

USES AND REQUIREMENTS OF ECOLOGICAL NICHE MODELS AND RELATED DISTRIBUTIONAL MODELS

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Abstract.—Modeling approaches that relate known occurrences of species to landscape features to discover ecological properties and predict geographic occurrences have seen extensive recent application in ecology, systematics, and conservation. A key component in this process is estimation or characterization of species' distributions in *ecological* space, which can then be useful in understanding their potential distributions in geographic space. Hence, this process is often termed ecological niche modeling or (less boldly) species distribution modeling. Applications of this approach vary widely in their aims, products, and requirements; this variety is reviewed herein, examples are provided, and differences in data needs and possible interpretations are discussed.

Key words.—ecological niche, ecological niche modeling, distribution modeling, geographic distributions.

Recent years have seen impressive growth in use of modeling approaches based on relationships between known occurrences of species and features of the ecological and environmental landscape (Guisan and Zimmermann 2000; Pearson and Dawson 2003; Peterson 2003a; Soberón and Peterson 2004). These models are often termed 'distribution models,' 'climatic envelope models,' or (most generally) 'ecological niche models.' The aim of these studies is generally to reconstruct species' ecological requirements and/or predict geographic distributions of species.

The earliest applications in this realm were undoubtedly those of Joseph Grinnell, in the 1910s and 1920s (Grinnell 1917; Grinnell 1924), who used the spatial distribution of occurrences of species to infer factors limiting their distributions, and laid a firm foundation for subsequent work in this field. The diversity of such applications, however, has now grown considerably. Distributional models and ecological niche models are being used not just to understand species' ecological requirements, but also to understand aspects of biogeography, predict existence of unknown populations and species, identify sites for translocations and reintroductions, plan area selection for conservation, forecast effects of environmental change, etc. (Table 1).

A basic dichotomy that pervades both the list of uses to which these methods are put and even the terminology used to refer to them is that of ecological niche modeling (ENM) versus distributional modeling (DM). A recent paper (Soberón and Peterson 2005) formalized the idea of niche modeling, and clarified the differences between these two views. Niches and distributions of species were visualized as a set of 3 intersecting circles, representing diagrammatically 3 classes of determinants: physical conditions necessary for a species' survival and reproduction ("abiotic niche"; e.g., correct combinations of humidity, temperature, other biophysical variables, substrate types, disturbance regimes), biotic conditions necessary for a species' survival and reproduction ("biotic niche"; e.g., presences of mutualists, absences of diseases and predators), and accessibility (i.e., within the dispersal capabilities of the species, either historically or at present) (Figure 1, top). This latter set of factors is not a niche dimension, but rather is a set of non-ecological factors that constrain the species to inhabit less than its full distributional potential, and may indeed not be permanent—as shown in the case of invasive species, dispersal limitations often with time are overcome.

In this framework, where abiotic conditions are appropriate can be compared with the fundamental

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Table 1. Summary of uses to which ecological niche models have been put, and the requirements that these uses have in terms of output and information content.

Quality of interest	Understand ecological requirements of species		Understand biogeography and dispersal barriers		Find unknown populations		Find new species		Identify sites for translocations and reintroductions		Conservation planning and reserve system design		Predict effects of habitat loss		Predict climate change effects			
	Any	Any	Any	Any	Any	Population	Any	Absolute	Absolute	Individual-population	Individual-population	Absolute	Any	Any	Any	Any		
Form of prediction (e.g., binary, ranked, absolute)	Any	Any	Any	Any	Any	Population	Any	Absolute	Individual-population	Individual-population	Individual-population	Absolute	Any	Any	Any	Any	Any	
Grain required	Any	Any	Any	Any	Any	Population	Any	Absolute	Individual-population	Individual-population	Individual-population	Absolute	Any	Any	Any	Any	Any	
Causal variables needed, or surrogates OK?	Causal	Causal	Causal	Causal	Surrogates	Surrogates	Surrogates OK if within range; causal necessary if extrapolating	Surrogates OK if within range; causal necessary if extrapolating	Surrogates OK if within range; causal necessary if extrapolating	Surrogates OK if within range; causal necessary if extrapolating	Surrogates	Surrogates	Surrogates	Causal	Causal	Causal	Causal	Causal
Need model response curve or parameter retrieval	Yes	Yes	Yes	Yes	No	No	No	No	Useful, to avoid error	Useful, to avoid error	Useful, to avoid error	Useful, to avoid error	No	No	No	No	No	No
Error needs	Overall low error needed	Overall low error needed	Overall low error needed	Overall low error needed	Low omission (don't mind searching extra localities, but don't want to leave anything out)	Low omission (don't mind searching extra localities, but don't want to leave anything out)	Low omission (don't mind searching extra localities, but don't want to leave anything out)	Low omission (don't mind searching extra localities, but don't want to leave anything out)	Low commission (very high cost of errors)	Low commission (very high cost of errors)	Low commission (very high cost of errors)	Low commission (very high cost of errors)	Overall	Overall	Overall	Overall	Overall	Overall
Potential distributional model versus realized distribution? Uncertainty estimates needed?	Potential	Potential	Potential	Potential	Realized	Realized	Potential	Potential	Realized	Realized	Realized	Realized	Realized	Potential	Potential	Potential	Potential	Both
	No	No	No	No	No	No	No	Yes	Yes	Yes	Yes	Yes	No	No	No	No	No	No

