Contemporary perspectives on the niche that can improve models of species range shifts under climate change

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Pioneering efforts to predict shifts in species distribution under climate change used simple models based on the correlation between contemporary environmental factors and distributions. These models make predictions at coarse spatial scales and assume the constancy of present correlations between environment and distribution. Adaptive management of climate change impacts requires models that can make more robust predictions at finer spatio-temporal scales by accounting for processes that actually affect species distribution on heterogeneous landscapes. Mechanistic models of the distribution of both species and vegetation types have begun to emerge to meet these needs. We review these developments and highlight how recent advances in our understanding of relationships among the niche concept, species diversity and community assembly point the way towards more effective models for the impacts of global change on species distribution and community diversity.

Keywords: global change; species distribution; biodiversity; modelling; cross-scaling;

1. INTRODUCTION

The impacts of climate change on species distribution and biodiversity will be amplified as global warming becomes stronger, making it all the more urgent that we develop methods to better assess and then mitigate these impacts (Lovejoy & Hannah 2005). Modelling is the most relevant approach to predicting range shifts under global change, but existing models have only coarse spatio-temporal resolution insufficient for the challenges of adaptive management of climate change impacts (Thuiller *et al.* 2008). We can predict the future range of a species but not its local abundance or the habitats within the range where the species might be found. Accurate predictions at finer spatio-temporal resolution require a new generation of species distribution models (Midgley *et al.* 2007),

and these models need to take account of developments in allied fields. Here, we outline existing approaches to modelling species distributions and show how contemporary ecological perspectives on the niche, species diversity and community assembly can inform and inspire novel approaches to predicting the impact of global change on the distribution and abundance of species across a range of spatio-temporal scales.

2. CONTEMPORARY APPROACHES TO SPECIES DISTRIBUTION MODELLING

Current approaches to modelling species distribution, which rely on Hutchinson's (1957) concept of fundamental and realized niches, fall into the following two categories.

(i) *Correlative models* (or habitat models) establish statistical relationships between environmental variables and observed distributions. These models are calibrated using species distributions observed in nature to predict the distribution realized in the face of competition and other factors that restrict the geographical expression of the fundamental niche (Pearson & Dawson 2003).

(ii) *Mechanistic models* quantify the interactions between the organism and its environment through functional relationships known to affect fitness. The mechanistic models can be cast at the level of functional groups or species (Chuine & Beaubien 2001; Sitch *et al.* 2003). They typically assess the fundamental niche, modelling the potential response of a species to environmental conditions by explicitly incorporating biological processes calibrated with observations on individuals in natural populations. The mechanistic approach can be extended to the realized niche, e.g. gap models that consider competitive processes (Bugmann 2001).

Most predictions for range shifts under climate change have been made with correlative models (reviewed in Thuiller *et al.* 2008), which can be quickly fitted provided that large and reliable datasets on the distribution and relevant environmental variables are available. They offer useful and necessary first approximations for distribution modelling at coarse scales. The accuracy of correlative predictions for future distributions, however, hinges on the constancy of the correlations on which they are based, an unlikely outcome given the complexity of organism–environment interactions (Suttle *et al.* 2007) and altered correlations among environmental factors under climate change. These limitations arise in the hierarchy of processes defining the niche at spatial scales ranging from a locality to the geographical range of a species (Pearson & Dawson 2003).

Attempting to resolve these scaling issues, Soberon (2007) argued that we should distinguish two different and independent types of niche: a Grinnellian niche defined by abiotic factors and an Eltonian niche defined by resource–consumer dynamics and biotic factors. We do not see this as a useful dichotomy for two reasons. First, both abiotic and biotic factors act together to influence the distribution and abundance of organisms at all spatial scales. Second, the

relative influence of environmental factors on distribution and abundance is scale dependent. There is no assurance that environmental factors defining a 'realized Grinnellian niche' at the scale of the geographical range will accurately predict outcomes at finer spatial scales. Mechanistic models that explicitly allow for the shifting, hierarchical relationships between environment and species performance offer a simpler and more realistic framework for predicting species distribution at finer spatial scales (Kearney 2006).

Three mechanistic modelling frameworks are used currently to predict shifts in distributions under climate change. Dynamic global vegetation models primarily predict the distribution of vegetation types (Sitch *et al.* 2003, and also Prentice *et al.* (2006) referenced in the electronic supplementary material 1). The gap models (Bugmann 2001 and references in the electronic supplementary material 1) are rooted in population dynamics at the level of individual trees competing in a stand and incorporate relationships associated with survival, growth and reproduction as a function of both biotic and abiotic conditions. Existing mechanistic niche models such as PHENO-FIT (Chuine & Beaubien 2001) are rooted in the functional ecology of species and explicitly incorporate physiological processes. We believe that such mechanistic approaches enriched by contemporary perspectives on the evolutionary ecology of the niche are most likely to yield predictions sufficiently accurate to address mitigation of the climate change impacts associated with species at risk and invasive species.

