MACIS

Minimisation of and Adaptation to Climate change Impacts on biodiverSity

Deliverable D2.1:

Review paper of the contribution of different models for assessing the impacts of climate change

Specific targeted research project (STREP)

Contract period 01 November 2006 – 31 October 2008
Contract no. 044399 (SSPI) MACIS

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Project Website www.macis-project.net

Predicting global change impacts on plant species' distributions: Future challenges

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Abstract

Given the rate of projected environmental change for the 21st century, urgent adaptation and mitigation measures are required to slow down the on-going erosion of biodiversity. Even though increasing evidence shows that recent human-induced environmental changes have already triggered species' range shifts, changes in phenology and species' extinctions, accurate projections of species' responses to future environmental changes are more difficult to ascertain. This is problematic, since there is a growing awareness of the need to adopt proactive conservation planning measures using forecasts of species' responses to future environmental changes.

There is a substantial body of literature describing and assessing the impacts of various scenarios of climate and land-use change on species' distributions. Model predictions include a wide range of assumptions and limitations that are widely acknowledged but compromise their use for developing reliable adaptation and mitigation strategies for biodiversity. Indeed, amongst the most used models, few, if any, explicitly deal with migration processes, the dynamics of population at the "trailing edge" of shifting populations, species' interactions and the interaction between the effects of climate and land-use.

In this review, we propose two main avenues to progress the understanding and prediction of the different processes occurring on the leading and trailing edge of the species' distribution in response to any global change phenomena.

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Deliberately focusing on plant species, we first explore the different ways to incorporate species' migration in the existing modelling approaches, given data and knowledge limitations and the dual effects of climate and land-use factors. Secondly, we explore the mechanisms and processes happening at the trailing edge of a shifting species' distribution and how to implement them into a modelling approach. We finally conclude this review with clear guidelines on how such modelling improvements will benefit conservation strategies in a changing world.

Introduction

There is now compelling evidence that species are already shifting their ranges in response to on-going changes in regional climates (Parmesan and Yohe, 2003; Root et al., 2005; Walther et al., 2005; Lavergne et al., 2006), that species are altering their phenology (Menzel and Fabian, 1999; Visser and Holleman, 2001; White et al., 2003; Zavaleta et al., 2003) and that some species are facing extinction, or have become extinct (Parmesan, 2006; Pauli et al., 2006; Pounds et al., 2006; Foden et al., 2007). Given the contemporary biodiversity crisis, effective conservation strategies that offset the climate change threats to species persistence will be critical in maintaining species and genetic diversity. To date, conservation planning has mostly focused on preserving pattern and has acted reactively. However, scientists and stakeholders recognize that the dynamic nature of biodiversity requires a paradigm shift in approach (Cabeza and Moilanen, 2001; Pressey et al., 2007). This should include proactive planning and focusing on processes rather than patterns. However, proactive responses are limited without forecasting and the implementation of advanced models to do this. Responses of biodiversity to land-use and climate change are receiving increasing attention in conservation planning science, with decision tools being developed to incorporate such forecasts (Hannah et al., 2007; Pressey et al., 2007).

The Millennium Ecosystem Assessment (MEA, 2005) mentions climate change as the largest forthcoming threat to biodiversity across most biomes, and in a recent review on systematic conservation planning, Pressey et al. (2007) recognize accounting for climate change to be an urgent issue and one of the major challenges for the future. However, Pressey et al. (2007) also emphasize the added problems due to the uncertainties associated with both climate change and projections of associated species' range shifts. Although methodological exercises have attempted to design protected areas while accounting for species' shifts (e.g. Hannah et al., 2007), conservation practitioners prefer to avoid the uncertainties in projections and concentrate on protecting current patterns of biodiversity. Nevertheless, several studies evaluating the future performance of protected areas (e.g. Araújo et al., 2004; Thuiller et al., 2006a) call for a need to include the dynamic nature of biodiversity in conservation planning.

To increase confidence in model projections, methodologies must acknowledge clearly the uncertainties involved and try to obtain conditional measurements of confidence in the forecasts made (Thuiller et al., 2004; Schröter et al., 2005; Berry et al., 2006; Araújo and New, 2007; Thuiller, 2007). Whereas confidence in model projections is likely to increase as the realism of key assumptions within a particular modelling approach are improved (Sutherst et al., 2000), tractability often decreases, due to more demanding parameterizations. Thus a trade-off exists between complexity and tractability in modelling species and identifying the most reliable and unbiased solution is not a trivial task (Thuiller, 2007). A second trade-off in modelling species' responses to environmental changes is between generality and specificity of predictions. At the generality end of the gradient, process-based dynamic global vegetation models (DVMs) are generalized to such an extent that they can simulate global patterns of vegetation distribution, as well as carbon, nutrient and water cycling from existing knowledge of the mechanisms driving these processes (e.g. Sitch et al., 2003; Woodward and Lomas, 2004; Thuiller et al., 2006c). The drawback is that primary producers are classified into a small number of "plant functional types" (PFTs), which provide a coarse classification of biodiversity for several conservation planning applications. Tree species-specific responses have been extensively explored with "forest gap models" (Botkin et al., 1972; Shugart, 1984; Sykes and Prentice, 1995, 1996; Bugmann, 2001). These models have been criticized for being highly parameterized for particular species and sites (Badeck et al., 2001), but there has been considerable progress in the development of generalized forest gap models, which can now be applied across different regions, at least in the temperate zone, and account for population demographics, species' interactions and physiological processes (Bugmann and Solomon, 2000; Hickler et al., 2004). At the specificity end of the gradient, habitat models (Guisan and Thuiller, 2005), which fit species environmental niches explicitly, ignore all mechanisms driving species'

