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PERSPECTIVES

Promising the future? Global change projections of species distributions

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Summary

Projections of species' distribution under global change (climatic and environmental) are of great scientific and societal relevance. They rely on a proper understanding of how environmental drivers determine species occurrence patterns. This understanding is usually derived from an analysis of the species' present distribution by statistical means (species distribution models). Projections based on species distribution models make several assumptions (such as constancy of limiting factors, no evolutionary adaptation to drivers, global dispersal), some of which are ecologically untenable. Also, methodological issues muddy the waters (e.g. spatial autocorrelation, collinearity of drivers). Here, I review the main shortcomings of species distribution models and species distribution projections, identify limits to their use and open a perspective on how to overcome some current obstacles. As a consequence, I caution biogeographers against making projections too light-heartedly and conservation ecologists and policy makers to be aware that there are several unresolved problems.

Zusammenfassung

Die Auswirkungen von Umweltveränderungen (Klima und Landnutzung) auf die zukünftige Verbreitung von Tier- und Pflanzenarten ist ein aktueller und gesellschaftlich relevanter Forschungsgegenstand. Solche Vorhersagen fußen auf einer sicheren Kenntnis der für die Verteilung relevanten Umweltfaktoren, gewonnen aus der statistischen Analyse der gegenwärtigen Verbreitung. Vorhersagen auf Grundlage einer Verbreitungsanalyse unterliegen verschiedenen Annahmen (z.B.: limitierende Faktoren bleiben limitierend; keine genetische Anpassung an veränderte Umweltbedingungen; keine Ausbreitungsbeschränkung), von denen einige ökologisch unhaltbar sind. Zudem gibt es eine Vielzahl statistischer Probleme (z.B.: räumliche Autokorrelation; Kollinearität von Umweltparametern). In diesem

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Beitrag stelle ich die wichtigsten Probleme von Verbreitungsanalysen und Verbreitungsvorhersagen vor, zeige die Grenzen dieser Methodik auf und weise auf Lösungsansätze hin. Schlussfolgerung dieser Erörterung ist, dass wir es uns mit Vorhersagen nicht zu leicht machen sollten, und dass Umweltschützer und Politiker sich der methodischen Unsicherheiten bewusst sein sollten.

Introduction

The publicity triggered by the publication of Thomas, Cameron, Green, Bakkenes, and Beaumont (2004) revealed the enormous public interest in projections of species extinctions due to global climate and land-use change. They use statistical matches of climate with present species distributions in combination with climate change scenarios to predict the future range of species distributions. Although Thomas et al. were the first to acknowledge the potential shortcomings of their approach, their conclusions have been challenged for conceptual and statistical reasons (Buckley & Roughgarden, 2004; Harte, Ostling, Green, & Kinzig, 2004; Thuiller et al., 2004): they assume that species distributions are affected overwhelmingly by climate, that species will have the same climate niche in the future, i.e. not adapt to climate and that the statistical methods are robust. Their projections, and those of others (e.g. Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005), are also contingent on the uncertainty attached to future climate and land-use. Regional climate and land use change projections and their problems were addressed elsewhere (Dockerty, Lovett, Appleton, Bone, & Sünnenberg, 2006; IPCC, 1998; Millennium Ecosystem Assessment, 2003).

Projections of species distributions are not merely generating hypotheses to be tested by later data. They are presented as predictions of tomorrow's diversity and policy makers and the public will interpret them as forecasts, similar to forecasts about tomorrow's weather. Hence, future projections based on species distribution models should show the same robustness as meteorological forecasts and not merely serve as hypothesis generators for future generations of ecologists. Here, I argue that the problems associated with the analysis of present distribution of species are so numerous and fundamental that common ecological sense should caution us against putting much faith in relying on their findings for further extrapolations.

The backbone of Thomas et al.'s extinction risk projections are species distribution models (also known as 'habitat suitability models', 'niche-based models' or 'predictive habitat distribution models': Guisan & Zimmermann, 2000). They describe the spatial distribution of a species – and in a wider sense also of species groups, traits, richness, performance – as a function of environmental predictors such as climate, land-use type, resource availability, topography, soil conditions, geographic isolation, landscape structure and so forth. Here, I want to evaluate the assumptions of this approach and point out some potential misuses (see also Davis, Jenkinson, Lawton, Shorrocks, & Wood, 1998; Van Horne, 2002; Vaughan & Ormerod, 2003). I do not intend to comprehensively review the state of the art (for this, see e.g. Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000; Latimer, Wu, Gelfand, & Silander, 2006), nor do I wish to cover all types of organisms addressed with species distribution models (for a glimpse at the wide range of approaches, contexts and problems see Scott, Heglund, Morrison, Haufler, & Wall, 2002). Rather, this paper is intended to call on the scientist employing species distribution models, for extrapolation or otherwise, to reflect more thoroughly on their merits and limitations (Table 1) than is often done.

