CLIMATE CHANGE AND BIODIVERSITY: SOME CONSIDERATIONS IN FORECASTING SHIFTS IN SPECIES' POTENTIAL DISTRIBUTIONS

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Global climate change and its broad spectrum of effects on human and natural systems has become a central research topic in recent years; biodiversity informatics tools—particularly ecological niche modeling (ENM)—have been used extensively to anticipate potential effects on geographic distributions of species. Misuse of these tools, however, is counterproductive, as biased conclusions might be reached. In this paper, I discuss some issues related to niche theory, geographic distributions, data quality, and algorithms, all of which are relevant when using ENM in climate change projections for biodiversity. This assortment of opinions and ideas is presented in the hope that ENM applications to climate change questions can be made more realistic and more predictive.

Key words: climate change, ecological niche, niche modeling, geographic distribution, bioclamatic envelope

The large-scale climatic changes observed and documented since mid-twentieth century represents a major and growing concern for the academic community. Considerable human and economical resources have been directed at understanding these phenomena and their possible consequences for humans and the natural world (Houghton et al. 1990; IPCC 1995; Watson 2001).

One dimension in which climate change effects on natural systems has been studied is in understanding its implications for potential geographic distributions of species. A common rule of thumb has been that species' potential distributional areas will likely shift poleward, as well as upward in elevation in areas of topographic relief. Although a useful generality, the predictive power of such sweeping statements is low; as such, the need for tools that produce species-specific, predictive tools regarding the details of climate change effects on species' distributions became clear.

Ecological niche modeling (ENM), also known as bioclimatic modeling or climate envelope modeling, has been applied increasingly to this task. This approach uses georeferenced primary occurrence data for species, in combination with digital maps representing environmental parameters, to build models of the ecological requirements of species—the set of conditions suitable and necessary for long-term survival of populations of the species without immigrational input. Then, such conditions are located on landscapes, and maps created to indicate the distributional potential of the species (Pearson and Dawson 2003; Peterson et al. 2001; Thuiller 2003). With this approach, distributional shifts caused by climatic change, in both the past and the future, can be estimated based on the fact that the niche model is characterized in ecological space—conditions with which a species is associated at present can be sought on modeled future or past climate scenarios (Fig. 1) (Hugall et al. 2002; Martinez-Meyer et al. 2004; Meynecke 2004).

The simplicity of the approach, improved availability of relevant data and software, and the importance of the topic have increased considerably the number of studies aiming to estimate effects of future climatic regimes on species' distributions. For instance, several studies have projected future potential distributions of species for conservation purposes (Aspinall and Matthews 1994; Bakkenes et al. 2002; Beaumont and Hughes 2002; Burns et al. 2003; Dunbar 1998; Erasmus et al. 2002; Iverson and Prasad 2001; Meynecke 2004; Midgley et al. 2002; Midgley et al. 2003; Ortega-Huerta and Peterson 2004; Peterson et al. 2002; Skov and Svenning 2004; Tellez-Valdes and Davila-
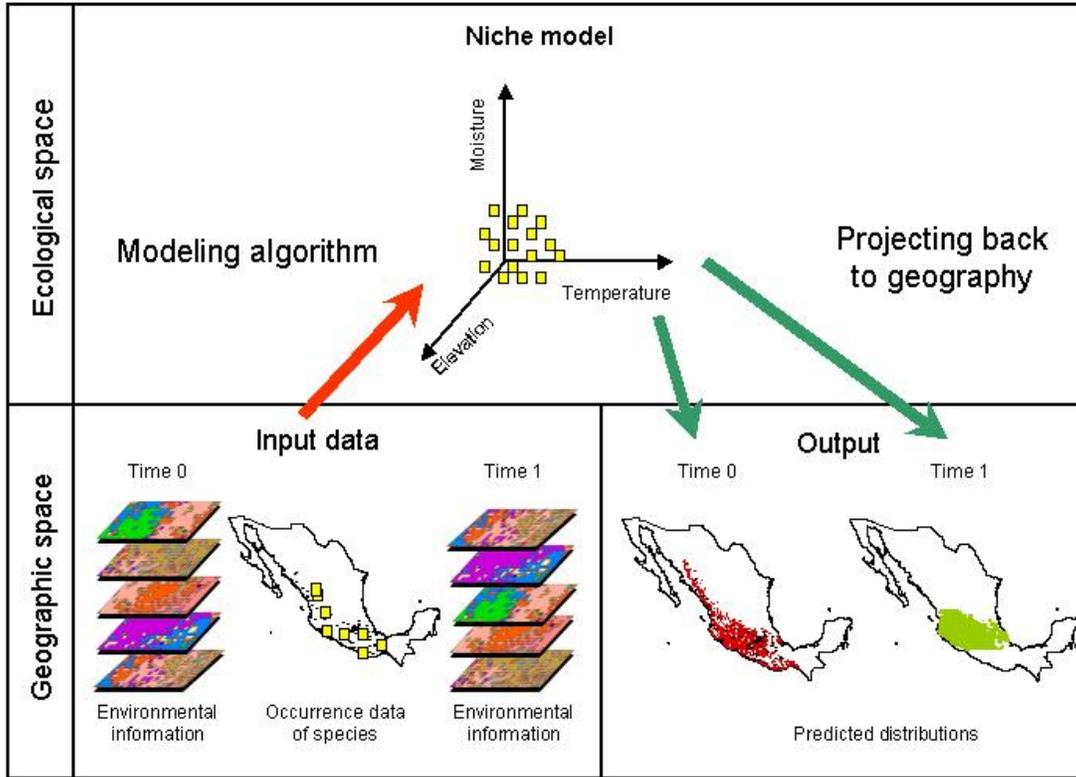
Figure 1. Diagrammatic summary of the ecological niche modeling process (see text for details).

