IDEA AND PERSPECTIVE

Grinnellian and Eltonian niches and geographic distributions of species

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Abstract

In the recent past, availability of large data sets of species presences has increased by orders of magnitude. This, together with developments in geographical information systems and statistical methods, has enabled scientists to calculate, for thousands of species, the environmental conditions of their distributional areas. The profiles thus obtained are obviously related to niche concepts in the Grinnell tradition, and separated from those in Elton's tradition. I argue that it is useful to define Grinnellian and Eltonian niches on the basis of the types of variables used to calculate them, the natural spatial scale at which they can be measured, and the dispersal of the individuals over the environment. I use set theory notation and analogies derived from population ecology theory to obtain formal definitions of areas of distribution and several types of niches. This brings clarity to several practical and fundamental questions in macroecology and biogeography.

Keywords

Bionomic, distributional areas, Elton, Grinnell, Niche, scenopoetic, spatial scaling.

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INTRODUCTION

The idea that ecological properties of species, loosely denoted as their ecological niches, and their areas of distribution are related, is an old one (Grinnell 1917; James *et al.* 1984). In recent years, growing numbers of scientists are estimating distributional areas by calculating 'environmental', or 'ecological', niches (Guisan & Zimmermann 2000; Peterson 2006). This useful set of techniques has recently experienced almost explosive growth, with great practical success (Guisan & Thuiller 2005; Araújo & Guisan 2006). However, discussions of the relation between species' distributions and niches tend to be muddled by lack of clarity in the usage of terms (Kearny 2006).

Unequivocal interpretation of these concepts requires explicitly stating assumptions about the spatial extent and resolution at which areas are measured; the types, mechanisms and effects of the biotic interactions that affect the distributions; the different roles that variables that are or are not depleted by consumers should play in niche definitions; and the scope of spatial displacements in ecological and evolutionary time frames.

Discussions of the above factors are still incipient. Pulliam (2000) analysed the importance of source–sink dynamics to niche theory. Kearny (2006) emphasized a distinction between mechanistic vs. correlative modelling, hinting at a hierarchical view in which 'niches' would be defined mechanistically, using physiological experiments, and 'habitat' would be defined by the correlative methods more characteristic of ecological niche modelling. Pearson & Dawson (2003) introduced an explicitly hierarchical point of view suggesting that, to define distributions, abiotic variables may be more important at coarser spatial scales. This idea was developed further by Guisan & Thuiller (2005), who analysed most of the factors relevant to using niche modelling to estimate areas of distribution, and stressed the importance of assumptions of dispersal equilibrium and the role of spatial extent and resolution. Finally, Araújo & Guisan (2006) pointed out several difficulties of using the concepts of fundamental and realized niches of Hutchinson(1957) in the area of species distribution modelling, highlighting ambiguities related to biotic interactions and the issue of the spatial resolution at which such interactions are relevant.

Here I provide further conceptual discussion of these problems, from the fundamentals of population dynamics, relying heavily on a distinction between types of variables and the importance of scale. Using ideas from population ecology several kinds of distributional areas are defined in terms of the actual or potential spatial locations that

individuals comprising a species can occupy and one particular type of niche in terms of the parameters of population equations. Throughout this contribution, the key role of spatial resolutions and extent is emphasized.

AREAS AND NICHES IN RELATION TO SPATIAL SCALE AND VARIABLE TYPES

Areas of distribution of species are generally represented as maps, but maps are abstractions. Underlying the abstractions are our observations of the temporal and spatial patterns in which individual organisms are distributed over the planet (Brown *et al.* 1996; Mackey & Lindenmayer 2001; Gaston 2003). What factors determine such patterns? Three important groups of such factors are (Guisan & Thuiller 2005; Soberón & Peterson 2005): (i) the dispersal capacities of the species, whether by their own movements or by propagule dispersal by external agents, because this element determines what parts of the world are accessible to individuals of the species; (ii) the spatial distribution of environmental conditions favourable to the establishment, survivorship and reproduction by the individuals (mostly in a physiological sense), because these consideration establish the broad limits of the distributions; and (iii) the biotic environment constituted by the species' competitors, predators, and pathogens, together with the availability and dynamics of resources. This last set of factors determines the fine-grained structure of distributions, and can also modify the limits determined by the second set of factors. Although other factors certainly exist, such as the pattern of disturbances in the environment, these three are fundamental to understanding the relationships between distributional areas and niches.