ecological niche of the species, and where abiotic and biotic conditions are fulfilled can be compared with the realized ecological niche of the species (Hutchinson 1957), although Hutchinson focused mostly on competition among the broader suite of potential biotic interactions; these interactions could potentially be integrated more intimately into the niche modeling framework (Araújo and Guisan 2006). The geographic projection of these conditions (i.e., where both abiotic and biotic requirements are fulfilled) represents the potential distribution of the species (Figure 1, top, blue area)—areas where the species could survive if introduced. Finally, those areas where the potential distribution is accessible to the species is likely to approximate the actual distribution of the species (Figure 1, top, black area). Other authors (Araújo and Guisan 2006) have further distinguished between my ‘actual’ distribution and the area actually occupied at any point in time, taking into account stochasticity, metapopulation dynamics, etc.

ENM proponents are interested in using distributional information (i.e., known occurrences sampled from the actual distribution) to estimate ecological niches and potential distributions of species, which then provides a means of understanding and anticipating ecological and geographic features of species’ distributional biology (Soberón and Peterson 2005). This approach has the advantage of allowing the effects of the three components listed above to be distinguished, which offers greater interpretability as to causation of phenomena, and permits predictability of phenomena that depend on the differences between components—e.g., the invasive potential of a species depends on the difference between potential and actual distributional areas. This approach, nonetheless, requires additional complexities of interpretation to produce estimates of actual geographic distributions, given that the data on which the niche models are based are not drawn from the entire abiotic niche or even from the potential distribution, but from the actual distributional area (Araújo and Pearson 2005; Pearson and Dawson 2003; Soberón and Peterson 2005; Svenning and Skov 2004).

DM proponents, on the other hand, include effects of abiotic, biotic, and accessibility considerations in their models from the outset. They argue that because distributional information is an expression of a realized ecological niche, as such the realized niche (only) is the target of modeling. As such, DM proponents would often include in the modeling approach independent variables that summarize biotic considerations (e.g., distributions of other species in the region) and that bring in spatial considerations that may be relevant to dispersal ability and accessibility (Leathwick 1998; Latimer et al. 2006). Whereas DM is simpler in producing estimates of species’ actual geographic distributions directly, predictivity across scenarios of change is largely lost, and assumptions regarding accessibility of areas may still be required (Soberón and Peterson 2005). A further discussion of the differences between ENM and DM is provided below.

This diversity of ideas can place different demands on features of algorithms and approaches used to develop models—and clearly has the potential to lead to debate and perhaps misunderstanding between workers with distinct needs and interests. Nonetheless, contrasts between different conceptualizations of the process (e.g., ENM versus DM) have seen little direct discussion in the literature (Araújo and Guisan 2006; Soberón and Peterson 2005). Such is the purpose of this contribution: to survey the diverse uses to which these approaches have been put, and discuss differences in data needs and interpretation that this diversity demands.

