global centroid to the centroid of one particular cloud of points. Other methods to compare niche shifts exist (Warren et al., 2008), but we wanted to use one that has already been used to document niche shifts in an evolutionary context.

Results

The occurrence points falling in N_F^* of the species in the northern and southern regions in the map, respectively, are shown as blue and red in Figure (3), respectively. Despite wide overall overlap, the climatic combinations corresponding to the 2 ranges are different, and a species capable of reaching every grid cell would have different N_F^* (and thus realized niche) in the northern and the southern regions. This result holds true even assuming: (i) constant N_F , (ii) no competitors or interactors of any kind, and (iii) full dispersal equilibrium within each subregion.

We plot the N_F^* of the 2 regions (Fig. 4), showing substantial niche shift between them. This result parallels

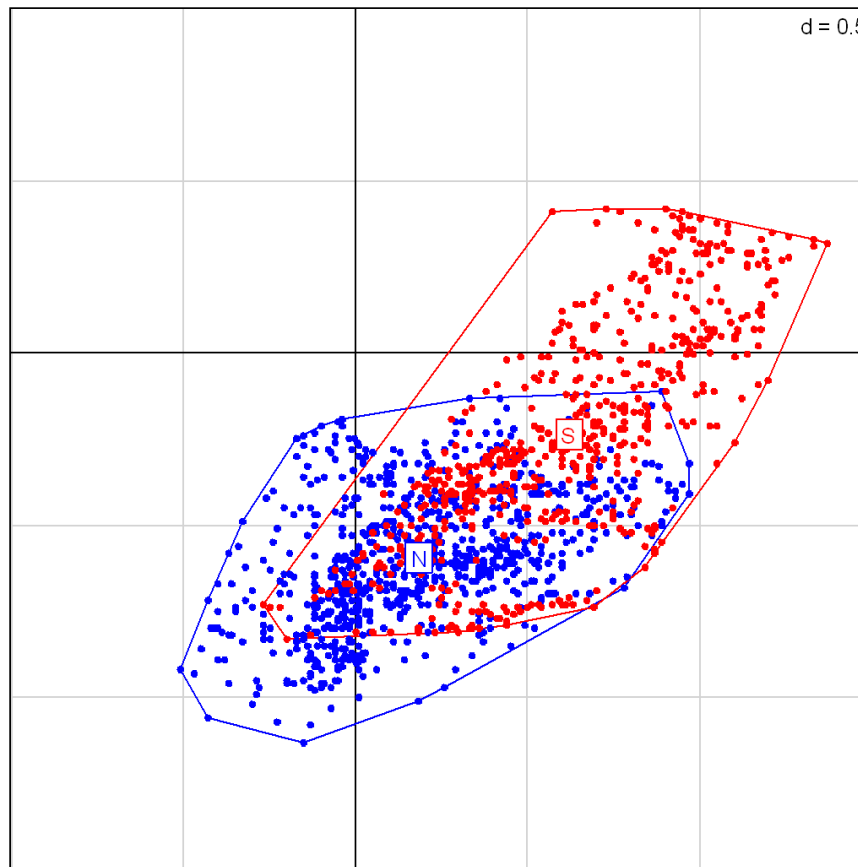


Figure 4. Co-inertia analysis of niche shift due to environmental space anisotropy. The northern and southern existing niche spaces are compared. The between classes inertia-ratio is 0.273, and a Monte Carlo simulation indicates that $p < 5 \times 10^{-5}$.

strikingly the niche shifts observed by Broennimann et al. (2007) when analyzing invasion by *Centaurea*, which they explained in evolutionary or ecological terms. Our example, however, mimics realized niche shifts resulting only from the anisotropy of E-space, which may be frequently be a more parsimonious explanation for niche shifts.

Discussion

The conclusion is straightforward: documenting shifts in an estimated realized niche, which is what correlative methods most likely do, yields little information about the evolution of the fundamental niche, since shifts in N_R result from combinations of evolutionary, ecological and geographic effects. Without ancillary information, documenting shifts in estimates of N_R does not inform about changes in the physiologically- defined N_F , nor about ecological changes in N_F^* . The correct null hypothesis when transferring niche predictions spatially should be lack of change in the centroids of the N_R conditioned

to the anisotropies in E ; in other words, appropriate comparisons will include considerations of the structure and composition of the E space in each region. Such tests have been implemented in the background similarity tests of Warren et al. (2008), which consider niche differences relative to a specific area of interest, and see also Dormann et al. (2010) and Godsoe (2010). Notice, however, that documenting stasis in the N_R probably implies stasis in N_F as well.

Beginning with Broennimann (2007) and Fitzpatrick et al. (2007), numerous studies have addressed the question of niche shifts during the invasion process (Pearman et al., 2007; Broennimann and Guisan, 2008; Rödder and Lötters, 2009; Dormann et al., 2010; Medley, 2010). In general, they have concluded that niche shifts are occurring, an idea with which we concur if the understanding is that they refer to the realized niche. As should be clear from the example we have presented herein, the question of which niche is shifting is crucial. It is clear that the *same* fundamental niche N_F , expressed in different regions with correspondingly distinct environmental spaces E' and

E'' will produce different *existing* fundamental niches and therefore, in all likelihood, different N_R , even in the absence of competitors and evolutionary processes.

The idea that niche comparisons should be performed in relation to available ecological space is not new. The literature of niche measures very often makes explicit reference to available ecological space (Colwell and Futuyma, 1971; Green, 1971; Doledec et al., 2000; Elith and Burgman, 2002; Hirzel et al., 2002; Calenge et al., 2008; Warren et al., 2008; Dormann et al., 2010). It is important that niche modelers appreciate more fully the fact that environmental spaces are highly heterogeneous and that attempts to understand changes in either N_F or N_R must therefore take into account the structure of the available environmental space E . The problem of the definition of the available niche space is a deep one, which is the subject of a separate treatment (Barve et al., 2011).

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