The description of the area of distribution of a species based on the locations of the individuals composing it would reveal an extremely complex and dynamic structure (Erickson 1945; Brown *et al.* 1996; Mackey & Lindenmayer 2001; Gaston 2003). Although at present such fully explicit descriptions are impossible, conceptually, they suggest a way for defining rigorously and operationally the relations between, on the one hand, the individual- and population-level processes that determine the ecological success of individuals (related to niches), and on the other, different aspects of the spatial distribution of those individuals and, therefore, of the area of distribution of the species.

Pulliam (2000) proposed a spatially explicit model of two competitors dispersing over a grid with heterogeneous environmental parameters. In his model, areas of distribution are sets of cells in the geographic grid where the species were actually or potentially present. This definition of area of distribution is straightforward, but requires clarification. From a biogeographic perspective, areas of distribution are

generally defined at large extents ($> 10^5$ km^2: for example, in countries or regions within continents) and low resolutions, with cells of 10^4–10^5 km^2 and larger being common (Gaston 2003). On the other hand, ecological variables important at the individual level (demographic, physiological and behavioural) are usually measured at scales small in extent (10^{-3}–10^0 km^2) and of high resolution (Whittaker *et al.* 2001; Pearson & Dawson 2003). The precise scale of what is 'high resolution' depends on the species. Therefore, to define areas of distribution useful in biogeographic or macroecological questions, it is necessary to find ways of scaling-up population processes, adopting conventions about the types of individuals and populations (i.e. breeding, migratory, source and sink) for which abundance above some threshold would be abstracted to 'presence' to highlight a cell as a part of the area of distribution (Brown *et al.* 1996). The concept of the area of distribution of a species then includes the ideas of probability of observation of well-defined types of individuals or populations at spatial and temporal resolutions and extents that are normally much coarser than autoecological scales. In what follows, I will thus define areas of distribution as: 'sets of grid cells in geographic space, defined by actual or potential ways in which presences of individuals of a species can be detected'. This concept is operationalized and developed in greater detail below.

The problem of defining niches is less straightforward. Three factors are important to clarify 'niche' in relation to areas of distribution. In the first place, niche as habitat must be distinguished from niche as function (Whittaker *et al.* 1973; Leibold 1996). In recent literature, this distinction is almost always made, if only implicitly. Second, it is important to distinguish niches as defined locally, at the scale of the ecology, behaviour, and physiology of small populations or individuals, from niches defined at larger spatial extents, where distributional limits matter (Holt & Gaines 1992; Pulliam 2000). This distinction is seldom made.

Finally, it is useful to distinguish between niche variables as resources or as conditions. Resources can be consumed, and populations may impact them and compete for them; to define niches using resource variables therefore one must not only specify their rates of supply, but also the mechanisms and parameters of consumption and the impacts that consumers have on the resources (Tilman 1982; Leibold 1996; Chase & Leibold 2003). These interactive, resource-related variables were called *bionomic* by Hutchinson (1978). The second type of niche variables are environmental conditions for which competition is not relevant (Hutchinson 1978; Austin & Smith 1989): these variables can be specified without resorting to models of exploitation or densities of competitors. Hutchinson (1978) called such variables *scenopoetic*, from the Greek roots of

'scene setting.' These two extremes have been distinguished repeatedly in the literature, albeit with different terminologies. For example, Austin & Smith (1989) and Austin (2002) have distinguished *direct* and *resource* variables, stressing the profound differences between them (Guisan & Zimmermann 2000). Begon *et al.* (2006) distinguished between *conditions* and *resources*.

The above points suggest that separating niches into two main classes is useful. One is the Grinnellian class, which can be defined by fundamentally non-interactive (scenopoetic) variables (James *et al.* 1984; Austin & Smith 1989; Austin 2002) and environmental conditions on broad scales, relevant to understanding coarse-scale ecological and geographic properties of species (Grinnell 1917; Whittaker *et al.* 1973; James *et al.* 1984; Jackson & Overpeck 2000; Peterson 2003). The other is the Eltonian class, focusing on biotic interactions and resource–consumer dynamics (bionomic variables), and which can be measured principally at local scales (Elton 1927; MacArthur 1969; Vandermeer 1972; Leibold 1996). The seminal ideas of fundamental and realized niches of Hutchinson (1957, 1978) can be applied to both classes, as well as the concept of multidimensional spaces of niche variables (James *et al.* 1984; Chase & Leibold 2003), but the details change significantly as the challenges of measuring scenopoetic and bionomic axes are totally different. Besides, data sets for the largely non-interacting or slowly interacting variables of Grinnellian niches (e.g. average temperature, precipitation, solar radiation, terrain aspect, etc.) are becoming increasingly available for the entire planet (Turner *et al.* 2003), whereas data sets for Eltonian niches remain a matter of detailed field studies of specific cases, as the dynamic and complex axes of multidimensional Eltonian niches are difficult to measure at broad geographic scales (Austin 2002; Araújo & Guisan 2006).