Aranda 2003; Thomas et al. 2004; Williams et al. 2003), resource management (Bradshaw et al. 1992; Clark et al. 2001; Holden et al. 2003; Loukos et al. 2003; Mati 2000; Rafoss and Saethre 2003; Schwartz et al. 2001; Sykes 2001; van Staden et al. 2004; Williams and Liebhold 2002), public health (Ando 1994; Craig et al. 1999; Peterson and Shaw 2003; Wittmann et al. 2001), and invasive species (Kriticos et al. 2003).

In many cases, however, insufficient attention has been paid to the limitations of the approach and the data, and analyses rely on untenable assumptions that may bias conclusions (Thomas et al. 2004; Thuiller 2003; Thuiller et al. 2004b). In this paper, I present and discuss what I consider the most critical issues—both conceptual and operational—that should be taken into account when using ENM to anticipate climate change effects on geographic distributions of species.

CONCEPTUAL CONSIDERATIONS

ENM depends conceptually on the theory of the niche, developed in the early 20th century (Soberón and Peterson 2005). The contribution of niche theory to biogeography is highly relevant, since it provides key conceptual elements to understand why species have limited ranges, and how abiotic and biotic factors interact to mold species' geographic distributions (MacArthur 1972). An understanding of these concepts is necessary for adequate and appropriate application of ENM tools to produce future potential distributional maps, and for correct interpretation of the results.

Although several often disparate niche definitions have been proposed through the years (Elton 1927; Grinnell 1917; Hutchinson 1957), in the context of biogeography, a generally accepted definition refers to the set of environmental conditions—biotic and abiotic—under which *populations* of a species can survive indefinitely without immigration (Grinnell 1917; Hutchinson 1957). According to Hutchinson (1957), measurements of a population's performance along an environmental gradient (e.g., temperature) can be used to define tolerance limits along that axis—i.e., the niche limits. Extending this notion to two dimensions (e.g., temperature and humidity), the niche takes the form of a polygon; considering multiple (n) axes, we can envision an n-dimensional hypervolume encompassing the set of appropriate conditions. Hutchinson termed this hypervolume the *fundamental niche*—the full range of possibilities *-in ecological space-* where the population can persist. In most cases, though, negative biotic interactions (chiefly competition and predation) prevent species from occupying the entirety of the fundamental niche; according to the theory, the portion of the fundamental niche actually occupied by the species in geographic space was called the *realized niche* (Hutchinson 1957). Hence realized niches are subsets of fundamental niches.

