Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change

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Recent greenhouse gas emissions exceed the highest IPCC SRES scenario (Raupach et al. 2007); global warming this century is thus on track to exceed the 1.5°C lower limit cited by the IPCC Fourth Assessment Report as resulting in increasingly high extinction risk for 20–30% of Earth's biodiversity (Parry et al. 2007). Minimising negative impacts on biodiversity requires effective conservation strategies that will enhance species' opportunities to adapt to climatic change, especially as their capacity for natural adaptation very likely will be exceeded this century (Parry et al. 2007). Developing and applying such strategies requires insight into species' responses and an integrated approach to identifying vulnerable species and regions (Williams et al. 2008). Robust predictive models of species' and community responses to climatic change are essential to this approach, and vital to inform policy and management (Barnard and Thuiller 2008).

Species exhibit a variety of responses to climatic changes, the magnitude and rate of change determining which response type predominates (Fig. 1). Apart from macro-evolution, that is elicited by relatively slow, larger-magnitude changes, species have exhibited all these generic responses to the climatic changes of the past half century (Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006). Behavioural and micro-evolutionary changes offer limited scope for adaptation, however, being constrained by

species' inherent plasticity and/or genetic variance (Huntley 2007). Local abundance changes are principally precursors to, or symptoms of, spatial responses. Extinction results from a species' inability to achieve a sufficient response of any other type. As the Quaternary record shows (Huntley and Webb 1989), geographical distribution changes are species' predominant response to relatively rapid, large-magnitude climatic changes, such as are projected for this century. Our aim in this paper is to outline a strategy for developing robust predictive models of species' spatial responses and the associated changes in abundance patterns.

Current state of the art

To-date, bioclimatic envelope models have been the principal approach used to project potential species' distribution changes resulting from climatic change (Midgley et al. 2002, Araújo and Guisan 2006, Thuiller et al. 2006, Huntley et al. 2008). Although their underlying assumptions and inherent simplifications have been debated (Gaston 2003, Pearson and Dawson 2003) and their reliability questioned (Davis et al. 1998, Beale et al. 2008), several studies have demonstrated their general robustness. They can successfully simulate species' distributions for regions (Beerling et al. 1995) or times (Hijmans and
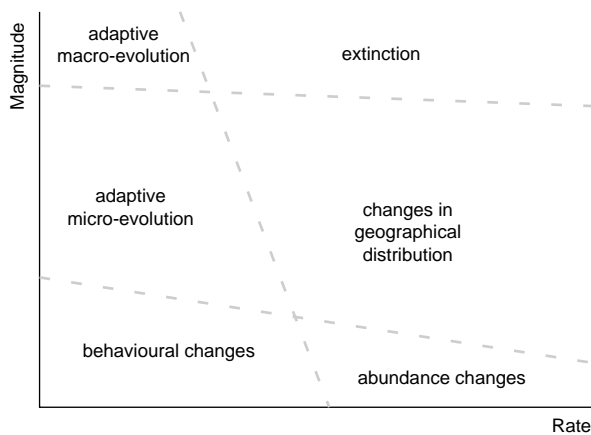
Figure 1. Schematic representation of species' responses to climatic changes. Species' predominant response to climatic changes depends upon the combination of the magnitude and the rate of those changes. Spatial responses, i.e. changes in geographical distribution, predominate for relatively large magnitude and relatively rapid changes, such as those projected for the present century.

Graham 2006) independent of those from which data were used in model construction, and retrodict species' abundance changes both near range margins (Green et al. 2008) and throughout sub-continental regions (Gregory et al. 2009). Their application has highlighted the potential magnitude of climatic change impacts upon species' distributions (Thomas et al. 2004, Fitzpatrick et al. 2008, Huntley et al. 2008), and potential species' losses from protected areas (Hannah et al. 2007, Hole et al. 2009, Coetzee et al. 2009).

However, these static models may give an unrealistically optimistic impression of species' capacities to adapt to climatic change because dispersal and colonisation rates will limit realisation of potential range shifts (Huntley et al. 1995, Midgley et al. 2006), as may barriers to dispersal. Efforts to address this have focused mostly on dispersal limitations, especially of plants (Neilson et al. 2005), relative mobility of animals (Warren et al. 2001) and habitat availability and/or fragmentation (Collingham and Huntley 2000, Hill et al. 2001). Demographic processes, however, especially intrinsic rates of population increase, are also fundamentally important determinants of species' rates of range expansion (Willis et al. 2009). Climatic change may also de-couple existing relationships between species' range extents and abundances, because of changes in relative range quality (Wilson et al. 2004). Demographic processes thus affect species' ability to achieve range expansions from source populations and to persist under less favourable climatic conditions. Only by developing dynamic models of species' potential range shifts, that incorporate population and dispersal processes, as well as ecological processes that influence habitat suitability (e.g. disturbance), can we move beyond simply simulating species' potential range changes (Guisan and Thuiller 2005). This is critical to our ability to assess climatic change impacts upon species' relative extinction risks (Thomas et al. 2004, Schwartz et al. 2006) and to develop climatic change-adapted conservation

management strategies (Hannah et al. 2002) that will enhance species' likelihood of persistence.