ECOLOGICAL NICHE MODELS AND EVOLUTIONARY CONSERVATISM OF NICHE

In general, readers are referred to recent conceptual reviews (Chase and Leibold 2003; Pulliam 2000; Soberón and Peterson 2005) of relationships among autecology, synecology (i.e., species interactions), and history and accessibility. Once again, this general approach was pioneered by Joseph Grinnell (Grinnell 1917; Grinnell 1924), who was directing detailed series of biological inventories, and was thinking about why species are where they are, and why they are not where they are not. Grinnell’s approach, obviously

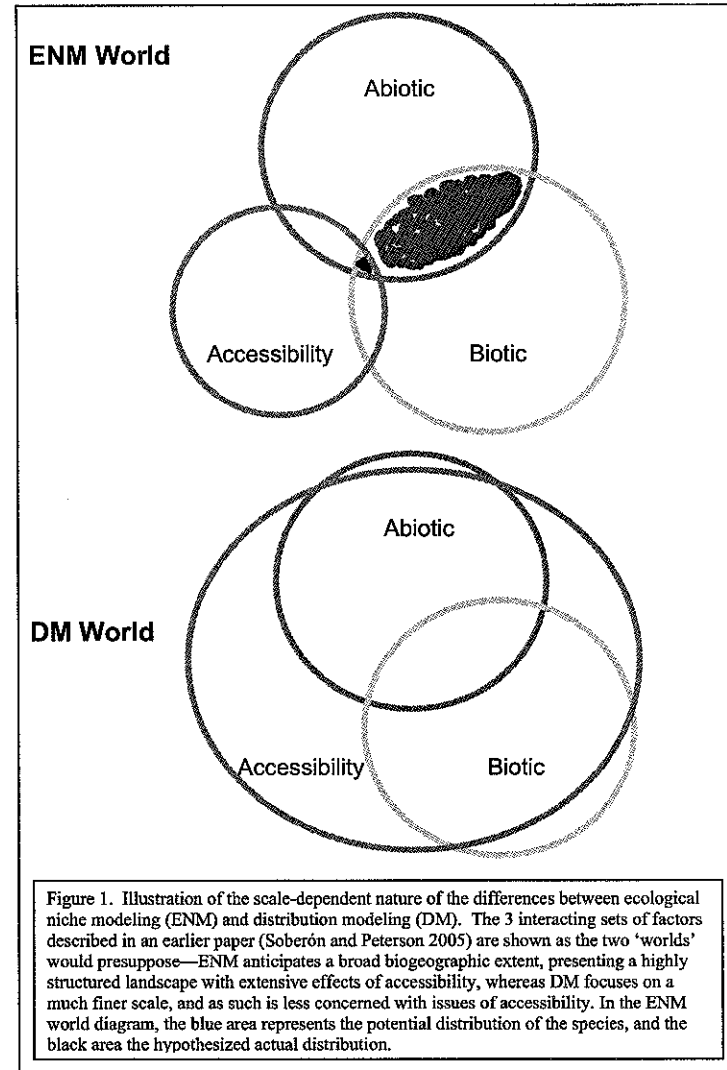


Figure 1. Illustration of the scale-dependent nature of the differences between ecological niche modeling (ENM) and distribution modeling (DM). The 3 interacting sets of factors described in an earlier paper (Soberón and Peterson 2005) are shown as the two ‘worlds’ would presuppose—ENM anticipates a broad biogeographic extent, presenting a highly structured landscape with extensive effects of accessibility, whereas DM focuses on a much finer scale, and as such is less concerned with issues of accessibility. In the ENM world diagram, the blue area represents the potential distribution of the species, and the black area the hypothesized actual distribution.

developed without benefit of computer aids for analysis, was to compare environments inside and outside of species' distributions, asking what is different. What is more, Grinnell fully appreciated the independent nature of ecological needs, versus barriers that can interrupt or truncate distributions (Grinnell 1914).

The concept of an ecological niche has—obviously—evolved quite a bit since Grinnell. It was generalized to include biotic as well as abiotic dimensions, evolving to fit into modern community ecology and associated bodies of theory via treatments by several key workers (Hutchinson 1957; MacArthur 1972). Curiously, though, more modern conceptualizations of ecological niches have become successively less useful for geographic, continental-scale views of species' ecological requirements. As such, in ENM applications, a Grinnellian view of niches has generally been adopted—a species' ecological niche can be defined as the set of conditions that permits it to maintain populations without immigrational subsidy.