demography (but see Sutherst, 2000; Kriticos et al., 2003) and species' interactions (but see Leathwick and Austin, 2001). They assume that the fitted relationship between the presence/absence or abundance of a given species and the environmental conditions measured in a site is a good surrogate for such demographic processes (Araújo and Guisan, 2006; Austin, 2007). These habitat models are simplistic but they focus explicitly at the species level, allowing the modelling of numerous species, and can thus be used to estimate patterns of current and future diversity (Box 1; Peterson et al., 2002; Thomas et al., 2004; Thuiller, 2004; Ferrier and Guisan, 2006).

Most efforts in the past have attempted to understand and predict how the distribution of a selected species or group of species as a whole will be modified in response to a given environmental change (mostly climate and land-use changes). However, little attention has been given to simulating processes at the leading and trailing edges of the distribution where range change happens (migration, persistence, extinction, Hampe and Petit, 2005). The leading edge is fundamentally important under global change, as it is commonly accepted that range expansions depend mostly on populations at the colonization front. The leading edge is also seen as controlled by rare long-dispersal dispersal events followed by exponential population growth (Hewitt, 1993; Hampe and Petit, 2005). Alternatively, the trailing edge remains largely understudied, but recent reviews have demonstrated their crucial role by maintaining long-term stores of species genetic diversity and places of speciation (Hampe and Petit, 2005). The aim of this review is therefore to highlight and discuss two research avenues that should provide better ecological understanding and better predictions. First we review, discuss and propose new avenues to understand and predict the processes happening at the leading edge of species' distributions. New directions are proposed to include population dynamics, land-use and biotic interactions more explicitly in the models. Then, following the same scheme, we analyse the processes happening at the trailing edge of species' distributions (persistence, mortality, genetic adaptation) and propose avenues to include them in a modelling framework.

Because it was impossible to cover all organisms and associated processes, we explicitly deal with plant models in this review, but most of the concepts discussed also apply to other organisms.

Box 1. Species' distribution model definition.

It is relatively difficult to classify models as they all share some theories, concepts or assumptions. In this review, we follow Kearney (2006):

We refer to ''*habitat models*'' as any model which relates the physical nature (biotic and abiotic) of a region with respect to a species, with no direct mechanistic links necessarily occurring between those descriptors and the species. Typical habitat models are reviewed in Austin (2002, 2007), Guisan and Thuiller (2005) and Guisan and Zimmermann (2000). They are purely descriptive and relate to a particular space and time frame.

We refer to ''*process-based models*'' as any model that uses mechanistic links between the growth and fitness of species, or more abstract plant functional types (PFTs), and a range of environmental or biological (e.g. competing species or PFTs) variables. Examples range from dynamic vegetation model (based on PFTs, Woodward, 1992), population viability analysis (based on population dynamics, Possingham and Davies, 1995), plant population modelling (Jeltsch et al., this issue) phenological models (based on phenology; Chuine et al., 2000), or diffusion/spread models (With, 2002).


Predicting the leading-edge response – forecasting species migration

Background

Evidence from paleo-ecological studies (Huntley, 1991; Prentice et al., 2000; Davis and Shaw, 2001) and multiple observations of current species' range shifts (Walther et al., 2005; Parmesan, 2006) show that migration (i.e. a directional shift in a species' range) will be a very likely response of plant species to ongoing and future climate change. In this paper, we define migration as the result of four processes: fecundity, dispersal, recruitment and population growth. Understanding migration holistically is important because: (i) it is clear that the rate of change in local conditions threatens to outpace the migration capabilities of many species with limited dispersal abilities (Solomon and Kirilenko, 1997; Pounds et al., 1999); and (ii) current levels of habitat modification and fragmentation further reduce the ability of most plant species' propagules to disperse across landscapes (Collingham and Huntley, 2000). This has obvious negative implications for species' persistence, including range reduction and possible extinction (Solomon and Kirilenko, 1997; Midgley et al., 2007).

Despite the acknowledged importance of plant migration in response to global change (Higgins et al., 2003a; Neilson et al., 2005; Midgley et al., 2007), few
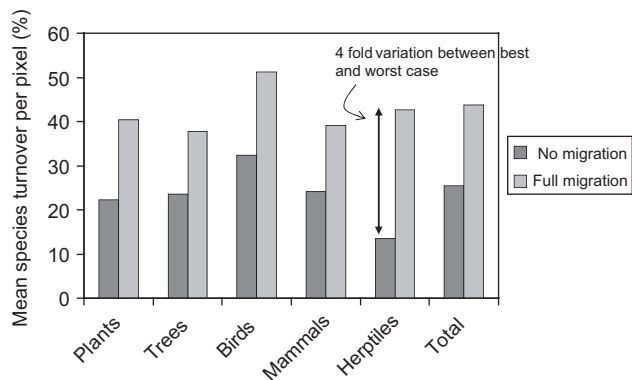
Fig. 1. Uncertainties in projected mean species turnover in Europe by 2050 associated with two extremes in migration assumptions (from Thuiller et al., 2005a, 2006b; Araújo et al., 2006, and Araujo and Thuiller, unpublished data). Two extreme assumptions, no or unlimited migration, were used to account for the migration ability of each species. The histogram highlights the uncertainty entering through these assumptions (see herptiles for the most striking evidence, showing almost four times the turnover with unlimited migration).