3. CONCEPTS OF THE ECOLOGICAL NICHE AND SPECIES DISTRIBUTION MODELLING

There are fundamental links among concepts of the niche, species diversity and community assembly that are not widely appreciated in modelling species distribution, and that should be considered in a mechanistic downscaling context. Whittaker (1975) distinguished three classes of species diversity associated with different spatial scales: α-; β-; and γ-diversities. He recognized α-diversity as the number of species in a given locality, β-diversity the number in a region and γ-diversity the number at spatial scales embracing many ecological regions. Silvertown *et al.* (2006) have promoted the idea that there are in turn α-, β- and γ-niches defined by traits and environmental factors critically influencing species distribution at each of these different spatial scales. For example, traits such as frost tolerance or leaf habit can influence species distribution on latitudinal or elevational gradients (γ-niche), flooding tolerance among habitats on landscape gradients (β-niche) or on flooding gradients in a riparian habitat (α-niche). This perspective helps to place the Hutchinsonian niche in a spatial context directly relevant to choices about critical parameters for the species distribution models.

The α-niche is relevant at the scale of community assembly and diversity in a single locality, the β-niche to species affinity for particular habitats in a region and the γ-niche to range-wide distribution. Correlative approaches to modelling distribution are entirely consistent with predictions at the level of the γ-niche, but are limited in predictions at the level of the α- or β-niche for the lack of data to fit models at fine spatial scale. On the other hand, no approach to distribution models can efficiently predict the probability of species occurrence in a given locality on a heterogeneous landscape (α-niche); those predictions are better suited to trait-based approaches to community assembly that draw species from the regional pool without direct consideration of environmental factors (Shipley *et al.* 2006; Ackerly & Cornwell 2007). We therefore turn to ways that the distribution models can better predict species occurrence patterns at the level of the β-niche, that is, at the spatial scale of species turnover among diverse habitats within regions in the continental range of a species.

4. DOWNSCALING PREDICTIONS OF SPECIES DISTRIBUTION

How should we approach downscaling models to predict the habitats within the future ranges of species where populations will colonize at the leading edge of an expanding range, or persist at the trailing edge? We favour a hierarchical and mechanistic modelling framework (figure 1) that focuses on key processes involved in the environmental filters that determine range-wide distribution (γ-niche dimensions) and then the sometimes different processes that determine habitat selection (β-niche dimensions). Decisions on the focal processes in the model need to consider constraints that operate at different life stages including dispersal and seedling establishment (Grubb 1977) as well as adult survival and reproduction, because early life stages are likely to be particularly sensitive to climate change (Svensson *et al.* 2005, referenced in the electronic supplementary material 1). The mechanistic modelling of range-wide distributions in this hierarchical framework has begun, but needs to be refined and extended to predictions at the scale of the β-niche.

The framework we propose (figure 1) requires assessing the influence of traits affecting the distribution at continental versus regional scales, i.e. discriminating among possible γ- and β-traits. The mapped ecoregions of the world (Olson *et al.* 2001, referenced in the electronic supplementary material 1) provide a framework for doing so. The ecoregions are characterized by an assemblage of communities and species that interact dynamically in the context of environmental conditions within a geographically coherent landscape. A γ-trait would facilitate predicting in which ecoregions a species might be found. For instance, a parameter such as foliar resistance to late spring frosts can predict exclusion of a given species in an ecoregion based on seasonal temperature regimes that fall wholly outside the tolerance of the species (γ-niche, figure 1). In ecoregions where a species is predicted to occur, a binary γ-trait such as frost tolerance can also play a significant secondary role as quantitative β-trait (i.e. degree of frost tolerance) acting through microclimatic temperature regimes to predict occurrence in different habitats along topographic gradients (β-niche). On the other hand, the ability to fix nitrogen might be a β-trait critical in

