Forum

Tools for integrating range change, extinction risk and climate change information into conservation management

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Ecological niche models (ENMs) are the primary tool used to describe and forecast the potential influence of climate change on biodiversity. However, ENMs do not directly account for important biological and landscape processes likely to affect range dynamics at a variety of spatial scales. Recent advances to link ENMs with population models have focused on the fundamental step of integrating dispersal and metapopulation dynamics into forecasts of species geographic ranges. Here we use a combination of novel analyses and a synthesis of findings from published plant and animal case studies to highlight three seldom recognised, yet important, advantages of linking ENMs with demographic modelling approaches: 1) they provide direct measures of extinction risk in addition to measures of vulnerability based on change in the potential range area or total habitat suitability. 2) They capture life-history traits that permit population density to vary in different ways in response to key spatial drivers, conditioned by the processes of global change. 3) They can be used to explore and rank the cost effectiveness of regional conservation alternatives and demographically oriented management interventions. Given these advantages, we argue that coupled methods should be used preferentially where data permits and when conservation management decisions require intervention, prioritization, or direct estimates of extinction risk.

Changes in geographical distribution and abundance patterns have been observed in a variety of taxa under 20th century climate change (Parmesan 2006). Forecasts are that many more species will be affected in the near future (Pereira et al. 2010) with impacts potentially transforming the structure of ecological communities (Hoegh-Guldberg et al. 2007). To meet global and regional biodiversity conservation targets (Butchart et al. 2010), we need an improved understanding of the mechanistic underpinnings of range limits (Holt et al. 2005, Sexton et al. 2009) and model architectures to extend this new found knowledge (Schurr et al. 2012). This is because forecasts of future distributions of species using traditional correlative approaches may underestimate the climatic tolerances of species, or fail to account for unforeseen

evolutionary changes in populations and important species interactions (Norberg et al. 2012).

Forecasting species' responses to rapid human-induced climate change requires both models designed to forecast changes in range edges (Huntley et al. 2010), and methods for simulating changes in occupancy and abundance within species ranges (Caughley et al. 1988). However, to date, forecasts of species range changes have been mainly modelled using correlative ecological niche models (ENMs), which explore the relationship between occupancy or abundance data with environmental variables (Peterson et al. 2011). Although ENMs convey practical advantages over alternative, more mechanistic approaches (owing to simplicity and flexibility of data requirements), the importance of underlying assumptions and inherent simplifications continue to be debated (Franklin 2010, Huntley et al. 2010, Kearney et al. 2010, Araujo and Peterson 2012, Dormann et al. 2012). Specifically, ENMs seek to characterize the sets of environmental conditions that are habitable for the species, but typically disregard species' life-history traits that constrain

demographic responses to environmental factors as well as information on the spatial structure of suitable habitats that may constrain local population processes (Araújo and Rahbek 2006). Consequently, ENM predictions do not characterise demographic and ecological processes at the population level and therefore cannot be used for direct estimates of extinction risk or to explore range dynamics explicitly (Fordham et al. 2012b).

As detailed in some recent multi-species case studies (Keith et al. 2008, Anderson et al. 2009, Lawson et al. 2010, Aiello-Lammens et al. 2011, Harris et al. 2012, Regan et al. 2012, Swab et al. 2012), coupled ecological niche-population models (NPMs) that link habitat suitability (ENM output) with demographic processes offer a potentially improved approach for estimating extinction risk and spatial distribution shifts under climate change because they account for important biological and landscape processes, and their interactions. Demographic models of population and metapopulation dynamics used in this 'coupled' statistical-demographic approach incorporate processes of survival, growth, reproduction and dispersal. Each of these processes may change stochastically (e.g. owing to weather-related fluctuations) or deterministically (e.g. owing to temporal trends because of climate change) and may be reliant on the age, size and/or sex of the individuals and on the density of the population (Brook et al. 2009). Moreover, dispersal is conditioned by the distribution of suitable patches (i.e. location, size, and shape), which can vary in time as a result of shifting habitat suitability. Although NPMs have tended to use complex metapopulation models, the framework could also be adapted to utilise much simpler stochastic patch occupancy models (Levins model and its variants; Hanski 1991).