modelling studies explicitly include migration processes when simulating geographical plant response (but see Collingham et al., 1996; Lischke et al., 2006; Midgley et al., 2006; Albert et al., 2007). DVMs do not consider migration either, the plant functional type or species of interest being expected to grow wherever the conditions are suitable. Habitat models usually assume either no migration or unlimited migration (Peterson et al., 2002; Thuiller et al., 2005b; Schwartz et al., 2006, Fig. 1), although most published future projections have assumed unlimited dispersal. As a consequence, seed dispersal and the associated patterns of plant migration are considered to be among the most significant uncertainties in projecting climate change impacts on plant species' ranges (Fig. 1, Higgins et al., 2003a; Neilson et al., 2005; Pearson, 2006; Midgley et al., 2007).

Key issues

The simplest way to incorporate migration into models of species or plant functional type distributions is to assume that all populations of a species migrate at identical rates (Williams et al., 2005; Broennimann et al., 2006; Midgley et al., 2006). Estimates of such migration rates can be derived from observed rates of contemporary migration (Cain et al., 2000; Bullock et al., 2006; Kunstler et al., 2007), from the paleo-records (Davis, 1981; Clark et al., 1998), from genetic isolation by distance slopes (Hamrick and Loveless, 1989; Petit et al., 2001; Kinlan and Gaines, 2003), from expert knowledge or from a mix of these sources. For instance, Midgley et al. (2006) assumed the rate of plant migration to be a maximum of 1 km per decade for ant- and rodent-

dispersed Proteaceae species of the Cape region, and 3 km per decade for wind-dispersed species. Such an approach can be easily combined with habitat models and may be used in global change analyses to assess risks (e.g. Williams et al., 2005) and to reduce the uncertainty of projections related to dispersal (e.g. Broennimann et al., 2006).

One shortcoming of this simple approach is that there are still few available data on dispersal distances, let alone migration rates of non-invasive plant species in present-day landscapes (for a summary see Parmesan and Yohe, 2003). Moreover, the assumption of identical migration rates across a species' range is likely to be untenable in many cases since the migration capacity of a population depends on its local dynamics (e.g. Skellam, 1951). Furthermore, external factors such as the land-use change, landscape fragmentation and the connectivity of patches of suitable habitat are bound to complicate the modelling of dispersal since probabilities of dispersal in heterogeneous habitats can become anisotropic (e.g. Pitelka et al., 1997; Higgins et al., 2003b; Pearson and Dawson, 2005). Similarly, as shown with the rapid spread of plant invasive alien species throughout the globe (Wadsworth et al., 2000; Kowarik, 2003; Levin et al., 2003), human-mediated dispersal plays a major role in long-distance dispersal events although it remains difficult to actually measure and integrate this into a modelling framework (Schmidt, 1989; Hodkinson and Thompson, 1997; Tikka et al., 2001; Zwaenepoel et al., 2006).

These problems can be partly avoided through the combination of a migration model with projections from habitat models. For example, Iverson et al. (2004) coupled a habitat model with a simple model of habitat colonization to predict the future distribution of North American tree species. The colonization model uses a cellular automaton that predicts the colonization of suitable cells based on habitat quality, a correlate of local abundance in occupied cells, and the distance between occupied and potentially colonized cells. For all of the studied species, Iverson et al. (2004) parameterized the dispersal component of their colonization model to produce a migration rate of 50 km/century in fully forested landscapes, a value inspired by maximum estimates of average Holocene tree migration in North America. Using the estimated dispersal parameter, the colonization model was then used to simulate the spread of species in present-day landscapes with lower habitat quality. This approach is computationally efficient and innovative in that it uses paleo-ecological information. However, it also has a number of limitations including the lack of consideration of population dynamics, the use of ad-hoc dispersal kernels (e.g. the modelling of dispersal with an inverse power law that does not integrate to 1), the assumption of identical Holocene migration rates for all studied species, and indeed the

assumption that migration estimates based on the paleo-record are correct, and relevant for today's fragmented landscapes (for discussion see Clark et al., 1998; Pearson, 2006).

More complex hybrid approaches entail models of local population dynamics and mathematically adequate descriptions of dispersal and recruitment (Jongejans et al., this issue). Classical metapopulation models represent recruitment processes by a single function (Hanski, 1994), whereas sophisticated spatially explicit gap models like LANDIS/LANDCLIM (He and Mladenoff, 1999; Schumacher and Bugmann, 2006), or landscape models like LAMOS (Cousins et al., 2003; Albert et al., 2007) model components of the recruitment process, such as seed production, seed dispersal, and seedling recruitment, separately. The spatially explicit forest gap model TREEMIG (Lischke et al., 2006) includes probably the most complete representation of seed dispersal and subsequent regeneration processes, by including density-dependent antagonists and intra- and inter-specific seedling competition.