The next generation − fully integrated models

Addressing this challenge requires integrated models that bring together the necessary component sub-models as modules within a unified framework. We envisage such models as grid-based, operating on discrete, normally annual, time steps, and with modules to simulate: 1) climatic suitability; 2) habitat availability/suitability; 3) population dynamics; and 4) dispersal. Although candidate models are available for all four components, integrated models are still in the early stages of development (Keith et al. 2008, Anderson et al. 2009). There are three core challenges in developing such models: 1) integrating across different spatial and temporal scales at which their components operate. For example, climatic suitability operates principally at extensive spatial scales to determine species' overall potential geographical ranges, whereas habitat availability/suitability is more relevant when considering where in a local landscape a species may occur, and in what numbers. 2) Providing realistic uncertainty estimates for model outputs. As with other complex models, analytical statistical approaches to assessing uncertainty are unlikely to be possible. 3) Balancing a desire for biologically "realistic" process representation with model complexity, data requirements and computational demands. It is likely that, as with earth system models (ESMs), there will be a need for complementary models differing in their degree of complexity. Much can be learned by developing and applying models of intermediate complexity, as the application of ESMs of intermediate complexity has shown (Claussen et al. 2002, Sánchez-Goñi et al. 2005).

1. Climatic suitability module

This module will be needed for most species, although in a minority of cases it will be redundant. The latter will be the case where: 1) the species' inherent physiological limits are known; 2) available data allow the species' growth, performance, survival and reproduction to be modelled mechanistically, including the effects of climate; or 3) a physiologically mechanistic approach is possible (Kearney and Porter 2009). The module will usually be based primarily upon observed correlations between the species' present distribution and present climate, and the necessary assumption that the species' distribution is at least approximately in equilibrium with that climate. The approach is thus precluded for those, usually rare, species that violate this assumption. It is essential that variables used, whether acting directly or indirectly, have plausible, preferably known, mechanistic roles in determining species' range limits. These bioclimatic variables generally are not solely those recorded in meteorological data, but are derived from these. It also is important that the implicit and/or explicit assumptions of the modelling approach are consistent with observations, especially with respect to the form

of the relationships between species' occurrence probability and bioclimatic variables.

2. Habitat availability/suitability module

This module may be simple or quite complex. At its simplest, it may be a binary mask (Midgley et al. 2010), with areas categorised either as suitable or unsuitable for the species. Such masks often will be derived from earth observation data, usually using a classified land-cover data product. Where the data product has a finer grain than that of the model, habitat availability within each model cell can be quantified (Hill et al. 2001). At the opposite extreme, complex niche models may include many habitat dimensions (Catling et al. 1998, Franco et al. 2000). Such models may be fitted using many different approaches, some more appropriate in their assumptions than others (Austin 2007). Although recent emphasis has been on applying more complex functions, and thereby more realistically relating species' responses to environmental predictors (Austin 2007), such approaches are limited by data availability. Generally, the more complex the responses, the more data are needed to construct a reliable model (Barry and Elith 2006) whilst avoiding over-fitting (Araújo and Guisan 2006). In practice, data limitations will preclude use of more complex models for most species.

Whichever approach is adopted, a key issue is how to incorporate changes in habitat availability and/or suitability arising mainly from three processes: 1) disturbance, whether natural (e.g. wildfire, extreme weather events) or anthropogenic (e.g. forest harvesting, burning), triggers episodic regeneration of vegetation. This leads to rapid changes in both the nature and extent of habitats available at spatial scales from landscapes to regions. 2) Vegetation structure and composition determine habitat suitability for most terrestrial animals and sub-dominant plants. Climatic change and increasing atmospheric CO_2 concentration are expected to lead to changes in these vegetation attributes over most of the global land surface, through shifts in plant species' distributions, CO_2 fertilisation and differential benefits to C3 vs C4 plants (Woodward and Kelly 2008) and to woody vs herbaceous plants (Bond et al. 2003). These changes will take place across a range of temporal scales, depending upon disturbance frequency and the rates at which individual species' responses are realised. 3) Changes in human land use resulting from both climatic change and socio-economic factors will result in loss and/or fragmentation of many species' habitats.