Which explanatory variables to choose? Issues of surrogates, equilibrium and scale

One key issue in species distribution models is the selection of explanatory variables. Candidate environmental factors are entered into the analysis and the best model is selected as the most likely driver of a species' distribution. Which environmental factors we chose depends largely on data availability and to a regrettably lesser extent on our understanding of the causal mechanisms behind species distributions. Because the most important causal mechanisms are often not readily quantifiable, we have to resort to substitutes and proxies. For example, when modelling kestrel occurrence, the abundance of voles, their primary prey, may not be known, so instead we may resort to using vegetation height as a surrogate for vole

Table 1. Overview of problems associated with species distribution models

General species distribution model issues:	Causal drivers are rarely quantifiable.
	Species may not be at equilibrium with environmental drivers
	Limiting factors may differ throughout a species' range
	Distribution patterns are governed by processes at multiple spatial scales
Extrapolation issues:	Identity of limiting factors may change with environmental change
	Biotic interactions are probably affected by environmental changes
	Genetic structure of species is likely to be affected by environmental changes
	Trends may not be valid beyond the range of present data
	Environmental change scenarios are spatially uncertain
Statistical issues:	Drivers have non-linear effects on species distribution patterns
	Drivers interact in their effects
	Causal drivers may be correlated with each other
	Data points in space are non-independent (spatial autocorrelation)
	Presence-absence data have low information content
	Low sample size and parsimony may lead to inadequately simple models

For details and examples see text.

abundance. Similarly, the distribution of specific ecto-mycorrhizal fungi has never been quantified at a scale relevant for the distribution of their symbiontic trees, but we may hope that soil moisture correlates with mycorrhization and hence we can use this as a proxy.

Many researchers have chosen to employ only climate variables as explanatory variables. The argument being that at large spatial scales climate is ultimately determining the fundamental, physiological niche (Pearson & Dawson, 2003). The caveats of this approach were recognise' early (Brereton, Bennett, & Mansergh, 1995, p. 343):

1. "The realised niche of a species can be much less because other environmental attributes characterising a species' habitat were not included ..."
2. "The distributional data used may not represent the full geographic range of each species and thus climatic profiles may be underestimates of realised or realisable distributions."
3. Uncertainty about the local projections for future climate will necessarily render species' distributions inaccurate, too. Microclimate (and "micro" here refers to anything finer than the grain of the distribution analysis) may differ substantially from regional climate, and hence give some species habitat to hang on to for (potentially long) transient periods. Demographic stochasticity will mean the inevitable extinction of any non-connected population, however.

Opinions differ if climate is by itself sufficient or even the most important factor for explaining species distributions (Thuiller, Araújo, & Lavorel, 2004). Even for species long considered limited by climate, where distribution models seem to be very well suited, later range expansion may prove the statistical model wrong (as shown by Kanda, 2005 for Virginia Opossum *Didelphis virginiana*). Also, different factors may limit a species' occurrence in different parts of the investigated range (Graf, Bollmann, Sachot, Suter, & Bugmann, 2006; Huston, 2002; Schröder & Richter, 1999; Svenning & Skov, 2004). If land use precludes the presence of a species in parts of its range, it may appear not to be filling its climatic niche, while in fact it does.

Another crucial aspect of selecting the explanatory variables concerns their ability to proxy for infrequent catastrophic checks of populations that may not have occurred during the time period sampled. A species may not be in equilibrium with its environment (as discussed in Araújo & Pearson, 2005; Vellend et al., 2006), for the reason that since the last parasite outbreak or destruction by fire, the population has not fully recovered. Hence any model constructed on, say, climate parameters alone may not be able to capture the distribution appropriately (see Araújo & Rahbek, 2006, for an example of the potentially gross inadequacy of climate-only models).