Perspectives

Given that complex gap and metapopulation models are computationally very expensive when they are run at large spatial scales, it seems more promising to incorporate results of migration theory into species-distribution models. There is a well-developed body of theory on the migration of species, but so far only little pieces of the theory have been used to improve range shift projections. Migration theory has led to a suite of models for population spread (e.g. Skellam, 1951; Kot et al., 1996; Neubert and Caswell, 2000; Clark et al., 2001). While the classical model of Skellam (1951) described migration as a diffusion process characterized by mean dispersal distance, later models have emphasized the importance of kernel shape and long-distance dispersal (Kot et al., 1996; Higgins and Richardson, 1999; Clark et al., 2001). In their simplest form, these models require information on a population's finite rate of growth, λ (or on net reproductive rate, R_0, and generation time, T), and on the dispersal kernel of offspring as a function of distance from the mother plant ($f(x)$). In the following, we point out how better models and data on dispersal and demography may help us improve migration forecasts.

The understanding and quantification of long-distance seed dispersal has undergone considerable progress in recent years (Nathan, 2006; Kunstler et al., 2007). Mechanistic models for wind dispersal now make reliable predictions at scales relevant for the long-distance movement of seeds and can be parameterized for large numbers of species (Nathan et al., 2002;

Tackenberg et al., 2003; Schurr et al., 2005). Moreover, these models seem to be informative for the biogeographical dynamics of plant species. For South African Proteaceae, Schurr et al. (2007) showed that mechanistically derived estimates of wind dispersal potential (Tackenberg et al., 2003; Schurr et al., 2005, Fig. 2) explain inter-specific variation in the ratio between realized and potential range size (the latter estimated with habitat models by Midgley et al., 2003). This suggests that for these predominantly wind-dispersed species, the incorporation of mechanistic models for wind dispersal may considerably improve distribution forecasts.

Mechanistic models for other dispersal vectors are less advanced than models for wind dispersal. In the case of seed dispersal by animals this is partly due to the fact that the environmental and behavioural factors influencing animal movement are so varied that models are often highly case-specific (e.g. Westcott and Graham, 2000). However, Powell and Zimmermann (2004) have demonstrated how mathematical homogenization techniques allow combining information on the behaviour of animals across different spatial scales with simple plant population models. The results are promising in that (a) considerably better historical migration estimates result from these analyses and (b) a general method to derive dispersal kernels is provided, which can be extended to other dispersal vectors that operate at multiple spatial scales. The further development of such generic models for seed dispersal by animals and abiotic factors other than wind will greatly improve our ability to forecast range dynamics (Nathan, 2006).

Statistical techniques also provide a promising avenue for estimating dispersal kernels from easily available information such as parent and seedling distributions (Ribbens et al., 1994; Clark et al., 1998; Clark, 2005) or molecular data (Cain et al., 2000; Godoy and Jordano, 2001). In the case of molecular methods, however, it remains unclear how widely applicable they are (Rousset, 2001) and whether they can be used to infer the shape of dispersal kernels.

While the quantification of long-distance dispersal is a comparatively new field, data on population growth rates have been collected by population ecologists over decades (see e.g. Franco and Silvertown, 2004). It should be noted, however, that these data typically stem from dense populations in the "core" of a species' range (Franco and Silvertown, 2004). The dynamics of such dense populations may differ in important ways from the dynamics of sparse populations at the spreading front that drive species expansion (Kot et al., 1996; Sagarin et al., 2006). For example, reduced intraspecific competition at the spreading front may result in increased population growth rates, thereby promoting migration. On the other hand, sparse populations at the expanding edge of a moving population may suffer from
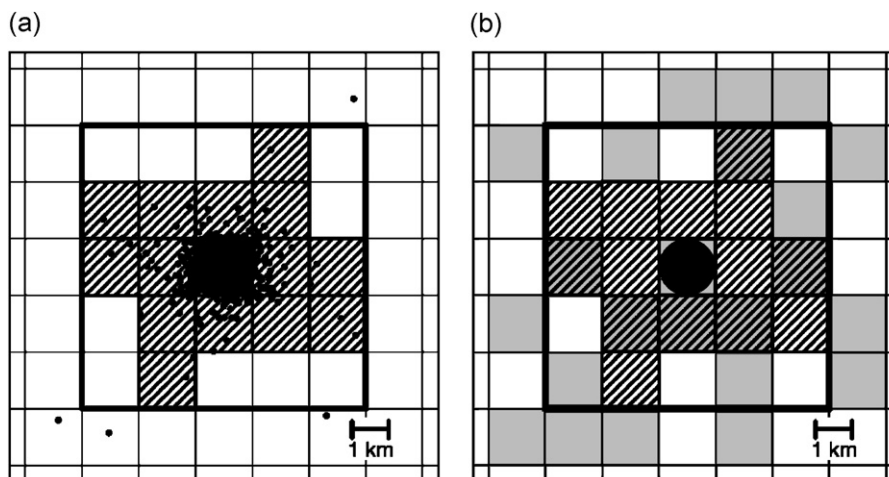
Fig. 2. A protocol used to estimate the dispersal ability of 37 species of South African Proteaceae. The protocol combines species-specific simulations of a mechanistic model for seed dispersal by wind with species-specific estimates of habitat distribution: (a) for each of 10,000 different dispersal environments, the dispersal model simulated the post-dispersal locations of 10,000 seeds (black dots) starting from the central source cell. The neighbouring cells reached by at least one seed (hatched cells) were determined from this seed shadow. To represent barriers to Proteaceae seed dispersal that arise from limited fire extent, only the 5 × 5 cell neighbourhood (delimited by the bold line) was considered. (b) The distribution of cells reached (hatched) was overlaid on the distribution of suitable habitat (grey), yielding the number of suitable cells that can be reached from a potentially suitable source cell (black circle) (from Schurr et al., 2007).