Finally, the scant direct evidence available (Mackey & Lindenmayer 2001; Holmes *et al.* 2005) suggests that many (although by no means all) scenopoetic variables may have broad spatial structures, whereas bionomic variables probably tend to have much more fine-grained spatial structures. This issue remains an unexplored research question. The distinction between scenopoetic and bionomic variables is somewhat artificial, as they can interact, and certain variables can act in either way, depending on the scale (i.e. solar radiation as a function of latitude, and radiation on a forest understory). It also depends on the biology of the organisms in question, and it becomes less useful at higher resolutions, when habitat variables are often included as niche axes. Despite all the above, it helps to clarify the problem of relationships between distributional areas and niches and makes possible to operationalize their definitions, and in the following discussion it will be used as an essential first approximation.

The different Grinnellian niches then will be defined as 'subsets of scenopoetic variable space corresponding to geographic areas defined by actual or potential properties of species'. As will be seen, the concept of fundamental niche and to some extent of realized niche (Hutchinson 1957) can be rephrased operationally in terms of the above definition without major changes in meaning. Both classes of niches are relevant to understanding the distribution of individuals of a species, but the Eltonian class is easier to measure at the high spatial resolutions characteristic of the most ecological studies, whereas the Grinnellian class is suited to the low spatial resolution at which distributions are typically defined. This hierarchical view of niche is consistent with theories about how factors affecting the structure of biological diversity act at different scales (Shmida & Wilson 1985; Mackey & Lindenmayer 2001; Whittaker *et al.* 2001; Pearson & Dawson 2003). In the vein of Pulliam (2000), I analyse how population dynamic considerations can suggest definitions for different kinds of areas of distribution, and then, define Grinnellian niches on the basis of such areas of distribution.

NICHES, AREAS AND POPULATION DYNAMICS

I begin by phenomenologically (Vandermeer 1972; Meszena *et al.* 2006) breaking the total population growth rate of a species in any given locality (cells in a grid) into three elements. (i) An intrinsic, density-independent growth rate will be defined mostly by the scenopoetic environment at coarse resolutions ($> 10^0$ km^2) and assuming that any essential resources are present; the intrinsic growth rate is therefore, in view of the previous section, the main avenue to define Grinnellian niches. (ii) A resource-interaction component, which is dominated by the biotic milieu [competition, predators and pathogens, mutualisms; see McGill *et al.* (2006)] at spatial and temporal resolutions commensurate with the activities or movements of individuals; this term in the growth rate is dominated by Eltonian niche processes. Finally, (iii) another component defines the probabilities of any given cell receiving and sending immigrants or propagules within a period of time defined according to the problem in question. This term determines the metapopulation structure and the source–sink dynamics. The set of all cells where the species can be observed will be determined by these three factors. This scheme is represented heuristically in Fig. 1, with **A** representing the geographic region where the abiotic factors that influence the *intrinsic* growth rate would allow it to be positive; **B** is the geographic region where the biotic factors that affect resource use and biotic interactions would allow positive *total* growth rates, and **M** summarizes the region(s) in the world that are accessible to the dispersal capacities of the species (Soberón & Peterson 2005).
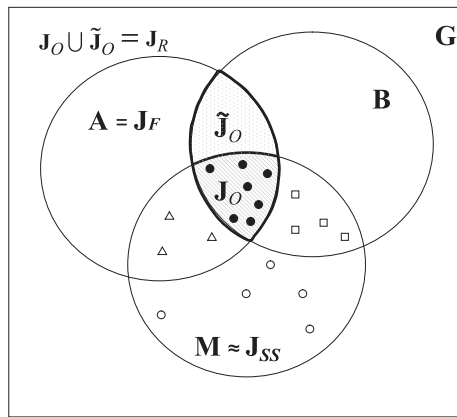
Figure 1 Heuristic representation of factors affecting the distribution of a species. **G** represents the total area of study. $\mathbf{A} = \mathbf{J}_F$ represents the geographical area where the intrinsic growth rate of the species would be positive. **B** represents the geographical area where the species can exclude or coexist with competitors. **M** represents the total area that has been or is accessible to the species within a time period of interest. Solid circles represent source populations. Open triangles are sink populations with negative growth rates due to competitive exclusion. Open squares represent sink populations due to negative intrinsic growth rates. Open circles are combinations of the above. $\mathbf{J}_R$, which is often (see text) assumed to be the union of the occupied area $\mathbf{J}_O$ and the potential occupied area $\tilde{\mathbf{J}}_O$, represent the entire region in **G** where both the scenopoetic and bionomic environment are adequate for the species, regardless of movements. $\mathbf{J}_{SS}$ is the area where individuals of the species may be found, regardless of whether populations are sinks or sources. By definition, $\mathbf{M} \approx \mathbf{J}_{SS}$.