Finally, species distribution analyses are carried out at only one spatial resolution and extent. Environmental drivers differ in their variability and relevance with scale (Wiens, Addicott, Case, &

Diamond, 1986): climate varies more on the continental, land use more on the regional scale. Hence, large-scale studies will find climate more important than soil properties (Bjorholm, Svenning, Skov, & Balslev, 2005; Borcard, Legendre, Avois-Jacquet, & Tuomisto, 2004). Land cover impacts become apparent at smaller scales than climate (Pearson & Dawson, 2003; Pearson, Dawson, & Liu, 2004).

In summary, hypothesis testing with species distribution models is often hampered by the lack of ecologically relevant data at the required spatial or temporal resolution.

Extrapolating from here and now to there and then

Can we extrapolate to values beyond the observed parameter range and present spatial distribution? The assumptions of species distribution models for extrapolation are (e.g. Austin, 2002):

1. The factors that limit a species' occurrence/abundance under observed conditions will also be the limiting factors under the extrapolated conditions.
2. Biotic interactions (competition, predation, symbiosis) will be the same under extrapolated conditions.
3. Genetic variability, phenotypic plasticity and evolutionary changes are negligible.

Any extrapolation is burdened with hugely increasing uncertainty the further we leave the observed data range behind us. A simple and ad-hoc rule of thumb, not to extrapolate further than 1/10 of the parameter range, may serve as guidance. Far more problematic is the projection of a species' range under a *combination* of environmental conditions it has never encountered before (Thuiller, Brotons, Araújo, & Lavorel, 2004).

Even more problematic is the projection of a species' range under a combination of environmental conditions it has never encountered before. Thuiller et al. (2004) recommend to use a large (ideally the full) range of a species for modelling, even if only a regional subset is of interest (see Pearson, Dawson, Berry, & Harrison, 2002, for an example). Thereby the entire niche can be modelled and the probability of encountering novel combinations of environmental conditions is reduced.

In addition to encountering novel combinations of abiotic conditions, also the biotic environment is likely to change (Lawton, 2000). As an example, consider how the effects of increased CO_2 on plant distributions will be modified by other factors: on a species' ability to acclimate or adapt to the new conditions (Ainsworth & Long, 2005; Jump & Peñuelas, 2005); on the changes in the plant–plant interactions due to altered water use efficiency and hence shifts from competition for nutrient to competition for water (Hely & Roxburgh, 2005; Joel, Chapin, Chiariello, Thayer, & Field, 2001); on the way humans manage the habitat in response to altered plant community composition (Polley, 1997; Rosenberg & Scott, 1994; Passioura, 2006). Another example is the climate-change induced mistiming of breeding and food abundance in a migratory songbird (Both, Bouwhuis, Lessells, & Visser, 2006), which would have been near-impossible to predict with a static statistical model. The semantic 'solution' employed by species distribution modellers is to call the extrapolation 'potential distribution under altered environmental conditions'. But even this rather vague term is not correct, since the probability derived from the model is conditional on the correctness of the three above assumptions. So far, our understanding of species' responses to altered environmental conditions in its community context is too limited to even allow a ranking of the three assumptions. A better phrase for extrapolated distribution would therefore be 'potential distribution under altered environmental conditions and unaltered species' ecological and physiological behaviour'. Now, that would restrict the use of such an extrapolation to long-lived organisms, relative to the changes modelled. However, even for long-lived species, extrapolations can be very poor, as shown for birds of prey (Fielding & Haworth, 1995).

Relying on present day analysis for projecting species distributions into the future can be fallacious (Davis et al., 1998). Even if a species moves further North in its distribution following climate change, we have no way of knowing if it will ever occur there, because small-scale environmental factors have been neglected. For example, a calcicole forest understorey plant species cannot extend its range into low-pH Siberia, no matter what the climate will be like (Skov & Svenning, 2004).

How much phenotypic plasticity or the evolution of species traits matters to a species' ability to maintain a population under new environmental conditions is largely unclear. Although rapid evolutionary change has been documented (Endler, 1986; Thompson, 1998), there are only few known case studies where species evolved in response to new physical conditions (Reznick & Ghalambor, 2001).

If species display high genetic or phenotypic plasticity, the projected range of distribution under altered environmental conditions may well be larger than forecasted under the assumption of genetic and phenotypic constancy (see Rehfeldt, Wykoff, & Ying, 2001, for an example).