Current reviews of techniques for modelling species distributions under climate change have suggested that these coupled approaches (including techniques where ENM and demographic models are simultaneously fit to data; Pagel and Schurr 2012) provide an important advance over entirely correlative models, at least under non-equilibrium conditions (i.e. under climate change and commercial over exploitation), because they incorporate a greater level of ecological realism by combining dispersal and metapopulation dynamics (Brook et al. 2009, Franklin 2010, Huntley et al. 2010, Dormann et al. 2012, Schurr et al. 2012). Although ENMs can be strengthened by adding information on an organism's physiological tolerance (Kearney et al. 2010), and through informed selection of environmental factors and spatial scales (Austin and Van Niel 2011), the addition of a demographic model is needed to: 1) account for important metapopulation processes such as source-sink dynamics and density dependent growth and dispersal; 2) incorporate interacting effects of habitat fragmentation and demographic stochasticity, and 3) explicitly evaluate demographically oriented management interventions.

Simple applications that seek to integrate life-history traits (dispersal and persistence) into ENMs might provide important insights into 'climate paths' that range shifts might follow (Early and Sax 2011), and reduce uncertainty in estimates of range movement (Engler and Guisan 2009). However, NPMs (or similarly sophisticated methods) are needed to explore the influence of climate change on extinction risk and spatial patterns of abundance. The disadvantages of NPMs are that spatial abundance data from across the species' range is needed to validate model structure and in some cases fit the model (Cabral and Schurr 2010), which are rarely available. Moreover, they are much more difficult to parameterise, potentially amplifying uncertainty in model predictions. Although Bayesian approaches (Pagel and Schurr 2012) could be used to inform parameterisation, independent evaluation of such models is extremely complex.

Here, we use new analysis and findings from published plant and animal case studies to better illustrate three key reasons for shifting emphasis towards NPMs in studies of climate change effects on species actual (instead of potential) distributions.

1) They provide direct measures of risks of population declines and extinction (e.g. extinction risk, expected minimum abundance, time to extinction, and risk of quasi-extinction) in addition to measures of vulnerability based on climate-driven changes in geographical range area or the quality and quantity of suitable habitat.

2) They simulate spatially varying patterns in life-history traits, permitting population density to vary in different ways in response to key spatial drivers (e.g. habitat status, harvest pressure, species interactions) conditioned by climate change and other anthropogenic forcing (an important point also raised by Schurr et al. 2012).

3) They can be used to explore and rank the cost effectiveness of regional conservation alternatives and demographically oriented management interventions (e.g. managed relocations, habitat restoration directed at improving vital rates, creation of protected zones) that might be available to mitigate the influence of climate change on a species. This is information urgently needed by policy makers and conservation practitioners (Wintle et al. 2011). By contrast, ENMs can only inform questions of habitat management directed to area, connectedness and relative suitability (Araújo et al. 2011).

Method

Modelling technique

We have described the technique of coupling correlative ENMs to demographic models in detail elsewhere (Keith et al. 2008, Brook et al. 2009, Fordham et al. 2012a). The procedure consists of creating a time series of ENMs, defining their output in terms of patches of suitable habitat and modelling populations of organisms occurring in those patch networks in a temporally changing landscape.

ENMs are first used to quantify the importance of environmental conditions that define present-day patterns of occurrence (Peterson et al. 2011). Environmental suitability is then scaled (using spatial abundance data) to obtain an estimate of the carrying capacity of each subpopulation. Carrying capacity forms the link between the spatial and demographic models, because the demographic rates at each time step are determined as functions of the current population size and carrying capacity (Akcakaya 2005). The

environmental predictive relationship is then forecast into the future using an annual time series of downscaled global climate model predictions (Fordham et al. 2011, 2012d); and land-use layers based on retrospective analysis of long-term data sets, LandSat imagery, and expert advice (Fordham and Brook 2010).

Metapopulation structure (size and location of subpopulations) is centred on spatial patterns of abundance defined through the ENM step, and connected via dispersal (the rates of which can be determined by distance, matrix quality, physical barriers, etc.). Each subpopulation is modelled with a demographic model that incorporates processes of survival, growth, reproduction and dispersal (Akçakaya 2000). Each of these processes may change stochastically or deterministically and may be reliant on location in the range. Model outputs include estimates of population size, how these vary temporally and spatially for sub-populations, and direct estimates of extinction risk, such expected minimum abundance (across the entire population) and quasi extinction risk.

Measures of population and range declines

There have been few efforts to link patterns of population decline with changes in species distribution directly. This is probably because estimating population size across space is an exhaustive process. Fordham et al. 2012b provided a rare attempt to examine this issue using Australian plants. Here we build on this research by comparing estimates of change in total population abundance with estimates of change in range area for three native Australian plants (*Angophora hispida*; *Banksia baxteri*; and *Xanthorrhoea resinosa*), two lagomorphs (*Oryctolagus cuniculus*, *Lepus timidus*) and a reptile (*Tiliqua adelaidensis*). These plants and animals were chosen because they represent a range of plant and animal life-history types (Supplementary material Appendix 1) and because they had NPMs already built for them (Anderson et al. 2009, Fordham et al. 2012a, b, c).