From these ideas, several issues relevant to ENM and studies of climate change can be identified. Soberón and Peterson (2005) developed a conceptual framework to answer a fundamental question—what precisely are we modeling with ENM tools? As they described, differences exist between fundamental niches, realized niches, and geographic distributions, with each one implying a distinct set of influencing factors. According to the Soberón and Peterson framework, in a modeling exercise, depending on the nature of the input occurrence data (presence-only *versus* presence/absence data; source [within-the-niche] *versus* sink [outside-the-niche] populations), the model may reflect the fundamental niche, realized niche, or actual geographic distribution of the species. In general, these authors argue that in most cases ENM summarizes something more towards the fundamental niche, which explains the fact that some (or a lot) overprediction is generally contained in resulting maps.

Clearly, previous manifestations of niche theory are insufficient to explain geographic distributions of species for two reasons. (1) Niche theory simply does not account for influences of historical factors, such as biogeographic barriers and life history traits of species such as dispersal capacity, which are manifested exclusively in geographical, rather than ecological, space. (2) Although interactions may take place in ecological space (e.g., species A is able to survive at some temperatures only because its competitor species B cannot), they may also exist exclusively in geographic domains (e.g., under identical environmental conditions, species A is absent from site 1 because

species B is present, but species A is present at site 2 because species B has never been there for historical reasons), or in both realms.

Therefore, finding in the field a stable population of a species likely means that that place presents suitable environmental conditions—biotic and abiotic—and thus lies within the species' realized niche. Hence, neglecting the possibility of sink populations biasing model results, occurrence points can be assumed to represent within-the-niche populations. In such cases, maps resulting that show true overprediction (i.e., not owing to a poorly specified model), would represent a projection of the realized ecological niche model of the species onto an *unconstrained fundamental geographic space*: a landscape in which historical factors and/or interactions acting in the geographical domain are not reflected. Put another way, this map would identify the potential geographic distribution of the species.

If the additional factors of history, limited dispersal ability, and biotic interactions were incorporated into the modeling process, then we would be truly modeling the realized ecological niche projected onto its *realized geographical space*—in other words, the actual geographic distribution of the species. Currently, to approximate actual geographic distribution maps from potential distributional models, *post hoc* procedures have sometimes been used. For example, electronic maps of biogeographic provinces, ecoregions, or vegetation types can be used as "cookie-cutters" to trim potential distribution maps under the assumption that the species' distribution is well-sampled at the level of ecoregions, and that disjunctions among such regions represent distributional barriers for the target species (Anderson and Martínez-Meyer 2004).

In studies in which the goal is to anticipate geographic shifts in species' distributions resulting from climate change, additional problems arise. In the best-case scenario, a species' present-day (modeled) potential distribution map resembles fairly well its known geographic distribution; in this case, an investigator may assume that environmental factors (rather than biotic or historical factors) are most influential in molding the species' distribution. When this model is projected onto future climate scenario, the resulting map identifies areas

likely to become habitable or uninhabitable for that species. Several authors have argued that this sort of result should be taken cautiously, since biotic interactions may shift in the face of changing conditions, and may thus affect the distributional potential of species (Davis et al. 1998a; Davis et al. 1998b; Pearson and Dawson 2003).

In situations in which a potential distribution map for present-day conditions shows broad areas of overprediction, biogeographic barriers to dispersal and colonization, biotic interactions, or both have an important influence on the geographic distribution of the species. Such potential distribution maps would need to be reduced to the species' actual geographic distribution prior to interpretation, based on explicit assumptions regarding which sorts of areas are likely to represent actual distributional areas as opposed to potential distributional areas (Fig. 2).

Projecting such models to future scenarios poses important complications. If potential distribution maps are not processed *post hoc* into actual distribution maps, then establishing which habitable areas are likely to be reachable by the species is difficult, and projections to future conditions may become totally unrealistic (Fig. 2). If the same scheme as for present-day maps is followed, and distributions are adjusted via maps representing biogeographic barriers, the outcome may be misleading because the barriers may also shift under effects of climate change. In other words, what is today a barrier for a species may not be a barrier in the future, because ecological differences become less abrupt and make previously inhabitable areas habitable for the species (Thomas et al. 2001). Sadly, no straightforward solution to this problem exists.