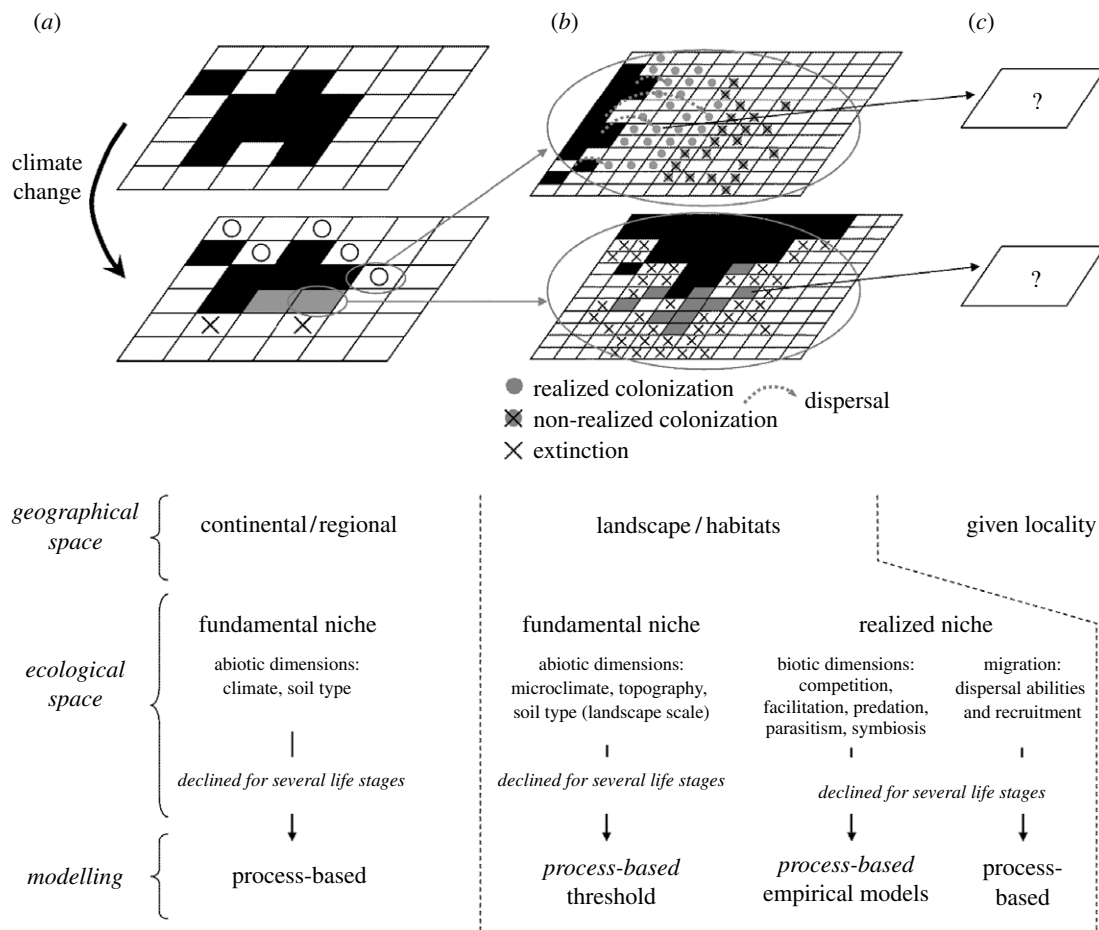(a)   (b)   (c)

Figure 1. A conceptual framework for building species distribution models that predict occurrence in specific habitats in regions within the continental range, i.e. models to scale down from the (a) γ- (crosses, extinction; circles, possible colonization) to (b) β-niche level. (c) So many interacting factors determine community assembly in a particular locality (α-niche level) that the process-based models are likely to be less useful than trait-based predictions at this spatial scale (question marks). Bold entries suggest where progress is more likely in the next few years. Black regions, presence; grey regions, altered presence, white regions, absence.

predicting habitat selection within the ecoregions but insignificant in predicting occurrence in different ecoregions.

At the continental scale, it is most often γ-traits associated with climate that set limits on the distribution (Morin *et al*. 2007). PHENOFIT (described in the electronic supplementary material 2) is an example of a mechanistic niche model that uses processes associated with survival and reproduction in seasonal environments to decide the fundamental climatic niche for a species, and then predict the γ-niche under current (Morin *et al*. 2007) or future climate regimes (Morin *et al*. in press). In our hierarchical modelling perspective, existing models such as PHENOFIT or LPJ-GUESS (Hicker *et al*. 2004, referenced in the electronic supplementary material 1) can and should be scaled down to the level of the β-niche. Once an analysis at the level of the γ-niche places a species in an ecoregion within its continental range, then the processes defining the fundamental β-niche of the species must be assessed to decide its realized β-niche in that ecoregion (figure 1). Macroclimatic factors that define the γ-niche can also scale down as β-traits influencing the distribution of species along regional or local environmental gradients (Ackerly & Cornwell 2007).

For example, species in an ecoregion at their northern range edge are restricted to ridge habitats where their seedling tolerance of chilling due to cold-air drainage into downslope habitats is avoided. Ideally a fundamental β-niche model should be strictly process-based, although for some species the relevant β-traits may be as simple as tolerance of a peculiar soil type (calciphilic species) or strong dependence on a seasonal water regime (obligate wetland species). Similar categorical simplifications may be helpful in modelling the complex processes associated with life stage and colonization dynamics, which are natural foci in terms of range shifts under climate change (Thuiller *et al*. 2008). Recent work shows that process-based modelling on seed dispersal and seedling establishment is feasible (Lischke *et al*. 2006, referenced in the electronic supplementary material 1), and there is no reason that biotic effects cannot also be considered in modelling the realized β-niche.

In closing we note that developing and parametrizing process-based models in this hierarchical framework (figure 1) requires pilot sites with characteristics such as those at the Gault Nature Reserve (www. mcgill.ca/gault/). The reserve lies in the transition zone between two major biomes, the boreal and

deciduous forests of eastern North America; both the leading and trailing edges of range shifts therefore are observable. The local topography is rugged, leading to a wide range of habitats and microenvironmental conditions in a relatively small area; environmental and biotic gradients within the reserve are well characterized, facilitating quantification of the β-niche. Finally, this site is protected and longitudinal and experimental studies can be carried out with minimal disruption. Using species at such pilot sites to develop and test hierarchical models in the framework that we discuss here should yield better predictions of the species distribution under climate change as well as advancing contemporary perspectives on the ecological niche.

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