The idea that ecological niches place constraints on species' geographic distributions hearkens directly back to the very definition of ecological niches by Grinnell himself. However, this 'constraint' requires some clarification—particularly in light of modern population biological theory regarding metapopulations (Pulliam 1988; Pulliam 2000), in which some suitable areas are expected to be uninhabited, and source-sink dynamics may at times place populations in unsuitable conditions. Certainly, an appreciation of the basic tenets of historical biogeography would suggest that species will not inhabit all areas that meet their niche requirements—rather, barriers to dispersal will often restrict species to a subset of these areas (Peterson 2003a; Peterson et al. 1999). Moreover, the question remains as to whether species are restricted to this particular set of conditions only in the here and now, or are ecological niches evolved characteristics of species that would show inertia (conservatism) over evolutionary time periods? If the latter were the case, ENMs could offer considerable predictive ability for understanding the distribution of that species and perhaps related species.

The roots of the answer to this question came from a paper on beech (*Fagus* spp.) distributions in

Europe and North America, in which distributions of North American and European beech species were compared with respect to climatic dimensions; the result was that considerable coincidence exists between the two species (Huntley et al. 1989). A more recent paper revisited this idea in a broader suite of species (Peterson et al. 1999), testing coincidence of ecological niche dimensions in 37 sister species pairs separated across the Isthmus of Tehuantepec, in southern Mexico—once again, each species' ecological characteristics were highly predictive of those of its sister species. Significantly, this interpredictivity among sister species broke down when confamilial species pairs were compared (Peterson et al. 1999), suggesting the obvious—that evolutionary conservatism of ecological niches is not absolute, and that they do evolve on broader time scales (Martínez-Meyer 2002; Wiens and Graham 2005).

Further evidence for the stable nature of the constraint on geographic potential by ecological niches can be drawn from two additional types of studies. First, under rare circumstances, data availability permits direct before-and-after characterization of distributions for single species; take, for example, recent papers showing significant predictivity of species' distributions across major events of change, such as the end of the Pleistocene (Martínez-Meyer and Peterson 2006; Martínez-Meyer et al. 2004a). Finally, additional evidence comes from studies of invasive species, in which species are transplanted to a distinct geographic and community context. Although it has been suggested based on theoretical musing and limited laboratory experiments that shifting species' interactions would confound any possible predictivity (in this case in the context of anticipating climate change effects on species' distributions) (Davis et al. 1998), numerous studies have successfully predicted the invasive distributional potential of species based on native-range ecological characteristics (Beerling et al. 1995; Higgins et al. 1999; Honig et al. 1992; Iguchi et al. 2004; Panetta and Dodd 1987; Papes and Peterson 2003; Peterson 2003a; Peterson et al. 2003a; Peterson and Robins 2003; Peterson et al. 2003b; Peterson and Vieglais 2001; Richardson and McMahon 1992; Scott and Panetta 1993; Skov 2000; Sutherst et al. 1999; Zalba et al. 2000).

Hence, a diverse and growing body of evidence supports the idea that ecological niche evolution is conservative over short-to-medium periods of evolutionary time, and that models of ecological niches of species can hold significant predictive power for a variety of geographic and ecological phenomena related to biodiversity. Recent theoretical treatments suggest that such should be the case—that, under many circumstances, ecological niche characteristics should not prove particularly labile in their evolution (Brown and Pavlovic 1992; Holt 1996; Holt and Gaines 1992; Holt and Gomulkiewicz 1996; Kawecki 1995). Hence, in practice as well as in theory, ecological niches appear to represent long-term stable constraints on the geographic potential of species.

FUNCTIONALITIES AND POSSIBILITIES

The following is a set of examples of applications to which ENM approaches have been put. These uses are summarized in Table 1, examples and brief discussion are provided in the text that follows.

• Understand ecological requirements of species

Too often, elements of biodiversity are so poorly known that a key first step is simply that of understanding the basic ecological dimensions that are relevant to a species' geographic distribution. That is to say, for the vast majority of species, nothing more is known than a few geographic occurrences—effectively 'dots on maps.' All of the rich detail of natural history, ecology, and behavior can be essentially unknown, but some information can be inferred from ecological niche models. Several examples of this sort of study have been published (Austin and Meyers 1996; Costa et al. 2002; Guisan and Hofer 2003; Hirzel et al. 2002; Luoto et al. 2006; Peterson et al. 2004a; Ron 2005).