At present, projecting niche models onto changed-climate landscapes produces expected suitability maps. When the goal is to produce plausible future distributional scenarios for species, understanding and incorporating dispersal considerations becomes critical (Morecroft et al. 2002; Svenning and Skov 2004; Thuiller et al. 2004a; Travis and Dytham 2002). Previous studies have shown that dispersal patterns are species-specific, and also depend on the geography of the area, which can make predictions difficult (Clark et al. 2003; Davis
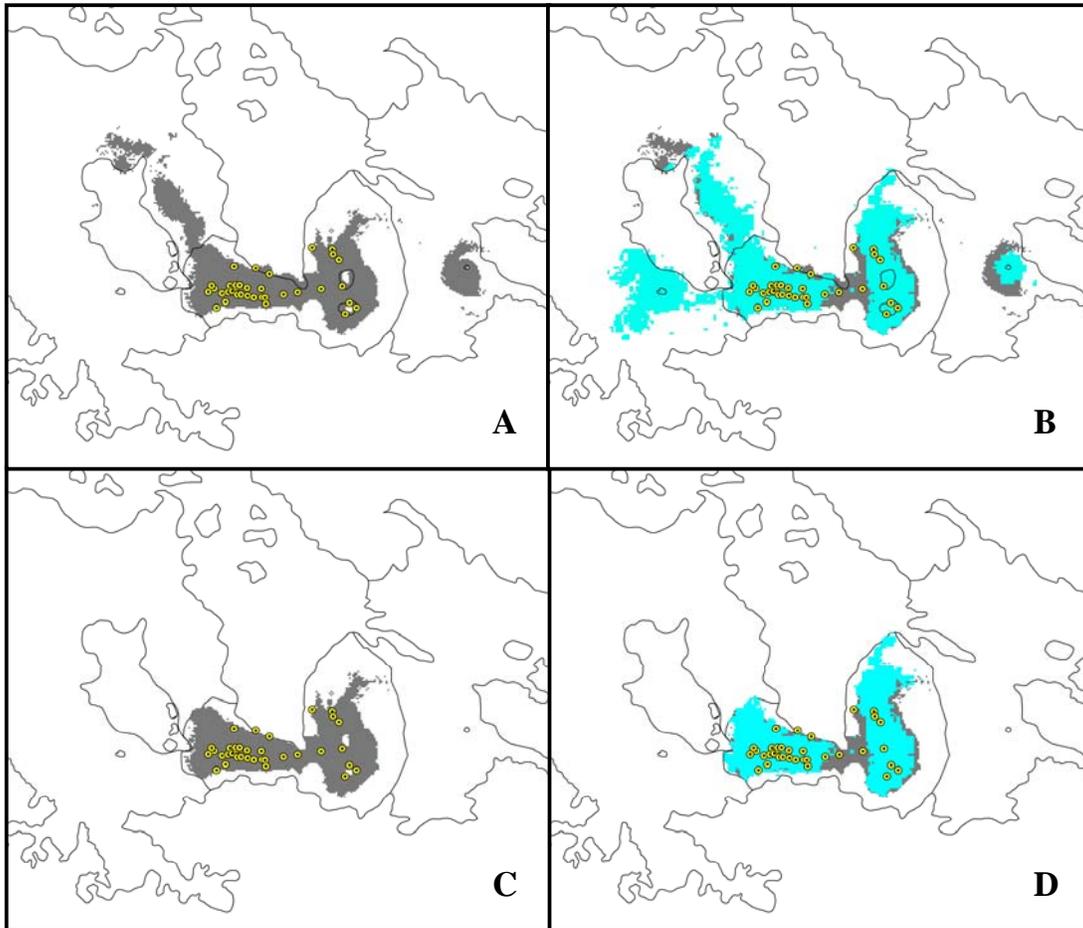
Figure 2. Distribution model of the Volcano Rabbit (*Romerolagus diazi*) in central Mexico, showing raw predictions for (A) the present and (B) in 2050. Overprediction (commission error) is reduced with a *post hoc* clipping process both in the present (C) and the future (D) using a map of the ecoregions (black lines), assumed to represent biogeographical barriers for the species. Gray areas represent the prediction for the present and blue areas are the modeled projection to 2050 under a future-climate scenario.

et al. 1998b; Dullinger et al. 2004; Post and Forchhammer 2002; Travis and Dytham 2002). As a result, some authors do not attempt to present definite future distributional predictions, but rather a set of possible scenarios based on different dispersal assumptions, ranging from no dispersal to universal dispersal (Peterson et al. 2001). In this way, one can at least bracket possible effects of climate change on species' distributions. Recent findings and new modeling tools regarding dispersal of species, however, are opening opportunities to incorporate dispersal information into predictive modeling to produce more realistic future distributional scenarios (Clark et al. 2003; Collingham and Huntley 2000; Nagelkerke and Alkemade 2003; Nathan et al. 2002).