A brief and final thought on extrapolation shall be devoted to future climate and land-use scenarios. While our understanding of climatic forcing yields relatively consistent projections of future climate at the global scale, regionalisation, i.e. downscaling, of these global scenarios is very difficult (e.g. Schröter et al., 2005). Hence, projections at a spatial scale of several square kilometres will be burdened with considerably larger uncertainty than those at several thousands of square kilometres. Even more problematic are scenarios for land use, since they have to embrace political, economic, demographic, technological and climatic developments (e.g. Holman, Nicholls, Berry, Harrison, Audsley et al., 2005; Holman, Rounsevell, Shackley, Harrison, Nicholls et al., 2005). Changing one law, e.g. subsidies for sugar or oil crops, may affect farming over huge areas (Rounsevell et al., 2006). Uncertainty in environmental change scenarios propagates through to projections of future species distributions.

Statistical stumbling stones

Several statistical issues provide obstacles for species distribution analysis. The first and foremost must be data availability. Data will be collected at different resolutions, during different time intervals, with different taxonomic concepts and for different purposes. To merge several data sources into one homogenous data set is an enormous challenge that usually dwarfs the time required to analyse these data (Graham, Ferrier, Huettman, Moritz, & Peterson, 2004). Nonetheless, I will here focus on a few statistical issues, once the data are ready for analysis.

The first point concerns the observation that in most analyses of species distributions (as well as other ecological data), only linear predictors are used (Austin, 2002). For most environmental drivers, we can expect a non-linear effect on species abundance or performance (Austin, 2002). Most plants have both upper and lower limits to how moist the soil may be and all animals have upper and lower bounds for the temperature they can tolerate. It seems strange to assume that all environmental variables in an analysis fall exactly on that stretch of the relationship where it is approximated linearly (see also Vaughan & Ormerod, 2003, for implications of ignoring non-linearity). As a first step, a quadratic term can be included, but sigmoidal or saturation transformations could also be employed if a specific causal mechanism (e.g. Michaelis–Menten kinetics) can be assumed. Using more flexible models, non-linearity can easily be incorporated in the analysis (e.g. GAM, neutral networks or other 'novel' methods: Elith et al., 2006).

Similarly, few analyses of species distributions have investigated interactions among environmental drivers (again see Austin, Nicholls, & Margules (1990) for raising and reviewing this problem and Thuiller, 2003 for a systematic improvement). Some argue that including interactions precludes a transfer to new regions because of the highly specific way that variables interact in a specific region (Beerling, Huntley, & Bailey, 1995; Gavin & Hu, 2006). Even so, to identify the causes of present distributions their present ecological demands should be the focus of the analysis. For example, the ecological expectation would be that a plant will tolerate low precipitation as long as the soil retains moisture. Hence the interaction of precipitation and soil texture should be crucial for many plant species. Similarly, a soil-breeding solitary bee will not occur in the best climatic conditions as long as the soil does not offer the right consistency for its nest. More importantly, without-interactions between main effects become unduly emphasised, because they take over some of the interactions' importance (Harrell, 2001). While this may suit mono-factorially minded policy makers, it will not help unravel the causes of species distributions.

Another problematic issue is posed by interrelated drivers. Soils, climate and land use are historically related in that climate shapes soils and soil determines land use. Environmental drivers will, therefore, often be correlated. In mountains, topography drives precipitation, exposition drives temperature and slope determines soil depth. Correlated environmental drivers cannot readily be dealt with in species distribution analysis (as is true for all fields of ecology: Mac Nally, 2002; Graham, 2003). Obviously, an organism does not respond to altitude as such, but rather to temperature or rainfall. Therefore, biological knowledge may help us to discard some of these variables (Poff, 1997). But how about soil pH and percentage of forest affecting the diversity of carabid beetle? Which of the two factors should we retain, and which should we discard? One solution is to construct uncorrelated dummy variables, e.g. by means of a principle component analysis, but they are difficult to interpret and hence unsuitable for hypothesis-testing models. A better approach would be to use residual regression (Graham, 2003), where correlated variables are regressed with each other and the residuals are used instead of the raw values. Alternatively, averaging the projections from different models reduces the model-specific uncertainty (Araújo, Whittaker, Ladle, & Erhard, 2005; Hoeting, Madigan, Raftery, & Volinsky, 1999), but they are still burdened with the fundamental uncertainty of which drivers were used in the first place.