Now, assume that the region of interest, **G**, is subdivided by a grid with cells of a resolution commensurate with the processes taking place at the Eltonian scales (e.g. 10^{-3}–10^0 km^2). In each cell j, three sets of parameters can be defined, corresponding to the population dynamics components described above: (i) the values of the scenopoetic variables, which, as they are by assumption non-interactive, can be represented by a simple vector of numbers $\vec{e}_j$. (ii) A vector $\vec{R}_j$ of bionomic parameters of a model that define the dynamics of the usage of the resources in cell j, their supply and the impact of the species on them, as well as the interactions with other species. This summarizes the population ecology of the species, and cannot be defined simply as a set of numbers, as it requires hypotheses (i.e. models) about specific interactions. The best example of this is the theory of the Eltonian niche developed by Chase & Leibold (2003) on the basis of ideas of MacArthur (1969) and Tilman (1982). Finally, (iii) a transition matrix **T** summarizes rates of dispersal of individuals among cells. This simplified scheme allows definition of niches in terms of sets of parameters, and areas in terms of sets of cells with actual or potential kinds of populations (e.g. with positive

intrinsic rates or with positive actual rates or with population densities above a certain threshold). The actual relation between those niches and areas is determined, in principle, by the population dynamics equations.

A full mathematical statement of the population dynamics of a species as a function of the above three factors would be extremely complicated (Vandermeer 1972; Rescigno & Richardson 1973; Tilman & Kareiva 1997; Pulliam 2000; Solé & Bascompte 2006) and this contribution is not the place to present it. Here, as a result, I ignore many complications. For example, bionomic variables and dispersal can be modulated by the scenopoetic variables (Davis *et al.* 1998; Bullock *et al.* 2000; Leathwick & Austin 2001; Meszena *et al.* 2006), so the simple dichotomy between the intrinsic and the total growth rates is not clear cut. Still, this scheme is a useful first approximation, and I will use the diagram in Fig. 1 as a heuristic tool to discuss it.

THE FUNDAMENTAL GRINNELLIAN NICHE

When Hutchinson (1957) defined the fundamental niche as the set of all the '…states of the environment which would permit the species…to exist indefinitely,' he did not make the difference between biotic and scenopoetic variables, although later he realized its importance (Hutchinson 1978). If one makes the difference, then two fundamental niches can be defined, one Grinnellian and another Eltonian. The best recent definition of the fundamental Eltonian niche is provided by Chase & Leibold (2003), based on the position of resource-supply points in relation to zero net-growth isoclines of species.

What would be a definition of the Grinnellian fundamental niche, or $\mathbf{N}_F$? By the arguments above, $\mathbf{N}_F$ can be defined rigorously as the set of all values of the vectors of scenopoetic variables for which the intrinsic growth rate is positive, or in symbols $\mathbf{N}_F = \{\vec{e}_j \mid r(\vec{e}_j) > 0\}$, where $r(\vec{e}_j)$ represents the density-independent intrinsic population growth rate as a function of the environmental variables in j. It is worth repeating that, under this definition, niche axes are measured at explicitly geographic scales. Many scenopoetic variables known to affect distributions of species (e.g. like macroclimatic variables, large scale-topography, solar radiation, etc.) are measured at low resolutions (10^{-1}–10^2 km^2) and show high spatial autocorrelations. Therefore, the range in their semivariograms is probably much larger than for bionomic variables (Holmes *et al.* 2005), making it feasible to aggregate values of such variables in neighbouring cells to coarser grids, compatible with the definition of areas of distribution. In other words, **A** is defined at coarse resolutions, aggregating adjacent sets of individual-resolution cells with similar values of the scenopoetic variables.