Allee effects that can substantially slow down spread rates (e.g. Kot et al., 1996; Taylor and Hastings, 2005). So far, only a few empirical studies have looked for Allee effects at expanding range edges, but for invasive plant species there is some evidence that Allee effects indeed occur at the invasion front (Cappuccino, 2004; Davis et al., 2004). This calls for further empirical research on the importance of Allee effects for the spread of native and invasive plant species. Moreover, we currently lack data on the post-dispersal survival of long-distance dispersed seeds (Nathan, 2006).

We suggest that empirical observations and experiments should urgently be combined with habitat modelling approaches to allow the spatial simulation of climate change impacts on demographic rates. A number of modelling approaches exist for providing such a mechanistic link. Metabolic theory makes very simple and generic predictions on the temperature dependence of population growth rates and carrying capacities (Brown et al., 2004). However, these predictions are probably too coarse to be useful in models for the range dynamics of individual species and independent tests using a broad range of taxa across different regions have found limited support for some of the general predictions in the theory (Hawkins et al., 2007). To develop and test more refined models of climate effects on demography, data are required on demographic rates collected across climatic gradients. More complex climatic effects on population growth rates are embedded in DVMs (e.g. Sitch et al., 2003; Woodward and Lomas, 2004 ♯2633), but species-specific predictions

cannot be made from these, and the formulations of population dynamics are very simplified (Moorcroft et al., 2001). Some forest gap models represent many of the processes that are thought to influence climatic effects on population growth rates, including competition and indirect effects on dispersal through earlier reproduction or seed numbers (Lischke et al., 2006). In these models, tree growth is commonly assumed to be maximal if the climate corresponds with the current climate in the centre of a species' distribution (e.g. Bugmann, 2001; Schumacher et al., 2004, 2006).

Towards the edge of the distribution, growth and establishment is reduced, while growth efficiency-related mortality increases. Plant species are limited not only by their absolute limits of survival but also through competition from other species, which might grow better in a given climate. Parameterizing these models for large numbers of plants other than trees in the temperate and boreal zones or PFTs, however, might not be possible in the near future. Instead, process-based vegetation models can be used to predict general changes in vegetation structure, such as canopy density or vegetation type, which implies information on changes in habitat type and quality for most species.

By altering demographic rates, inter-specific interactions may speed up or slow down spread rates, as well as decrease or increase the area a species can occupy (e.g. Travis et al., 2005). Modelling the effect of inter-specific interactions on spread rates is particularly challenging since, at the spreading front, a species is likely to interact with species it has not encountered before. These novel

interactions may not be captured by the extrapolation of habitat models and call for the incorporation of process-based interaction modules into range shift models. As an example, the range shift model of Lischke et al. (2006) contains a submodel describing intra- and inter-specific competition for light. For more complex interactions such as competition for multiple resources, facilitation, pollination and herbivory we lack generic models. While the development of such generic models is highly complex, it also seems highly rewarding: generic models for species' interactions may greatly expand our ability to (1) replace descriptions of potential ranges by mechanistic range models, (2) assess the impact of invasive species on biodiversity, and (3) predict the dynamics of novel communities arising under global change.

The combination of habitat models for potential ranges with mechanistic models of species spread holds great promise for the improvement of range shift projections. It should be noted, however, that such hybrid models provide no general solution for the incorporation of migration processes into range shift projections. Consider, for instance, a species that is expanding poleward in response to past climatic changes, as seems to be the case for many European tree species whose range still appears to be limited by post-glacial expansion (Svenning and Skov, 2004). A habitat model fitted to the present-day distribution of such species would tend to underestimate its cold tolerance and hence the extent of its current and future potential range. Consequently, a process-based migration model based on these bioclimatic projections is likely to underestimate the future range of this species, thus overestimating extinction risks from models of range. This problem may be somewhat reduced by not using the "best fit" between a species' distribution and climate; but instead the most extreme value of any bioclimatic variable found within a species' geographic range (Bugmann and Solomon, 2000).