• Understand distributions, biogeography and dispersal barriers

ENM techniques also have considerable potential in identifying geographic phenomena that limit species' distributional potential. As such, ENM provides a tool by which the biogeography of species can be illuminated, providing information about species' distributions that is otherwise basically unavailable. This use of ENM hearkens directly back to Grinnell's original efforts. Examples of this sort of ENM application are numerous (Anderson et al. 2002a; Graham et al. 2004; Manel et al. 1999; Pearce et al. 2001; Robertson et al. 2004; Rojas-Soto et al. 2003;

Skidmore et al. 1996; Svenning and Skov 2004). Further extensions of these applications has addressed the seasonal distributions of migratory species (Joseph 2003; Joseph and Stockwell 2000; Martínez-Meyer et al. 2004b; Nakazawa et al. 2004), detection of species' interactions (Anderson et al. 2002b), and fine-scale temporal distributions of ephemeral species (Peterson et al. 2005a).

• Find unknown populations and species

ENM, in its simplest manifestations, provides a framework by which one can interpolate between known populations of a species to anticipate existence of other, unknown populations. Some species are sufficiently poorly known, or are sufficiently endangered, that encountering new populations can make a clear difference in understanding their distributions and in planning their conservation. Including dimensions of conservatism of ecological niche evolution, this same reasoning can be used to predict the geographic distributions of unknown species closely related to known species. Studies of this sort are growing in number (Bourg et al. 2005; Raxworthy et al. 2003).

• Identify sites for translocations and reintroductions

Recent discussions have noted that translocations and reintroductions of species closely resemble species' invasions (Bright and Smithson 2001). That is, these deliberate introductions will work only to the extent that the species encounters appropriate conditions in the new landscape, and to the extent that all of the other factors affecting invasion success also coincide (e.g., demographic effects, biotic interactions). Nonetheless, previous studies have focused mainly on factors affecting success of 'establishable' populations (Armstrong and Ewen 2002; Carroll et al. 2003; Howells and Edwards-Jones 1997; McCallum et al. 1995; Nolet and Baveco 1996; Schadt et al. 2002; South et al. 2000; South et al. 2001; Southgate and Possingham 1995)—few have asked the question of what parts of the landscape are suitable for establishment. As such, ENM provides a framework within which areas may be evaluated for their potential suitability for establishment of populations of species under intensive conservation management. Examples of this sort of ENM application are now beginning to appear (Danks and Klein 2002; Mladenoff et al. 1995; Peterson et al. 2006a).

• Conservation planning and reserve system design

Many exciting advances have been developed recently for prioritizing areas based on patterns of species' occurrences (Prendergast et al. 1999; Pressey 1994; Williams et al. 1996). These approaches

generally focus on the challenge of assembling optimal suites of areas for priority conservation action, and as such represent important new tools in the conservation realm. Nonetheless, the quality of the results of these analyses depends critically on the quality of the distributional information that is fed into them. Given the existence of biases and gaps in the existing sampling, a modeling step to improve the picture of species' distributional areas is warranted, and several efforts have now taken this step (Araújo et al. 2005b; Godown and Peterson 2000; Loiselle et al. 2003; Peterson et al. 2000; Sánchez-Cordero et al. 2005a; Wilson et al. 2005). Further advances in this realm can be derived from use of niche models to identify areas of high probability of population persistence (Araújo et al. 2002) and identifying optimal dispersal corridor locations (Williams et al. 2005); indeed now these place-prioritization algorithms are able to base analyses on probability data (rather than just presence-absence data) (Araújo and Williams 2000; Cabeza et al. 2004; Williams and Araújo 2002). An interesting discussion of issues related to these applications has recently been published (Rondinini et al. 2006).

• Predict effects of habitat loss

Species appear often to obey different suites of environmental factors at different spatial scales (Ortega-Huerta and Peterson 2003). That is to say, they may seek optimal suites of climatic conditions at relatively coarse conditions, but may respond to land cover type or soil type at finer scales (Coudin et al. 2006; Midgley et al. 2003), and to food distributions at micro-scales. As such, at times, investigators may be able to model species' niches at coarse scales, but then use additional information (e.g., land cover type) to refine the model's predictions. To the extent that species' responses to these finer-scale phenomena remain constant over time, then these models can be used to anticipate future distributional potential in the face of changing patterns of habitat distribution and land use. Explorations of applying these ideas in an ENM framework have been developed and applied now in several situations (Peterson et al. 2006b; Sánchez-Cordero et al. 2005a; Sánchez-Cordero et al. 2005b; Thuiller et al. 2004).