A particularly worrying case is the high correlation between mean, minimum, maximum and standard deviation of climate variables. Their ecological implications are vastly different: modelling palm trees in Europe using mean annual temperatures will give a very low probability for Ireland, where palms merrily grow because winters are warm. Means are appealing in predictive models because climate models are relatively consistent in predicting means and extremely poor and incomparable in variation around them (Cess et al., 1993). What if climate change leads to a new relationship between the mean and variance (as is predicted for temperature in Europe: little change in mean annual temperature, but increased summer and decreased winter temperature, with larger variability within weeks: IPCC, 1998)? Then a model employing means is useless because the plants and animals actually experience very different temperature conditions compared to those used for statistical analysis.

More recently, the non-independence of adjacent data points in space has raised statistical concerns (Lennon, 2000). Data points closer to each other in space are usually more similar to each other than to those farther away (Tobler, 1970), even after taking into account the dependence on spatially autocorrelated environment drivers (Legendre, 1993; Legendre et al., 2002). The main ecological reason is distance-related dispersal: the farther, the fewer propagules. The statistical implication is that data points are not truly independent replicates and hence should be treated as correlated. The statistical methods are available, but not even 20% of species distribution studies reviewed use them (Dormann, 2007). Surprisingly, none of the statistical tools presented in either Guisan and Thuiller (2005) or Elith et al. (2006) is able to incorporate spatial autocorrelation. In consequence, both the identification of environmental drivers and the estimation of their coefficients – and hence projection by these models – may be severely biased (Kühn, 2007).

Let us turn to the issue of the low information content of occurrence data. When a species is correctly recorded in a grid cell as present, we know it is there. If it is recorded as absent, we cannot be sure: it might have been overlooked or misidentified (McArdle, 1990). Abundance data usually give much better ecological information, allowing us to estimate population sizes and so forth (Cushman & McGarigal, 2004). And what is the ecological implication of knowing that pine has been recorded in a quadrat? We still do not know (and cannot infer) whether there is a forest. We still have no idea if loss of a species from a quadrat will affect the ecosystem in that cell.

Also the methods of choice to analyse presence–absence data, Generalised Linear or Additive Models with binomial error distributions, intrinsically yield far worse likelihood values for binary data than for Poisson-distributed abundance data. This is due to the low information content of 0/1 data. Overall, occurrence data are often the best we have, but that does not make them necessarily adequate for the problems they are being used to address.

Finally, we have to address the limits of parsimony, i.e. the philosophic principle of shaving every model to its barest minimum ("Occam's razor": Burnham & Anderson, 2002). Low prevalence poses a problem (Schwartz, Iverson, Prasad, Matthews, & O'Connor, 2006) since few data points allow only for very simple – probably too simple – explanatory models. Commonness of a species impacts model performance in unpredictable ways (Manel, Williams, & Ormerod, 2001). In any case a model's predictive ability is likely to be a function of the target species' prevalence (Karl, Bomar, Heglund, Wright, & Scott, 2002; Luoto, Poyry, Heikkinen, & Saarinen, 2005; McPherson, Jetz, & Rogers, 2004; Segurado & Araújo, 2004). Reducing model complexity too far may yield very crude models that do not do justice to the species' environmental requirements. As famously said by Einstein (although not strictly about species distribution models): "The supreme goal of all theory is to make the irreducible basic elements as simple and as few as possible without having to surrender the adequate representation of a single datum of experience" often paraphrased as "Theories should be as simple as possible, *but no simpler*".

What problems can be tackled by species distribution analyses?

The above paragraphs may leave a bleak impression and, I believe, rightly so. Species distribution analysis has potential for both, science and environmental management, but not as generally as it is presently employed. There are some brilliant and insightful studies on species distributions (e.g. Bonn & Schröder, 2001; Graf, Bollmann, Suter, & Bugmann, 2005; Lichstein, Simons, Shriner, & Franzreb, 2002; Özesmi & Özesmi, 1999; Schadt et al., 2002; Tognelli & Kelt, 2004). These studies show that several fields of research will profit from the analysis of species distributions. In these research fields, several of the above problems do not occur, simply because they do not try to extrapolate, because at smaller spatial scales more detailed and quantitative information is available, or because the distribution analysis is only one tool amongst many to solve ecological riddles.