An approach that completely circumvents this problem is the joint statistical fitting of a mechanistic range dynamics model and a habitat model to species records. A step in this direction has been taken by Wikle (2003), who used a hierarchical Bayesian approach to fit a Skellam-type model of population migration to a time series of House Finch records in the eastern US. Wikle's model allowed for random spatial variation in both population growth rate and mean dispersal distance. While he did not model these parameters as a function of climatic variables, the hierarchical Bayesian framework employed is flexible enough to incorporate functional relationships between demographic parameters and climatic variables. Limits to the broad application of this approach may be posed by the availability of high-quality data on the spatio-temporal dynamics of species and by the computational challenges encountered in the statistical fitting of complex models (Clark, 2005). However, the hierarchical Bayesian framework is a powerful way of linking process-based models and data, and this potential should be exploited for the improvement of range shift projections.

Predicting the trailing edge response – forecasting species probability of persistence

Background

To predict the future distribution of a species, one has to consider not only the ability of the species to colonize new sites, but also the ability to persist in current sites or face localized population extinction. The effects of local extinction may be seen at the level of entire species' ranges: in South African Proteaceae, species with life histories that are more vulnerable to population extinction tend to fill less of their potentially suitable range (Schurr et al., 2007). Extinction is also likely to be seen in small and isolated populations driven by reduced intra-population genetic variation and reduced fitness stemming from a greater degree of environmental stress and inbreeding depression (Willi et al., 2006). These small and isolated populations are often found at the rear edge of a range; indeed, the fossil record shows that extinction commonly occurred at rear-edge populations, particularly during periods of rapid climate change (Davis and Shaw, 2001).

Recent empirical evidence suggests that climate change already drives the extinction of rear-edge plant populations leading to a distribution with a 'trailing' edge (Lesica and McCune, 2004; Hampe, 2005; Lavergne et al., 2005, 2006; Wilson et al., 2005). For the desert tree *Aloe dichotoma* in southern Africa, Foden et al. (2007) found that trailing edge populations showed clearly negative demographic rates, and strongly positive rates were observed at the leading edge of the range, making population growth rate a sensitive and useful indicator of incipient change in range.

However, for the majority of species detecting any decline at the rear edge is hampered by a lack of available survey data (Thomas et al., 2006) and there is also a danger that the larger amount of evidence for leading-edge expansion may result in a lack of research on climate change effects on the rear edge (Hampe and Petit, 2005). Moreover, this lack of research is granted more urgency as it has been argued recently that population extinction at the rear edge of shifting ranges may be of disproportional importance for conservation because of the high level of regional genetic diversity between isolated populations (Hampe and Petit, 2005).

The short-term response of plant populations to environmental change partly depends on basic aspects of a species' life history: populations with long generation time, high reproductive rates, and persistent life cycle stages are likely to persist longer in the face of environmental change. Additionally, phenotypic plasticity is important for short-term reactions to environmental change, since it may allow a species to buffer short-term environmental change and maintain viable populations (Ghalambor et al., 2007).

For the long-term persistence of natural populations facing directional changes in environmental conditions, evolutionary adaptation becomes crucial (Etterson and Shaw, 2001). Ultimately, populations persist only if the rate of adaptive evolution at least matches the rate of environmental change (Bürger and Lynch, 1995). The two main ingredients necessary to predict how phenotypic traits in a population might change in response to environmental change are the magnitude of plasticity in the population (which determines the potential of the population to respond over the short term), and the speed at which the population can evolve (which determines the potential of the population to respond over the longer term). However, there is little data to quantify the speed of evolution in the face of climate change (but see Berteaux et al., 2004). This lack of hard data was emphasized by Hedrick (2001), who highlighted that "determining the potential for adaptation of a population in a changing environment is a critical unanswered question in most cases". Alternatively, the fossil record favours the hypothesis of niche conservatism for most species in a climate change context (Prinzing et al., 2001; Ackerly, 2003; Wiens and Graham, 2005; but see Broennimann et al., 2007 for the case of biological invasions); this may be true for isolated populations at the rear edge of a shifting range because the relatively poor *intra*-population diversity will reduce the evolutionary potential in the face of rapid environmental change (Davis and Shaw, 2001; Parmesan, 2006; Willi et al., 2006).

Also, given that microevolutionary processes occur across generations, generation time is an important factor affecting the evolutionary potential of species if environmental change is rapid (Rosenheim and Tabashnik, 1991). From that, species with a long generation time such as perennial herbs, shrubs and trees should have a lower capability to respond to new selective pressures than species with a short generation time such as annual herbs (Rosenheim and Tabashnik, 1991). On the other hand, species with a long generation time have a higher probability of population persistence, at least over short timescales (see above). Thus, to predict the long-term fate of populations exposed to environmental change, one has to quantify the effects of both ecological and evolutionary processes on demographic rates (Botkin et al., 2007).

Key issues

The understanding and quantification of demographic processes is key to the modelling of population extinction under environmental change. The link between demography and population extinction has been studied extensively in the field of population viability analysis (PVA, see Menges, 2000; Reed et al., 2002 for reviews of PVAs of plants), leading to a substantial theory on population extinction (e.g. Lande, 1993; Frank and Wissel, 2002; Grimm and Wissel, 2004). A minimal spatial model for population extinction contains the growth rate and carrying capacity of individual populations, and the probability of dispersal between populations (the latter is relevant since immigration may rescue small populations from extinction, Brown and Kodric-Brown, 1977). The basic demographic quantities necessary for predicting population extinction are thus easily identified; the challenge to distribution modelling lies in predicting how these quantities will be modified by environmental conditions, inter-specific interactions, phenotypic plasticity and evolutionary change. In the following, we provide perspectives on how these modifications can be represented in distribution models.