Now imagine a relation $\gamma : \mathbf{E} \rightarrow \mathbf{G}$ that can be implemented in a geographic information system (GIS) and that map from $\mathbf{N}_F$ to the geographic space $\mathbf{G}$ (Guisan & Zimmermann 2000). This relation finds all cells in $\mathbf{G}$ with values of the scenopoetic variables belonging to $\mathbf{N}_F$. This set of localities, symbolized by $\mathbf{J}_F$, constitutes one type of potential (i.e. not necessarily occupied by the species) area of distribution of the species. It could be called the *fundamental area of distribution of a species*. In symbols:

$$\mathbf{J}_F = \gamma(\mathbf{N}_F) = \{ j \in \mathbf{G} \,|\, r(\vec{e_j}) > 0 \}.$$

In Fig. 1, the region $\mathbf{J}_F$ is represented by the circle $\mathbf{A}$ [compare with Fig. 3 in Pulliam (2000)]. As the same environmental combination can occur in several geographic cells (Aspinall & Lees 1994), numbers of elements in $\mathbf{J}_F$ and $\mathbf{N}_F$ are not necessarily the same.

From $\mathbf{N}_F$, it is possible to calculate the area $\mathbf{J}_F$, and the reverse operation is theoretically valid: if, in a thought experiment, a macroecologist knew $\mathbf{J}_F$, then a GIS would allow her to extract from each cell in $\mathbf{J}_F$ the scenopoetic values to obtain $\mathbf{N}_F$. In symbols, there is a relation $\eta : \mathbf{G} \rightarrow \mathbf{E}$ such as $\eta(\mathbf{J}_F) = \mathbf{N}_F$. Of course, $\mathbf{J}_F = \gamma(\mathbf{N}_F)$, which means that $\eta = \gamma^{-1}$. However, this equality is only true because $\mathbf{J}_F$ is a potential area of distribution, and factors such as movements and interactions among species are ignored. As we will see below, when complicating factors restrict occupation of potential areas, the equation $\eta = \gamma^{-1}$ does not hold anymore.

To check the above equalities using independent estimates of $\mathbf{N}_F$ (e.g. obtained in the laboratory) and $\mathbf{J}_F$ (requiring field observations and experiments) would require a great deal of information that is mostly unavailable. Estimation of $\mathbf{N}_F$ remains a thorny practical problem that probably can be solved only by resorting to direct experimental measures of intrinsic growth rates, or to first-principle models (Porter *et al.* 2002; Pearson & Dawson 2003; Kearny & Porter 2004; Kearny 2006).

THE REALIZED GRINNELLIAN NICHE

After defining the fundamental niche, Hutchinson (1957) introduced the idea of a realized niche, in which the effects of competition reduced the fundamental niche of a species and therefore, the area it could occupy. However, in the Grinnellian case, reduction of $\mathbf{N}_F$ to a realized niche is a complicated issue, beginning with the fact that, by definition, no competition can exist for scenopoetic variables. Therefore, reduction of $\mathbf{N}_F$ can only take place trough the Eltonian niche processes taking place at the scale of the cells j and reducing $\mathbf{J}_F$. As Chase & Leibold (2003) discussed, the fundamental Eltonian niche can be reduced by competitors, leading to realized niches that can be expressed in the space

of resource variables. This reduction can in turn create mosaics of localities at which only one competitor is present (Chase & Leibold 2003). In Fig. 1, this case is represented by the intersection of $\mathbf{A}$ and $\mathbf{B}$. As $\mathbf{B}$ is the set of all local-sized cells where the species of interest would coexist or dominate over competitors, then $A \cap \mathbf{B}$ is the region where both $r(\vec{e_j}) > 0$, and competition allows persistence; therefore, the total growth rate (in absence of recurrent migration) can be positive at low densities. Thus, following Hutchinson (1957), a realized area of distribution would be the set of cells defined by

$$\mathbf{J}_R = \left\{ j \Big| \frac{\mathrm{d}x_j}{\mathrm{d}t} \Big|_{x_j \approx 0} > 0 \right\} = \mathbf{A} \cap \mathbf{B},$$

where $\mathrm{d}x_j/\mathrm{d}t$ is the total population growth rate. Notice that, in contrast with the original argument of Hutchinson (1957), in general, since movements are ignored, this realized area may include regions that are suitable from both the scenopoetic and bionomic points of view, and yet remain inaccessible to the species (see Fig. 1). In other words, $\mathbf{J}_R$ may include potential areas. The realized Grinnellian niche would be $\eta(\mathbf{J}_R) = \mathbf{N}_R$. This superficially simple description hides many difficulties due to issues of scale and movement, and to the intrinsically complex nature of the Eltonian processes.