Finally, even resolving issues of interactions, barriers, and dispersal, some uncertainty remains in future projections as regards the ability of species to survive in novel environments. As climates change, environmental regimes novel to populations emerge; populations will be able to survive under these conditions if (1) those conditions are within their fundamental niches (Vetaas 2002); or (when such is not the case) (2) populations are able to adapt to conditions outside their present niches (Holt 1990; Holt and Gaines 1992). In the first case, projections to future scenarios may fail to predict areas within the fundamental niche but not represented in the modeled realized niche; as such, the models may underestimate potential future distributions of species. In the second situation, models will also underrepresent potential distributional areas, given the species' ability to adapt to new conditions; however, theoretical and empirical evidence strongly suggests that adaptation is less frequent than migration (Holt 1996; Hughes 2000; Martínez-Meyer et al. 2004).

OPERATIONAL CONSIDERATIONS

Modeling ecological niches and predicting geographic distributions of species frequently becomes complicated because input data are frequently far from ideal. As mentioned above, two main data streams are employed: (1) locality data documenting known occurrences of the species (some algorithms incorporate absence data as well), and (2) environmental data in the form of raster GIS maps, normally including some combination of climatic, topographic, and land-cover data. In climate change studies, parallel environmental variables must be available for the future (or the past; Fig. 1). In the following section, I discuss some important issues regarding data quality, both biological and geographic, that should be taken into account in this sort of analysis.

Biological data

Studies of climate change and biodiversity are frequently based on incomplete biological data; indeed, ENM emerged as a solution to this challenge. Perhaps the most frequent question from new workers in this field refers to minimum numbers of occurrence points needed to generate robust models. Sadly, no easy answer to this question exists. Controlled experiments and analyses have shown that minimum numbers of points required for modeling depends on the species in question, as well as on the number of geographic variables in the analysis, and the algorithm used (Kadmon et al. 2003; Stockwell and Peterson 2002).

In general, a rule of thumb is that the more occurrence data are available, the better, but even this seemingly obvious point is not necessarily true. Actually, the distribution of occurrence data in ecological space becomes much more important than the overall density of points, particularly for generalist, widespread species that likely have broad ecological niches (Kadmon et al. 2003; Thuiller et al. 2004b). When the distribution of occurrence points in geographic space is too biased (i.e., observations are clustered in small regions of the species' range), biases appear in ecological space as well, and models can misrepresent the species' ecological requirements (Fig. 3). In this case, systematic removal of points to "balance" their spatial distribution have resulted effective (Hidalgo-Mihart et al. 2004). Although methods for this manipulation need exploration and standardization, a useful approach has been to overlay a reticule on the study area, and randomly select one point per cell (Hidalgo-Mihart et al. 2004). Cell size for the reticule has to be large enough to eliminate clustered points, but not as large as to eliminate points from the same cell that represent different environments.