Perspectives

Environmental effects on demographic processes can be easily incorporated into distribution models if environmental change causes an abrupt change in demographic rates, leading to rapid population extinction. In the context of land-use change, such abrupt changes have already been incorporated into distribution forecasts by overlaying habitat models' forecasts with a post-modelling mask (Broennimann et al., 2006). Climate change and invasive species are, however, likely to induce gradual changes in demographic parameters and the probability of local extinction. Such gradual changes pose a greater challenge to distribution modelling because their description requires quantitative information on the relationship between demography and environment. In the context of species' migration, we have already discussed how distribution models can incorporate gradual effects of *mean environmental conditions* on demographic rates. In the context of population extinction, however, it seems particularly important to additionally consider the effects of *temporal and spatial variability in environmental conditions* (e.g. Higgins et al., 2000; Menges, 2000), especially extreme events (Parmesan et al., 2000).

Temporal variability in the environment is commonly believed to increase the probability of population extinction (e.g. Menges, 2000), and its consideration in distribution forecasts is particularly important if environmental variability increases due to climate change.

The more temporally variable the environment becomes, the more the persistence of a population will depend on its ability to maintain reproductive potential during unfavourable periods (e.g. Higgins et al., 2000). Plant populations can store reproductive potential in seed and sapling banks or in long-lived adults (Bond and Midgley, 2001). Higgins et al. (2000) noted that species with a high storage reproductive potential may even benefit from an environment becoming more variable, as this may lead to a higher frequency of conditions beneficial for recruitment. Their simple model for local population dynamics includes the storage effect as well as temporal variability in the environment, and could be embedded into process-based distribution models.

Broad-scale spatial variability in the environment is usually accounted for in habitat models and this information can be linked to demographic rates in a process-based approach. Small-scale spatial variability, however, poses a problem to distribution modelling. Existing distribution models are typically grid based and assume that environmental conditions within large grid cells are constant. Yet, small-scale environmental variability within grid cells may be crucially important for predicting species' responses to climate change. In a heterogeneous grid cell, a species may be able to escape to another habitat type or to higher altitudes and therefore persist longer than in a homogeneous environment (Jackson and Overpeck, 2000). Species' distribution models can account for small-scale variability in environmental conditions by considering the area covered by different habitat types or the altitudinal range within each grid cell. A similar approach has already been taken to describe habitat transformation through the incorporation of a data layer that gives the proportion of area transformed inside each grid cell (e.g. Latimer et al., 2006).

Biotic interactions are also likely to alter the demographic determinants of population persistence or extinction. Competition for resources is undoubtedly important for determining range size (Case et al., 2005; Brooker, 2006; Morin and Chuine, 2006). Leathwick and Austin (2001) showed how competition by *Nothofagus* shaped the distribution of other tree genera in New Zealand. Facilitation can have similar controls on rear-edge boundaries: Castro et al. (2004) have shown that Scot's pine (*Pinus sylvestris*) seedlings at their southern limit in Spain have higher survival rates under shrubs (that effectively shelter the pine seedlings from drought, frost, hail and trampling) than on bare ground or under woodland canopies. Both these examples highlight how interactions refine the broad-scale control that the environment has on a species' distribution and suggest that interactions may become increasingly important for range dynamics in the future. Approaches that can be used to model the effects of interactions on species' distribution and population spread may also be useful for modelling the consequences of interactions for population extinction.

Phenotypic plasticity and evolutionary adaptation in response to climate change are currently being studied (e.g. Willi et al., 2006; Bridle and Vines, 2007), and may find their way into process-based models over the next few years. Indeed, understanding the processes and patterns of gene flow and local adaptation requires a detailed knowledge of how geographic space and landscape characteristics structure populations (Antonovics et al., 2002). We foresee that such information will be transferable into distribution modelling in the near future. One promising research direction would thus be to simulate adaptive genetic responses in spatially explicit models of species' distribution, a new task for the field of landscape genetics (Manel et al., 2003; Metcalf and Pavard, 2007). Tools for jointly simulating the dynamics of plant populations and genotypes are now becoming available: the modelling framework AMELIE (Kuparinen and Schurr, 2007) links the spatio-temporal dynamics of plant populations and genotypes, and is flexible in its description of life histories, seed and pollen dispersal, reproductive systems, and demographic and environmental stochasticity. Individual life cycle stages can be described by a wide range of alternative submodels, allowing, for instance, plant growth to be modelled with a physiological model. The AMELIE framework can thus be used for including evolutionary processes into distribution modelling, given that sufficient demographic and genetic data are available.