The first problem with defining $\mathbf{B}$ in terms of the Eltonian niche is that, in practice, the results of interactions are seldom, if ever, predictable from sets of parameters. Under resource–consumer models (Tilman 1982; Chase & Leibold 2003), $\mathbf{B}$ can be defined in terms of parameters, but the definition is complex since it requires knowledge of the precise exploitation model, the resource supply points and their location in relation to the impact vectors, and the initial conditions (Tilman 1982; Chase & Leibold 2003). Therefore, for a realistic resource–consumer model, it would be in general impractical to measure parameters and define $\mathbf{B}$ operationally, in terms of sets of cells that fulfil the conditions. Even worse, under certain realistic scenarios, results of complex competitive interactions cannot be predicted even with knowledge of the parameters and the initial conditions (Huisman & Weissing 2001), so a definition of $\mathbf{B}$ in terms of the parameters of the equations may be fundamentally impossible. It is likely then that direct estimation of the region $\mathbf{B}$ from experimental data, as suggested by Kearny (2006), may be possible only for extreme situations when the competitive interactions are very simple and apparent, or phenomenologically, *a posteriori* from observations (Bullock *et al.* 2000; Leathwick & Austin 2001; Anderson *et al.* 2002).

The second problem with defining $\mathbf{B}$ in terms of Eltonian processes is one of scale. Owing to its Eltonian nature, $\mathbf{B}$ has a fine-grained structure. Competition for resources, or

through shared predators, takes place at the scale of cells, but **A** was defined at the scale of clusters of cells sharing similar values of the scenopoetic variables. A wealth of ecological theory and experience shows that at spatial scales large enough to include disturbances and some amount of spatial and temporal heterogeneity, competitors can coexist for long periods of time (Tilman 1982; Chesson 2000; Amarasekare 2003). Therefore, at the geographic scales at which distributions are defined, the presence of competitors does not necessarily imply that the distributional area is reduced. Many local populations can be reduced or even extirpated without the coarse-scale pattern being affected. Second, even if competitors were capable of excluding populations of a given species in the entirety of a coarse-resolution cell, unless the cell had a unique combination of niche variables, N_F as defined here would not be reduced (Pearson & Dawson 2003). The possibility of competitive exclusion taking place but not necessarily reducing the fundamental Grinnellian niche (a consequence of the different scales at which the two niches are defined) is in stark contrast with the case of the Eltonian niche, where competitive exclusion, at local levels, means both an alteration of the fundamental niche and a reduction of occupied local-level cells (Chase & Leibold 2003).

Finally, the region in **B** but outside **A** ∪ **M** represents an inaccessible area without the favourable environmental conditions but with the right biotic settings. An example of such situation may be an area with the right food plant and no competitors of a monophagous insect, but in another continent and outside its climatic envelope. This situation is probably only marginally interesting.

OTHER GRINNELLIAN NICHES

The third factor that affects the relation between niches and areas of distribution is dispersal and movements. In a Grinnellian approach, with an explicit spatial setting, movement is an essential factor that was ignored by Hutchinson and most papers on niche theory until very recently (Pulliam 2000; Pearson & Dawson 2003; Svenning & Skov 2004; Guisan & Thuiller 2005; Soberón & Peterson 2005; Araújo & Guisan 2006).

In Fig. 1, movement is depicted in a simplified way using the region **M**, which is the set of all localities in **G** that have been accessible to the species since some arbitrary point in time (e.g. the origin of the species in question, glacial maximum, etc.) By hypothesis, naturally occurring individuals can only be observed within **M**, and individuals in **M** but outside **A** ∩ **B** represent sink populations. The intersection $A ∩ B ∩ M = J_O$ represents the *occupied area of distribution* of the species (Gaston 2003), or the region where the total population growth rate is positive and naturally occurring propagules have been present:

$$\mathbf{J}_O = \left\{ j \,\middle|\, \frac{dx_j}{dt}\bigg|_{x_j \approx 0} > 0 \text{ and } x_j(t) > 0, t_0 \leq t \leq t_1 \right\},$$

where $t_0 \leq t \leq t_1$ represents some time interval within which propagules arrived.

In principle, it is possible to determine at low resolution the region of the planet, $\mathbf{J}_O$, accessible to a certain species and having viable populations of it (Svenning & Skov 2004). The GIS operation $\eta(\mathbf{J}_O) = \mathbf{N}_O$ yields the set of variables associated with $\mathbf{J}_O$. However, the variables that determine $A ∩ B ∩ M = J_O$ are both scenopoetic (and probably measured at low spatial resolutions) and bionomic (probably only measurable at high spatial resolutions). Therefore, ideally, the GIS that extracts the niche should be provided with high-resolution layers summarizing bionomic variables involved in definition of the Eltonian niche and the description of the realized niche should in theory be developed in terms of variables operating at different scales (Mackey & Lindenmayer 2001). As we have seen, however, this task presents serious practical and theoretical difficulties, so fully dynamic bionomic variables are seldom incorporated in niche modelling (although static maps of presence of important interactor species or habitat conditions can easily be added). This problem remains a difficult practical challenge, but also opens interesting avenues for research.