We modelled species' spatial abundance patterns and range limits as being driven by demographic processes, climate change and, for some species, catastrophic events (wildfires and droughts), and the interaction between these. With the exception of one species, the mountain hare *L. timidus* in Britain, range and total abundance was forecast under a high-CO_2 emissions future, as predicted under the WRE750 (Wigley et al. 1996) and MiniCAM-Ref (Clarke et al. 2007) greenhouse gas emission scenarios. For *L. timidus* we assumed a higher level of CO_2 mitigation (A2 emission scenario; Nakicenovic and Swart 2000), owing to data availability (see Supplementary material Appendix 1 for a detailed description of species specific models).

Modelling spatiotemporal variant vital rates

In Australia, the maximum finite rate of population increase (R_{max}, e^{rm}) in an infamous Australian invasive species – the introduced European rabbit *Oryctolagus cuniculus* – is influenced by climate and can be characterised according to

bioclimatic region (Hone 1999). We compared results from coupled niche-population models that treated R_{max} as spatially invariant (constant) ($R_{max} = 1.5$; Fordham et al. 2012a) with models where R_{max} was calculated as a spatially variable function of bioclimatic region (R_{max} varying between 0.77 and 2.06; Hone 1999). Anthropogenically driven changes in climate were simulated according to two greenhouse-gas-emission scenarios: a high-CO_2 concentration stabilising scenario (WRE750) and an alternative scenario that assumes strong mitigation of CO_2 (LEV1; Wigley et al. 2009). Modelling focused on the northern Australian range boundary north of $-25.5°$ latitude (see Supplementary material Appendix 1 for further details).

Assessing regional conservation alternatives

Climate-driven changes will adversely impact the expected minimum total abundance of *T. adelaidensis*. Relocating animals from climatically unstable to climatically stable habitats is critical for safeguarding lizard population persistence (i.e. their ability to exist; Fordham et al. 2012c). Here we build on previous research, by investigating whether introductions from an intensively managed 'captive' population with a carrying capacity of 2500 animals could avert the likelihood of extinction for *T. adelaidensis* this century. To simulate a more stable captive environment we modelled a 50% reduction in environmental variability in fecundity and assumed that catastrophic events (wildfires and droughts) did not effect this population. Animals were introduced to five patches of suitable habitat every five years at a rate of 5% of the captive population per patch. Sites for introduction were chosen according to area (largest to smallest) in each five-year period. The five largest populations were nominated as potential release sites. Other criteria for determining introduction sites included: a carrying capacity greater than 1000; not having had animals released at the site for at least 15 yr; having animals released no more than once at a given site. Animals were not removed from the captive population if local abundance dropped below 500 animals. Likewise animals were not released if the introduction site abundance was greater than 500 animals. Introduced animals were modelled as having similar survival and reproduction rates to native animals (Santos et al. 2009).

We compared extinction risk according to three management strategies modelled under a no-climate-policy emissions future (MiniCAM-Ref): 1) a climate adaptation strategy focused on reintroductions from a captive breeding population; 2) increasing carrying capacity through the creation of obligate habitat; and 3) no additional management (see Supplementary material Appendix 1 for specific model details).

Model simulations

All models were implemented in RAMAS GIS ver. 5 (Akcakaya 2005) and simulations were based on 1000 stochastic replicates and run over a 81yr period (i.e. 2000–2080). Depending on the case study, we estimated the following indices: 1) the smallest population size that is expected to

occur between 2020 and 2080 (expected minimum abundance; McCarthy and Thompson 2001), which is a continuous metric reflecting risks of both declines and extinction risk. 2) Proportional changes in mean annual total population abundance between 2020 and 2080. 3) Mean annual total population abundance and metapopulation occupancy between 2020 and 2080. 4) Range movement between 2020 and 2080 based on a weighted mean of the latitudes of the most northern 10% of the metapopulation. Weights were the average local population abundance of each patch in each year, and latitude was taken from the geographic centre of the patch (Anderson et al. 2009). 5) Annual change in range area calculated using correlative ENM maps of habitat suitability, with a threshold applied to distinguish between potentially occupied and unoccupied sites (Buisson et al. 2010).