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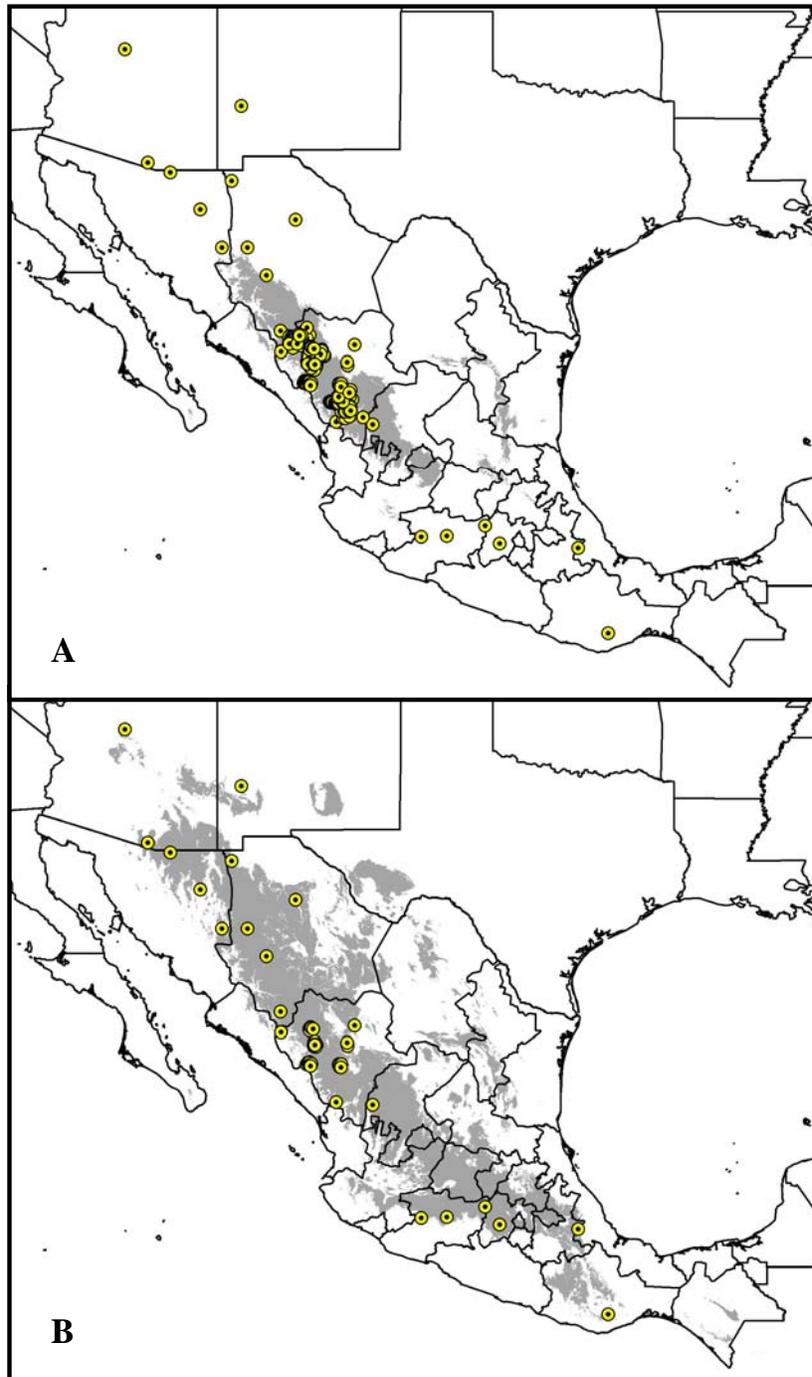
Figure 3. Geographic bias in occurrence data available for the Mexican wolf (*Canis lupus baileyi*). (A) Input points show strong geographic bias towards the center of the distribution of the species, causing a bias in the distribution model. (B) Systematic removal of points reduces the bias and produces better distribution models.

Not only are the amount and distribution of points important to producing good models, but some species are more difficult to model than others. In general, models for species with narrow ecological niches (e.g., habitat specialists) result better and more predictive than models for species with broad ecological niches (Thuiller et al. 2004b).

Of course, it is always highly recommended to validate model predictions prior to any extrapolation or interpretation (Oreskes et al. 1994). Validation usually takes the form of challenging models to predict the distribution of a suite of points that were not included in model development—a general, predictive, and usable model will be able to anticipate the distributions of such sets of points. Model predictions may also be validated via cross-time tests, which such is feasible (Martínez-Meyer et al. 2004). Different statistics have been used for this purpose, including the Receiver Operating Characteristic (ROC) curve, Cohen's Kappa statistic, and chi-square tests (Anderson et al. 2003; Elith and Burgman 2002; Fleishman et al. 2003; Oreskes et al. 1994); detailed reviews of statistical methods can be found elsewhere (Fielding and Bell 1997; Pearce and Ferrier 2000; Pearce et al. 2001), but a couple of comments will be provided here.

First, ROC curves and Kappa require both presence and absence data, whereas chi-square not. Of course, the former methods are more powerful, but interpretation of 'absence' information is complex—absences of *species* will frequently not coincide with absence of appropriate niche conditions, making the meaning of the absence data difficult to interpret (Soberón and Peterson 2005). In instances in which true absence data are lacking and sampling from non-presence areas is performed to obtain 'pseudo-absence' points (Engler et al. 2004; Hirzel et al. 2001; Zaniewski et al. 2002), these same concerns are relevant.