Maintaining the discussion restricted only to scenopoetic variables, as $\eta(\mathbf{J}_O) = \mathbf{N}_O$, we should ask what would be the region that has the environmental conditions $\mathbf{N}_O$. This is obtained by the GIS operation $\gamma(\mathbf{N}_O)$. If each cell has a unique environment, then $\gamma(\mathbf{N}_O) = \mathbf{J}_O$. But if the same or similar environments can be repeated in geographically different cells, there may be a potential area $\tilde{\mathbf{J}}_O$ disjoint from $\mathbf{J}_O$ but with identical (or similar) environments. In this case, $\gamma(\mathbf{N}_O) = \mathbf{J}_O \cup \tilde{\mathbf{J}}_O$, where $\tilde{\mathbf{J}}_O$ is outside the accessibility region **M** in Fig. 1. This means that the operation of extracting the geographical areas from the niche $\mathbf{N}_O$ may recover an area which is, in general, larger than $\mathbf{J}_O$. Would it be true that $\mathbf{N}_O = \mathbf{N}_R$? This equality is often assumed in species distribution modelling applications (Guisan & Thuiller 2005), but it is really just a hypothesis that depends on $\mathbf{J}_R = A ∩ B = \mathbf{J}_O \cup \tilde{\mathbf{J}}_O$. Invasive species for which actual and potential areas of distributions are known can provide ways of testing this hypothesis (Peterson 2003).

The area $\tilde{\mathbf{J}}_O$ has only recently been discussed in relation to niches (Peterson 2003; Svenning & Skov 2004). It is a potential area of distribution different from $\mathbf{J}_F$. The ratio of realized to potential area that Svenning & Skov (2004) analysed is simply $|\mathbf{J}_O|/|(\mathbf{J}_O \cup \tilde{\mathbf{J}}_O)|$, where the vertical bars denote the size of the area. The areas $\tilde{\mathbf{J}}_O$ and $\mathbf{J}_O$ coincide only if the region of accessibility **M** is large enough as to enclose the whole of **A** ∩ **B** and the species is in dispersal equilibrium within it (i.e. either the species has good

dispersal capabilities or the spatial extent of the analysis is small).

Figure 1 makes obvious that it is possible to define other biologically meaningful areas (and therefore niches). For example, since individuals of the species can disperse to areas beyond $\mathbf{J_O}$ anywhere within the region $\mathbf{M}$, it would be possible then to define the *source–sink area of distribution* ($\mathbf{J_{SS}}$) of a species as the collection of spatial localities where individuals of the species can be observed (regardless of whether their growth rate is positive or negative (Pulliam 2000). Ignoring complications from variation in the probability of detection of presences, then $\mathbf{M} \approx \mathbf{J_{SS}}$. Clearly, $\mathbf{J_O} \subseteq \mathbf{J_{SS}}$. Typical museum specimen or survey data, which seldom include information about the reproductive status of the population from which a specimen was extracted, yield information about $\mathbf{J_{SS}}$. Pulliam (2000), in the context of source–sink dynamics, stated that, as the range of niche conditions actually experienced by a species may be greater than the range of conditions for which the intrinsic population growth rate is positive, then 'the realized niche is often larger than the fundamental niche' (Pulliam 2000). The notation presented herein allows a more precise statement and clarification. Since $\mathbf{J_{SS}} \supseteq \mathbf{J_O}$, then $\mathbf{N_{SS}} = \eta(\mathbf{J_{SS}}) \supseteq \eta(\mathbf{J_O}) = \mathbf{N_O}$. In words, the sink-source niche contains (therefore it is equal or larger than) the occupied niche. As we saw, it is often hypothesized that $\mathbf{N_R} = \mathbf{N_O}$, and therefore the sink-source niche would also contain the realized niche. However, whether $\mathbf{N_{SS}}$ is larger than the fundamental niche $\mathbf{N_F}$, as Pulliam (2000) suggests, would depend entirely on the relative positions of the regions $\mathbf{A}$, $\mathbf{B}$, and $\mathbf{M}$ and thus on the configuration of the study area. Pulliam's (2000) suggestion will take place if $\mathbf{J_{SS}}$ entirely contains $\mathbf{A} = \mathbf{J_F}$, and therefore $\mathbf{N_{SS}} = \eta(\mathbf{J_{SS}}) \supseteq \eta(\mathbf{J_F}) = \mathbf{N_F}$.