Alternatively, when no data are available, simple adaptive scenarios may be drawn up and included into distribution modelling outputs (Berteaux et al., 2004). For instance, for a quantitative trait such as response to climate (influenced by multiple genes, each having a small effect), we can describe several situations depending on the magnitude of phenotypic plasticity (PP) and the speed of evolution. In one extreme situation, contemporary evolution is slow and there is virtually no PP for the trait considered. Sources of change in the average trait value are weak, and if the selection gradient acting on the trait (the slope of the relationship between the trait and fitness) is steep, the average fitness of the population decreases under the pressure of climate change (Berteaux et al., 2004). In the opposite case PP is high and contemporary evolution is fast, so that sources of change in the average trait value are strong, and the average fitness of the population remains stable. A particular situation may occur, where antagonistic plastic and genetic responses to environmental change will lead to apparent evolutionary stasis (no change or contradictory change in the phenotype with time), despite selection and genetic variation of the trait (Merilä et al., 2001). Depending on the magnitude of PP and the speed of evolution, one can draw optimistic or

pessimistic scenarios when predicting changes in species' distribution under environmental change (Berteaux et al., 2004).

To conclude, we argue that range gain and loss are two sides of the same coin: range loss is caused by the extinction of existing populations, whereas migration is driven by newly founded populations that escape extinction. The process-based modelling of range dynamics will thus greatly benefit from better data on the factors causing the extinction or persistence of small populations.

Conclusion

Models are simplifications of reality and often begin life by helping researchers to formalize their understanding of a particular process or pattern of interest. Models are thus primarily important aids to research. Difficulties may therefore arise when such theoretical models are used to guide conservation planning, management and to support the formulation of policy decisions (e.g. IPCC). The magnitude of uncertainties in species' range modelling is currently so great that it might lead conservation planners, policy makers and other stakeholders to question the overall usefulness of science as an aid to solve real world problems. Bridging the perceived gap between science and societal needs is of paramount importance if we want to make progress and contribute meaningfully, as scientists, to solving the global environmental change crises.

The conservation agenda is now moving on to consider adaptation to climate change and here a landscape approach is more applicable for testing strategies such as habitat re-creation, corridors and ecosystem resilience. Habitat models may contribute to this in providing a broader framework for understanding and predicting climate change impacts, delineating potential corridors for species migration (Williams et al., 2005) or testing the effectiveness of reserve networks to protect biodiversity (Burns et al., 2003; Araújo et al., 2004; Bomhard et al., 2005). Perhaps we should endorse Sutherland's suggestion (Sutherland, 2006) and ask conservationists to identify desired future states and then use models to backcast in order to identify strategies for achieving the desired state. The time is ripe for modellers to explore how far models can be taken to both fulfil the requirements of and answer the critical questions for conservation in a dynamic future.

One key point is still puzzling to us and generates lively discussions among the authors of this paper: Are more complex models (i.e. including a large number of parameters) likely to be more accurate than simple models (i.e. including few parameters)? When should we rely on complex versus simple models to aid policy decisions? This is a reflection of an older debate over the merits of accuracy versus realism, or between simplicity versus complexity. We could of course argue that adding dispersal and physiology makes models more realistic and closer to the truth, but are these models necessarily more accurate? This is a complex issue as habitat models have proved to be very accurate under current conditions even though they ignore species physiology and other properties (Hijmans and Graham, 2006). Nevertheless, some conclusions can be tentatively made: complex models are likely to be more accurate at finer resolutions, whereas simple models are likely to offer useful and parsimonious solutions at broader scales; complex models are probably more accurate under novel situations and for species with non-equilibrium distributions with current environmental conditions (Peng, 2000); the development of complex models is necessary not only as an academic exercise to help understanding of the importance of different drivers of change on the distribution of species, but also as an aid to identify the optimal trade-offs between precision and generality. Furthermore, future research may help develop models that are still simple yet have better predictive power (e.g. based on more advanced environmental predictors or including simple interactions; Leathwick and Austin, 2001; Robertson et al., 2003; Araújo et al., 2005; Guisan et al., 2006; Heikkinen et al., 2006).

In recent years we have seen a new generation of models, termed "hybrid" models (TreeMig (Lischke et al., 2006), LPJ-GUESS (Smith et al., 2001), Hybrid (Friend et al., 1997)). These models try to achieve a compromise between realism–accuracy and complexity–simplicity. Such developments are opening new pathways for research and are bound to provide many answers for the questions raised in this review. One of the limitations of these approaches is that they are highly sophisticated, data hungry, and require detailed knowledge of ecological processes that is usually unavailable for large numbers of species and regions. Nevertheless, the literature abounds with experimental and observational studies carried out at local scales which are only rarely used by modellers. These studies have been accumulating over at least two centuries and offer a powerful source of information. This, if appropriately synthesized and digested, could be extremely useful in helping to select and fine tune the parameters entering process-based models across a variety of species, functional types and regions (Midgley and Thuiller, 2005). A systematic use of the information available in the literature, and directed pairing of experimentalists with distribution modellers, would help in testing model performance against observations recorded with a moderate level of climate change already observed, and thus help to identify the gaps in

knowledge that need filling in order to efficiently set the targets for conducting large-scale experiments required to obtain meaningful information for the parameterization of distribution models. Existing global biological traits databases are an example of accumulated meta-information that will prove to be extremely helpful in a more realistic parameterization of models.

The future holds great promise for researchers in global change biology: there is indeed much to be done, but there is also real hope that integrative programmes and projects will help filling in gaps between distinctive fields of research, thus contributing to the emergence of the new generation of forecasting methodologies that are more useful for decision making.

Acknowledgments

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