• Predict potential for species' invasions

This ENM application is perhaps that which has seen the most intensive exploration by many laboratories, with examples developed for numerous taxa worldwide. Here, the idea is that—given apparently widespread evolutionary conservatism in ecological niche characteristics—species will often 'obey' the same set of ecological rules on invaded distributional areas as they do on their native distributional areas. As such, the geographic potential

of invasive species is often quite predictable, based on their geographic and ecological distributions on their native distributional areas (Beerling et al. 1995; Higgins et al. 1999; Hinojosa-Díaz et al. 2005; Hoffmann 2001; Homig et al. 1992; Iguchi et al. 2004; Panetta and Dodd 1987; Papes and Peterson 2003; Peterson 2003a; Peterson et al. 2003a; Peterson and Robins 2003; Peterson et al. 2003b; Peterson and Vieglaís 2001; Podger et al. 1990; Richardson and McMahon 1992; Robertson et al. 2004; Sindel and Michael 1992; Skov 2000; Sutherst et al. 1999; Welk et al. 2002; Zalba et al. 2000), although the factors that make a species invasive are clearly more complex than just niche considerations (Thuiller et al. 2005b).

• Predict climate change effects

To the extent that species' ecological niches remain fairly constant, and do not evolve to meet changing conditions, it is possible to project present-day niche models onto future conditions of climate, as represented in large-scale climate models (Flato et al. 1999; McFarlane et al. 1992; Pope et al. 2002). These projections, under assumptions made fairly explicit, provide hypotheses of species' potential geographic distributions and how they will change over the next few decades of evolving world climates, and this field has now seen extensive activity (Araújo et al. 2005a; Araújo et al. 2006; Berry et al. 2002; Carey and Brown 1994; Erasmus et al. 2002; Gottfried et al. 1999; Huntley et al. 1995; Kadmon and Heller 1998; Malanson et al. 1992; Pearson and Dawson 2003; Pearson et al. 2002; Peterson 2003b; Peterson et al. 2004b; Peterson et al. 2002; Peterson et al. 2001; Peterson and Shaw 2003; Peterson et al. 2005b; Porter et al. 2000; Price 2000; Roura-Pascual et al. 2005; Sykes et al. 1996; Thuiller et al. 2005a), including retro-projections aimed at reconstructing distributions in the Pleistocene (Hilbert et al. 2004; Hugall et al. 2002; Martínez-Meyer and Peterson 2006; Martínez-Meyer et al. 2004a). The complexities of these projections, however, are only beginning to be appreciated, given species' responses to other factors such as atmospheric gas composition (Thuiller et al. 2006).

DISTRIBUTIONAL MODELING

Distribution modeling, as it is usually depicted by its proponents, appears to constitute an effort not to overinterpret conceptually the models resulting in what would otherwise be ENM. That is, the usual argument goes, because the occurrence data on which models are trained are sampled from the actual distribution of the species, it is improbable that the model can say anything about the potential distribution or fundamental

ecological niche of the species. While these arguments have some merit if interactions were to occur universally and in ecological dimensions (rather than in geographic dimensions—'who gets there first'), I argue that such situations are rare, although this is clearly a topic for future detailed analyses. That is, I argue that many species interactions take place in geographic space, and that they are far from universal: in this way, ecological potential of species is manifest in some portion of the range, and good (dense, representative) sampling will usually reveal that potential (Araújo and Guisan 2006): a worked example is provided in a recent publication (Anderson et al. 2002b), and the theoretical issues have also been reviewed recently (Soberón and Peterson 2005).

Another interpretation of the ENM-DM debate focuses on the scale of the inquiry (see Figure 1). Here, whereas ENM proponents would anticipate a full-species-range scale for a study, DM proponents may be willing to examine a much smaller portion of species' distributions. As such, accessibility considerations become unimportant in DM (as the entire study area tends to be available to the species), whereas ENM—which is often developed at broader scales (such as that of an entire species' distribution) must take them into account more explicitly.

DM, given that it is able to rely on assumptions such as that dispersal limitation is relatively immaterial in sculpting species' distributions, is often able to produce more accurate local predictions within regions. However, DM results are often limited by spatial references in environmental data sets used to build models, and the limited spatial scales of inquiry may often provide incomplete characterization of niches of species. ENM, on the other hand, uses the conservative nature of ecological niche characteristics of species to open additional suites of predictive capabilities, and provides a clearer interpretation of causal forces affecting species' distributions. However, ENM models may be difficult to test and validate because special assumptions are required to turn potential distribution estimates into actual distribution estimates.