Figure 1 shows that source–sink dynamics allow species to 'explore' niche space outside $\mathbf{N_R}$ in two different ways. Sink populations can occur because lack of a favourable biotic milieu, like the triangles in Fig. 1, or because of a lack of scenopoetic conditions, like the open squares. The selective pressures in these two extreme cases will be entirely different and also sensitive to the actual shapes of the niches (Jackson & Overpeck 2000; Ackerly 2003).

DISCUSSION AND CONCLUSIONS

The preceding sections, largely an exercise of clarification of terminology, develop themes proposed by different authors over the past century, beginning with Grinnell (1917). This clarification responds to an empirical need [pioneered by Austin & Smith (1989)] that suddenly became overwhelming because of the explosion in availability of species-occurrence data (now $> 10^8$ records freely available through the http://www.gbif.org portal) and environmental electronic

coverages that began in the 1990s (Soberón *et al.* 1996; Graham *et al.* 2004), together with improvements in GIS technology and modelling techniques. Without much theoretical warning, scientists found themselves able to calculate, for thousands of species, abstract objects obviously *related* to niches and also obviously pertinent to estimating geographic areas of distribution. The need for clarification of terminology and concepts is now pressing (Guisan & Thuiller 2005; Soberón & Peterson 2005; Araújo & Guisan 2006; Kearny 2006).

In this contribution, I have not mentioned the many methods existing to estimate Grinnellian niches, nor precisely what parts in Fig. 1 are estimated by them. Of course the answer depends on specific assumptions about the relative positions of $\mathbf{A}$, $\mathbf{B}$, and $\mathbf{M}$, on whether absence data are available, and on the specifics of the methods used. However, any debate about what it is exactly that 'ecological niche modelling' calculates cannot proceed far without agreement on terms and meanings, which is the purpose of this contribution. By agreeing on distinguishing Grinnellian and Eltonian niches on the basis of spatial resolution and types of variables, and by accepting that Grinnellian niches are properties of a species defined through the areas that it occupies or may occupy, a whole set of questions becomes more sharply defined and operational. The ecological and evolutionary dynamics of Grinnellian niches can be studied through their shapes (Austin *et al.* 1990). How theses shapes are constrained by the environmental space $\mathbf{E}$ within which a species is evolving, and how $\mathbf{E}$ itself changes in time (Jackson & Overpeck 2000; Yesson & Culham 2006) can also be studied, empirically, using measurements of well-defined objects.

A clearer view of the hypothesis of niche conservatism and its many implications (Peterson *et al.* 1999; Ackerly 2003; Peterson 2003; Wiens & Graham 2005) is now possible, as evidence of conservatism applies mostly to Grinnellian niches; the question of whether we should expect niche conservatism also in Eltonian niches is open. The separation of the niche concept on the basis of scenopoetic and bionomic variables, simplified as it is, suggests that it would be interesting first to document, and then to understand, spatial autocorrelations and cross-correlations of the two types of variables. There is also the question of how far the simplification of scenopoetic vs. bionomic variables can be taken. At what scales the interactions between the two become hopeless to disentangle (Davis *et al.* 1998; Buckley & Roughgarden 2006)? The predictive success of distribution modelling at biogeographic extents and low resolutions suggests that, at least at this scale, the distinction is valid and useful, as has been noted by many authors (Austin & Smith 1989; Austin *et al.* 1990; Mackey & Lindenmayer 2001; Pearson & Dawson 2003; Guisan & Thuiller 2005; Araújo &

Guisan 2006). Finding the scope of validity of the distinction may be another interesting field of study. Finally, a full mathematical statement of the hierarchy of Grinnellian and Eltonian processes, linked by metapopulation structure, would constitute a promising way to study areas of distribution of species from their component factors (Mackey & Lindenmayer 2001), rather than as if they were objects existing with an intrinsic physical reality.

In conclusion, in contrasting the ratio of data to theory in the Grinnellian and the Eltonian domains, one is struck by the extreme differences. Immense stores of species-presences data and values of scenopoetic variables are now readily available that can be applied to questions of Grinnellian niche characteristics and variation. However, very little theory has been developed explicitly about this. The opportunity is wide open to develop it, on the basis of large quantities of data that have simply never been available in the much more dynamic and complex domain of the Eltonian niche.

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