Furthermore, the independence of data sets for developing models ('calibration') and for evaluating them ('validation') is critical. Different strategies have been followed here, including data partitioning, resubstitution, and independent sampling. In general, obtaining new and independent data directly from the field is preferable. When such new sampling is not feasible, data partitioning seems to provide better results than resubstitution

(Fielding and Bell 1997). When biases exist in particular sampling methods, calibration and validation data sets may *both* reflect them, and the model may not be generally representative of the distribution of the species.

In any case, true independence may not exist in the biological data because of the very nature of species' distributions. However, this situation overestimates model fit, necessitating development of validation techniques that incorporate effect of spatial autocorrelation (Hampe 2004). Projections onto scenarios of change over time bring additional complications, because frequently no data are available to validate future predictions. Projections to past climates are often the only means of obtaining statistical validation for cross-time predictions (Martínez-Meyer et al. 2004). In future climate change studies, a minimal step is validation of model predictions under current conditions—because errors are propagated or even exacerbated in projections (Thuiller 2003), species for which present-day models are poor should not be used for future projections.

Geographic data

Several issues related to environmental datasets used in ENM affect model performance in both present and future predictions, including the amount, type, and quality of variables included in analyses. Experimental studies have demonstrated that some environmental variables are more informative than others when modeling ecological niches. In general, climatic variables (e.g., maximum and minimum temperatures, precipitation) are particularly useful, as they coincide with physiological tolerances (Parra et al. 2004; Peterson and Cohoon 1999). However, a combination of climatic and topographic features, like elevation, slope, and orientation of slopes, yields better results (Parra et al. 2004) because topographic features modify how individual animals or plants experience a particular climate regime. In future projections, elevation certainly is not useful, as certain elevation-temperature associations break down under different climates.

Not only are the type and number of environmental variables important, but also their quality in terms of resolution (spatial, temporal, and metric) is crucial. Today,

thanks to efforts by individuals and research groups, global, regional, and local climatic and topographic data sets with different spatial and temporal resolutions are freely available (e.g., Hydro-1K[1], WorldClim[2]; Chapman et al. 2005). Nonetheless, at least until recently, many regions lacked adequate geographic information (Lim et al. 2002). In any case, a thorough understanding of the methods used to derive geographic datasets is highly desirable, since all of them have limitations (Chapman et al. 2005), and these limitations will affect modeling outcomes.

Spatial resolution (pixel size) is of particular importance when interest is focused on species with relatively small ranges or in complex landscapes (Chapman et al. 2005). Low-resolution maps do not capture such variability and models result too coarse or imprecise (Lim et al. 2002). High-resolution datasets may be difficult to generate for some regions because climatic station data are too sparse or are lacking (New et al. 1999). Even when high-resolution maps are derived (e.g., Worldclim), it is very important to validate their reliability with independent field data or other information (Magana et al. 1997) before using them for predicting species' distributions.

In climate change studies, simulated future climates are generally obtained for projections by one of two means: (1) increasing one or more present-day temperature variables (minimum, maximum or mean) by some quantity (e.g., Tellez-Valdes and Davila-Aranda 2003), or (2) from data output from General Circulation Models (GCM) (e.g., Peterson et al. 2002). Use of GCM results is clearly preferable since climate change involves complex rearrangements of numerous parameters; GCMs are currently the best means to account for these complexities (Murphy et al. 2004). However, inconsistencies among predictions from different GCMs available pose problems for users who may not be able to decide among alternatives. In recent years, research efforts have focused on quantifying uncertainties among models, with the aim of producing more reliable estimations (Allen et al. 2000; Murphy et al. 2004). Regional Climate Models (RCM) have been developed

for some areas as well, which improve spatial resolution, but which bring an additional suite of assumptions and potential complications (MacCracken et al. 2004). For now, statistical downscaling of GCM results remains the best option for producing high-resolution scenarios (Giorgi et al. 2001).

Modeling algorithms

As with biological and geographic datasets, ENM algorithms have seen considerable improvement and development in recent years. Currently, many ENM algorithms are available as stand-alone software packages (e.g., Biomapper, DesktopGarp, FloraMap, BIOCLIM), or are implemented in statistical or GIS packages (e.g., GRASP). This rapid development has led to a series of studies testing and comparing algorithm performance under diverse circumstances. Although results suggest that no single algorithm can be identifying as performing better than all others under all circumstances (Brotons et al. 2004; Pearson et al. submitted; Thuiller et al. 2003), some generalities can be drawn.