Sub-modules to simulate some of these processes, including disturbance and related vegetation dynamics, and vegetation structural responses to climatic change and increasing CO_2 concentration (Keith et al. 2008, Midgley et al. 2010), could be incorporated into the habitat module. Careful consideration of temporal and spatial scale differences between vegetation dynamics and species' range changes is necessary, as well as the need to balance complexity with computational efficiency. Alternatively, land-cover scenario series could be simulated using an ESM that includes a coupled dynamic global vegetation model (Cox et al. 2000, Sitch et al. 2003), although scale mismatches between the ESM grid and that needed to model species' range and abundance dynamics require consideration. Land-cover scenarios, therefore, might better be derived from offline runs of a vegetation dynamics model, driven by the changing climatic conditions simulated by an ESM, for the grid used in the integrated model. Potential human land-use changes could be incorporated using scenarios derived from models of societal and economic processes, and their impacts on land use (Alcamo et al. 1996).

3. Population dynamics module

This module too may have various levels of complexity. Where data describing the influence of climate on life-history (e.g. age-specific survival, reproduction) are available for a species, the climatic suitability module may be redundant. Instead, the population dynamics module can simulate how climatic changes affect key demographic processes that determine a species' range and abundance. In practice, such data are rarely available and then only from intensive, localised studies. It is unclear whether relationships between weather and fitness observed in such local studies apply also to longer-term climatic changes and, if so, how they lead to distribution changes at the extensive spatial scales at which ranges are limited principally by climate (Schwager et al. 2008). If such relationships do apply at extensive spatial scales, demographic parameters should vary with climatic gradients. Although demographic parameters do vary geographically (Frederiksen et al. 2005), we know of no study clearly relating this to climate. Ample evidence for local adaptation of life-history characteristics (e.g. counter-gradient variation, Laugen et al. 2003) suggests extrapolations from local studies to overall ranges require care. Nonetheless, where basic demographic data are available, a simple population dynamics module could simulate population changes. In a grid-based model, this module would simulate population changes in each grid cell, the maximum population each cell can support being determined by its climatic suitability and habitat availability/suitability (Hill et al. 2001, Keith et al. 2008). Where demographic data are not available for a species, generic estimates based upon similar species may suffice (Anderson et al. 2009). Sensitivity analysis of the demographic module will reveal which fitness components must be estimated most accurately to maximise reliability of the predictions. Minimally, data enabling estimation of the maximum population density and maximum intrinsic rate of population increase in optimal habitat and climate can provide a basis for simulating abundance changes as climate and habitat change.

4. Dispersal module

At its simplest, this module would, at each time step, take the propagules/offspring simulated for each grid cell by the population dynamics module and disperse them stochastically according to a function representing the species' dispersal characteristics. Whilst this may be adequate for passive dispersers, mobile organisms capable of directed dispersal and habitat selection may require more sophisticated treatment. For example, an offspring's eventual

destination may be simulated by a combination of a stochastic process, determining distance and direction of initial dispersal, and a subsequent directed movement if that grid cell is unsuitable. This allows occupation of the nearest suitable and/or not yet fully occupied grid cell within some maximum distance of that to which it initially dispersed (Hill et al. 2001). Density-dependent dispersal also requires consideration (Sutherland et al. 2002). Animals capable of strongly directed dispersal and habitat selection may disperse according to the rules of an ideal free distribution, electing to settle in the optimal reachable patch, as determined by habitat quality and population density. This can lead to a balanced dispersal process in which propensity to disperse is negatively correlated with local carrying capacity (McPeek and Holt 1992, Diffendorfer 1998). Dispersal of strongly territorial species, however, may accord with an ideal despotic distribution (Zimmerman et al. 2003). If dispersal propensity is unrelated to local population density, source–sink dynamics will dominate population dynamics at the range edge (Pulliam 1988), with more suitable areas supporting higher population densities and producing more emigrants than marginal areas. The module must be able to simulate these various dispersal modes. In addition, many mobile species disperse more than once during their life, often in age- and sex-specific ways (Greenwood and Harvey 1982), and the module also must accommodate these cases.