1. Small-extent, decision-support for conservation biology (such as Biological Action Plans: Zabel et al., 2003, and numerous others).
2. Testing specific hypotheses, e.g. on the spatial scale of habitat selection (Graf et al., 2005; Mackey & Lindenmayer, 2001), the species-energy hypothesis (Lennon, Greenwood, & Turner, 2000) or range-size effects on diversity pattern (Jetz & Rahbek, 2002).
3. Generating hypotheses, e.g. on correlation of species traits with environmental variables (Kühn, 2006), which can then be tested experimentally.
4. Identifying hierarchies of environmental drivers (Borcard & Legendre, 2002; Bjorholm, Svenning, Skov, & Balslev, 2005; Pearson et al., 2004).
5. Prospective design of surveys, e.g. optimising sampling schemes for rare species (Guisan et al., 2006).
6. Spatial interpolation/regionalisation, where the species distribution model can improve inverse-distance interpolation (Binzenhöfer, Schröder, Biedermann, Strauß, & Settele, 2005; Özesmi & Mitsch, 1997).

How can species distribution models be interpreted, and to which policy advice do they lead?

I acknowledge that in many cases we are constrained by the quality of available data, in particular for large-extent studies. At the same time, there is huge pressure from policy to provide estimates of species' future distributions (Thuiller et al., 2005), guide reserve selection (Araújo & Williams, 2000) or forecast ecosystem impacts of climate change (Schröter et al., 2005). However, I believe that many papers reporting on species distribution have not provided the scientific rigour to serve science or management. Methodological, technical and data shortcomings severely constrain the usefulness of extrapolations, but the most problematic issue is the unfeasibility of incorporating genetic flexibility and complex interactions between organisms into static, statistical models.

Species distribution analyses are no easy game: they require intimate knowledge of the species, of the statistics and a lot of thought about the question to which they are applied. Here, in short, and in no particular order, are the main thoughts one should have in mind when reading through a species distribution study offering advice on species management or contributing to the understanding of a species' ecology:

1. Only factors that were investigated can be interpreted and missing factors may be of overruling importance.
2. Many incorporated environmental parameters are proxies for some causal ecological mechanism we do not yet understand.
3. Confounded variables require disentangling before interpretation.
4. Interactions need to be considered as more important than main effects.
5. Management advice is restricted to the scale of analysis.
6. Ecosystem function cannot be inferred from occurrence data.
7. Biotic interactions act at a very small (spatial and temporal) scale compared to most distribution data.
8. We have (generally) little idea to what extent a species is able to adjust to new environmental conditions through either phenotypic plasticity or evolutionary change.
9. Extrapolated ranges are *potential* ranges and contingent on the assumption that limiting factors remain limiting factors.
10. All analyses are correlative and ideally require manipulative confirmation. Do not trust the results if you cannot identify a causal mechanism behind it. E.g. altitude (an indirect factor *sensu* Austin, Nicholls, & Margules, 1990) cannot in itself affect species occurrence; but the unavailability of forage (resource factor) due to permanent snow cover or permanently frozen soils can.

Overall, the phrasing employed by Guisan and Thuiller (2005, p. 994) gives the correct emphasis on the use of species distribution models. They may serve to "support appropriate management plans for species recovery" and "support conservation planning and reserve selection". The emphasis is on support, rather than guidance.

Conclusion: How to improve species distribution forecasts?

I consider the following three steps as vital to a further development of species distribution model-based projections. Firstly, we need to identify where the largest contribution to projection uncertainty comes from. In other words, which of the following links in the forecast chain introduce most variability: quality of raw data, choice and collinearity of explanatory variables, type of statistical modelling approach, or regional land-use and climate change scenarios? Once these more statistical questions have been addressed, we need to move forward, beyond statistical sophistication. A second step is a critical comparison and parallel construction of static statistical and dynamic individual-based species distribution models. We should ask, under which (if any) circumstances can ecological processes such as biotic interactions and movement be neglected? And finally, validation of model projections must play a more prominent role, especially with data sets from different time periods becoming available now, but also by using manipulative field experiments in various parts of a species' range to assess which drivers are acting. Thomas et al. (2004) may well be right with their forecast of high extinction risks within the next 50 years. However, it is their considerable ecological experience, not their models, that I put my faith in.

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