First, as mentioned above, all approaches face particular problems in dealing with widespread species. This effect results from increased probability of data being lacking or bias in representation of the niche (Brotons et al. 2004), or from reduced statistical power (Stockwell and Peterson 2002). In this case, algorithms able to handle "true" absence data (e.g., Generalized Linear Models, GLM; Artificial Neural Networks, ANN) seem to perform better than presence-only methods (e.g., Ecological Niche Factor Analysis, ENFA; BIOCLIM). However, most biological data sources provide only occurrence records; so methods that at least take advantage of "pseudo-absence" information (e.g., Genetic Algorithm for Rule-set Prediction, GARP) may have an advantage.

Second, since model performance varies among species, combining results of different methods may be desirable in cross-taxon studies (Thuiller 2003). Currently, only a few algorithms incorporate multiple methods in predicting distributions, like Biodiversity Modeling, Biomod (Thuiller 2003) and GARP (Stockwell and Peters 1999). Another useful approach to this challenge may be development of models using several distinct

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[1] http://lpdaac.usgs.gov/gtopo30/hydro/.
[2] http://biogeo.berkeley.edu/worldclim/worldclim.htm.

algorithms, and combining the results after modeling.

Finally, projections to future climate scenarios may produce very different results depending on the algorithm used, even when present-day results are very similar (Thuiller 2003). These differences arise because different algorithms make different assumptions when extrapolating to future scenarios presenting environmental combinations not found in the present (Pearson et al. submitted). Theoretical studies have indicated that significant elements in species' adapting to new conditions are the degree of dissimilarity between conditions within and outside the niche, genetic variation for key traits determining abundance and distribution, dispersal dynamics, etc. (Holt and Gaines 1992). A fundamental problem is that very little is known about species' responses to novel environments to permit their incorporation into the modeling process (Holt 1990). Probably, the most appropriate recommendation here is to evaluate algorithm performance in present-day predictions, to select only those algorithms that perform best, and to follow a 'consensus' approach with algorithms used in future projections. This approach at least provides a notion of ranges of distributional possibilities of target species, and strengths and weaknesses of algorithms employed. Clearly, more research is needed both in fundamental aspects of the ecology and evolution of species, and in implementation of these findings in ENM.

CONCLUSIONS

In recent years, climate change has come to rank among the most active research topics in science because of its immediacy, and the profound effects on natural systems and human welfare that are anticipated. Rapid development of biodiversity informatics tools has stimulated research focused on forecasting climate change impacts on biodiversity. ENM has become particularly important, because it provides one of few predictive approaches to understanding geographic dynamics of species. As more people turn to such tools, it becomes relevant to review key aspects of their use. Poor understanding of the ENM approach, both in terms of conceptual basis and practical implementation, might lead to inappropriate results or interpretations.

The first elements for consideration are the biological, ecological, and geographic characteristics of the species in question. Natural history aspects such as niche breath, ecological affinities, and dispersal capacity are crucial to understanding geographic distributions, and to interpreting model results. Here, the theory of the niche plays a key role—based on the this conceptual framework, we can affirm that the ENM approach does not produce a representation of the geographic distribution of species, but rather an unconstrained geographic projection of the realized niche, estimated in ecological space. Other elements that modify species' geographic distributions from their fundamental potential, e.g., biogeographical barriers and competitors, are not integrated into the ENM process. *Post hoc* procedures are generally implemented to convert potential distribution models into actual distribution models if the intention is to produce realistic scenarios of present and future distributions of species.

In addition to the conceptual framework, the quality of input data, both biological and geographic, is fundamental. Species' distributions and their responses to climate change processes are idiosyncratic. Spatial and metric resolutions of geographic data are decisive in the quality of modeling outcomes. In projections to future scenarios, notwithstanding several complications, GCMs are the most reliable source of future-climate information, but downscaling is mandatory to permit regional and local studies. Currently, it is impossible to identify any single modeling algorithm that performs better than all others for all types of species and data conditions, and I suspect that use of multiple methods may prove to be the most robust current option.

Despite all the limitations discussed herein, ENM is the best instrument currently available for anticipating effects of climate change on distributions of species. As more workers get involved in this field, I anticipate rigorous and critical evaluation of ENM tools, as well as filling key knowledge gaps and incorporating them into the modeling systems. In this way, this approach will become more reliably predictive, and results will be increasingly useful in preservation of both natural and human resources.

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