A practical challenge for simulating dispersal is that of obtaining reliable data from which to estimate the distribution of dispersal distances (Paradis et al. 1998, Clark et al. 2003). Suitable propagule dispersal data are available for only very few plant species (Schurr et al. 2005). Dispersal of mobile animal offspring is often easier to observe than plant propagule dispersal, especially where offspring can be individually marked at their natal site and observed or recaptured later. A key difficulty with such data, however, is how to account for varying detection probabilities (Bennetts et al. 2001, Tufto et al. 2005). Faced with these challenges, some authors have used arbitrary migration rates (Fitzpatrick et al. 2008) or simple rule-based dispersal models (Williams et al. 2005, Midgley et al. 2006) to simulate plant species' range expansion. Reliable estimates of dispersal characteristics are important, however, because the distribution of dispersal distances can critically affect species' rates of range shift (Anderson et al. 2009). In particular, much evidence indicates that species' occupation of newly suitable areas following an environmental change depends not upon relatively local, easily observed and more measurable dispersal of the majority of propagules/offspring, but upon inherently rare and difficult to detect long-distance dispersal of a very small minority of propagules/offspring (Clark 1998, Cain et al. 2000). Furthermore, such long-distance dispersal may depend upon mechanisms different from those involved in local dispersal (Wilkinson 1997, Higgins et al. 2003). Where possible, therefore, the form of the species' long-distance dispersal function should be estimated, including, where relevant, the maximum distance attainable by active dispersal. An estimate of the proportion of long-distance dispersed propagules/offspring also is desirable. When faced with a shortage of data upon which to base such estimates, however, simpler approaches to modelling long-distance dispersal will be necessary.

Discussion

Development of integrated models requires careful balancing of model complexity with data availability. For a few species, available data may permit a mechanistic approach to simulating all key processes; more likely, such an approach will be possible for only one or two processes. For most species, the data requirements of fully mechanistic approaches cannot be satisfied and various simplifications are necessary, such as using a binary habitat mask rather than a quantitative habitat suitability sub-model. Even simple integrated models (Keith et al. 2008, Anderson et al. 2009), however, represent an important advance upon climatic envelope models. Integrated model development should be pursued urgently for species that satisfy the necessary assumptions, and especially those for which at least minimum data requirements are met. Initially, these models will be valuable research tools, enabling hypothesis testing and sensitivity analyses to investigate, for example, how habitat availability and/or fragmentation limit species' realisation of their potential responses to climatic change. Development of these models will also highlight areas of critical data deficiency, whilst sensitivity analyses can help prioritise efforts to fill data gaps. Ultimately, and most importantly, these models will provide more and better policy-relevant information on species' responses to climatic change within a dynamic community and habitat context, and thus a sounder basis for decisions about how and where to allocate scarce conservation resources.

The data requirements of such models emphasise the vital contribution made by amateurs and the general public. It is often they who have provided most of the species' distribution and abundance data over extensive regions. Furthermore, model validation requires datasets from repeated mapping/atlas schemes and schemes recording long-term abundance or demographic data. Continuity of financial support for such activities is essential for future assessments of the success of biodiversity conservation strategies and for identifying needs for their adaptive modification (Sutherland et al. 2004). In addition, long-term detailed datasets collected by researchers for individual species are essential for development of the more complete and mechanistic models required to assess simpler models' performances. Although maintaining such long-term studies is unfashionable and difficult, the value of the data they provide in guiding climatic change adaptation options must be recognised by scientific funding agencies worldwide and appropriate resources provided to ensure their future continuity.

The development of integrated range–abundance dynamics models is an urgent research priority, although only the next step towards more realistic simulations of species' responses to climatic change (Barnard and Thuiller 2008). As such models are developed, an important challenge is provision of realistic uncertainty assessments for their outputs; these, in turn, require uncertainty assessments for the inputs. One potential approach to assessing uncertainties is to develop simplified models, often formulated using a Bayesian framework (Wynn et al. 2001), that emulate the behaviour of complex models but can be run many thousands of times to provide uncertainty estimates. In

the longer term, models able jointly to simulate the range and abundance dynamics of two or more interacting species can be envisaged. Such models can test competing hypotheses about the importance of species' interactions in determining geographical distributions (Heikkinen et al. 2007, Preston et al. 2008), and about assembly and dynamics of communities as climate changes (Guisan et al. 2006). They would also contribute to further improvements in robustness of range-change projections upon which conservation policy, planning and management decisions must be made.

In summary, bioclimatic envelope models produce valuable, first-order assessments of potential climatic change impacts on biodiversity. However, their limitations, together with the urgent need to provide more robust information to policy-makers and conservation practitioners, demand the development of integrated models with at least the components we outline here. Because data constraints will inevitably prevent use of complex, fully-mechanistic models for most species of conservation concern, however, we advocate development of models of intermediate complexity (Keith et al. 2008, Anderson et al. 2009) as a means to bridge the knowledge gap and provide more realistic projections of species' responses to climatic change.

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