DISCUSSION AND CONCLUSIONS

The diversity of applications discussed above suggests that important methodological requirements may also differ among applications. That is, different applications may require distinct assumptions and interpretations to make possible a particular result. Table 1 details a number of considerations that may be relevant in this respect.

These points are relevant also to the challenge of choosing among the many options for creating ecological niche models in the first place. The community of investigators that use these approaches use many different inferential techniques. These techniques include very simple range-rule approaches that detect limits along independent environmental axes, multivariate statistical approaches that fit response curves in environmental space, and evolutionary computing approaches that explore solution space randomly to produce 'best' solutions to the challenge. These different techniques interact with the uses listed in Table 1 as well—some techniques may be better suited to some uses.

Qualities of interest regarding uses and a brief discussion of their interaction with techniques and uses, are as follows:

- *Form of prediction* (e.g., binary, ranked, absolute) – Some uses (e.g., identification of sites for translocations and reintroductions, conservation planning and reserve system design) require an absolute, rather than a relative, answer to the question of suitability. That is to say, it does no good to reintroduce a species to the best site in a landscape if that site is not highly suitable for the species to become established. These uses will thus require inferential approaches that have some mode of calibration to indicate which sites are equally suitable as those where the species does maintain or has maintained populations.
- *Grain required* – Grain required for usable predictions varies from a grain relevant to individual or at least population distributions (e.g., identification of sites for translocations and reintroductions) up to broader-scale views (e.g., prediction of climate change effects). Although the details depend on the extent of the area under consideration, this factor will clearly demand that inferential algorithms be able to deal with large data sets in developing models.
- *Causal variables needed, or surrogates OK?* – The issue of what is a causal variable is not simple.

Causation is not a yes-no issue, but rather is an issue of relative immediacy. For example, humidity may be directly related to survival, but the most proximate manifestation of 'humidity' may be whether a species' eggs desiccate before they can hatch. Nonetheless, clearly, some variables are likely to be surrogates for 'real' causal variables. Similarly, many models use elevation as an independent variable—elevation nonetheless is really an excellent surrogate for temperature, but cannot be used in place of temperature, e.g., when climates change, because elevation would have a changing meaning in different climate regimes. The different uses break down about evenly as to whether surrogates are acceptable, or whether causal variables are needed (Table 1).

- *Need model response curve or parameter retrieval*—Some modeling approaches (e.g., multivariate statistical approaches) are able to reconstruct the roles of individual independent variables in model predictions, whereas others (e.g., evolutionary computing approaches) must reconstruct this information in a more *post hoc* manner. Although both approaches can potentially 'get at' the issue of the shape of the response curve to particular environmental variables, the former are clearly more convenient.
- *Error needs*—Two general types of error are possible in modeling species' niches and distributions—omission (leaving out of the prediction areas that are within the species' ecological potential), and commission (including in the prediction areas outside of the species' ecological potential). Different uses of modeling emphasize different error components as more or less important—for example, understanding ecological requirements of species would emphasize minimizing both error components simultaneously, whereas identification of sites for reintroductions would require low commission error (high cost of error as to which sites are suitable).
- *Potential distributional model versus realized distribution?*—Several of the uses detailed in Table 1 are clearly functions of potential distributions, rather than actual distributions of species. For example, all applications to predicting species' invasions would perforce have to be based on estimates of potential distributions, whereas other applications (e.g., conservation planning and reserve design) would either demand actual distributional estimates or potential distributional estimates refined by specific assumptions regarding interactions with other species and dispersal abilities.

- *Uncertainty estimates needed?*—Finally, because of high costs of being wrong in bases for decisions, applications such as identification of sites for translocations and reintroductions and conservation planning and reserve system design require careful estimates of uncertainty associated with predictions. Such estimates are most easily drawn from multivariate statistical approaches, although they are possible using other approaches as well.

In sum, the world of modeling ecological and geographic distributions of species is simultaneously complex (see the preceding list of considerations in choosing modeling methods) and promising (see the exciting list of uses farther above). This field is clearly just recently achieving much of the breadth of its potential, and as a consequence is seeing increasing interest and application.

This contribution is intended principally as a platform for discussion. That is, much of what is said regarding particular applications and uses and their requirements for inferential algorithms is opinion, and is intended to spark discussion and debate, laying out one point of view. My hope is that this contribution can serve to initiate such a debate, and by this means improve the conceptual platform on which an even-more-vibrant field of inquiry can be based.

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