Results and discussion

Measures of population and range declines

ENM techniques have advanced considerably in recent years (Elith et al. 2006, Thuiller et al. 2009), yet their use in assessing anthropogenic disturbances remains constrained to proxies rather than direct estimates of extinction risk. Range-area-type-measures, such as forecast shifts in geographic range area and habitat quality (using ENMs to derive habitat-suitability indices) continue to be used to draw inferences about the extinction risk of species (Thomas et al. 2004, Schwartz et al. 2006). This can be problematic, because it assumes a linear relationship between range area and total population abundance (Akçakaya et al. 2006). However, theory suggests it is unlikely that the abundance of individual species will decline at the same rate as its distribution since species are rarely evenly distributed throughout their range (Lawton 1993, Gaston et al. 2000).

Our results confirm that the relationships between rate of change in geographic range area (approximated using correlative ENMs) and total population abundance (evaluated using NPMs) are rarely linear (Fig. 1), the exceptions being: *X. resinosa* (Fig. 1c) and possibly *L. timidus* (Fig. 1f). The former is a long-lived plant distributed across a wide range in eastern Australia, with a slow generational response to climate-induced habitat change (Fordham et al. 2012b), and the latter is a more geographically constrained lagomorph in Britain with a relatively stable range (Anderson et al. 2009). Longevity and rate of habitat change are two functions that are likely to have a strong influence on the range area–abundance relationship because short-lived organisms respond more rapidly to environmental changes (Morris et al. 2008).

Figure 1 highlights that: 1) it is not clear, a priori, in what situations a linear range area–abundance relationship will hold; and 2) there is obviously a need to consider direct measures of extinction risk (population declines and other measures of stochastic viability), as well as measures of change in geographic range, when assessing climate change impacts on biodiversity. Furthermore, in the NPMs, total population abundance may be forecast to increase despite a decline in range area (e.g. Fig. 1d); or vice versa (e.g. Fig. 1a). These outcomes are not detectable by standard ENMs. Clearly, further research is needed to better understand the relationships between trends in range and abundance, potentially using simulated data and observer models to mimic real species (Zurell et al. 2010).

Modelling spatiotemporal variant vital rates

Biogeographic theory indicates that a species' local abundance and physiological state (influencing survival and fecundity) is typically greatest within the core (often near the centre) of its geographical range and declines toward the edge (Brown et al. 1995), where local extinctions are more frequent (Araújo et al. 2002). This implies an ordered response to environmental conditions: extreme conditions are lethal, marginal conditions permit survival and often temporally variable use, while average or better conditions allow reproduction (Townsend et al. 2000). However, species' densities rarely display central peaks and peripheral declines across geographic ranges (Sagarin et al. 2006, Yackulic et al. 2011) due to anthropogenic extinction forces (for example, habitat degradation, biocides and introduced species) that spatially propagate like contagions (Channell and Lomolino 2000), and non-linear population processes, including competitive exclusion, predation, non-equilibrial responses to disturbance regimes, Allee effects, and genetic swamping (Sexton et al. 2009). Consequently, core populations may even, counter intuitively, have a greater probability of extirpation than those at the edge of the range, particularly when populations are strongly influenced by anthropogenic extinction drivers (Channell and Lomolino 2000), including climate change.

Since complex causal agents can produce widely different spatial abundance patterns (Caughley et al. 1988), predictive models used to assess species' responses to climate change must be able to simulate spatially variable patterns in key vital rates that determine local abundance (Schurr et al. 2012). Indeed, NPMs accommodate variability in demographic rates across the species range, allowing them to change in different ways in response to key spatial drivers, conditioned by the processes of global change. Incorporating spatial (as well temporal) variability in life-history traits into NPMs can have a substantial influence on predicted responses to future environmental scenarios.

Results from our case study on rabbits in Australia (Methods) show that neglecting to recognize spatial patterns of variation in maximal growth rate at low population sizes runs the risk of underestimating expected minimum total abundance and overestimating change in mean total abundance between 2020 and 2100, especially for high-emission climate-change scenarios (Table 1). Also, failing to treat R_{max} as varying spatially influences the rate at which invasive species are forecast to shift their distribution in response to climate change (Table 1). The extent of northern range contraction differed by approximately 80 km depending on whether R_{max} was modelled as spatially variable or constant across populations. Interestingly, range contraction was faster for the variable R_{max} scenario under a low-emission scenario (compared to a constant rate of R_{max}), but slower for the emissions-intensive scenario. This reflects a greater number of habitat patches with below average R_{max} being maintained by dispersal inputs for longer on the trailing range margin under the low-emission scenario, which act as demographic sinks.
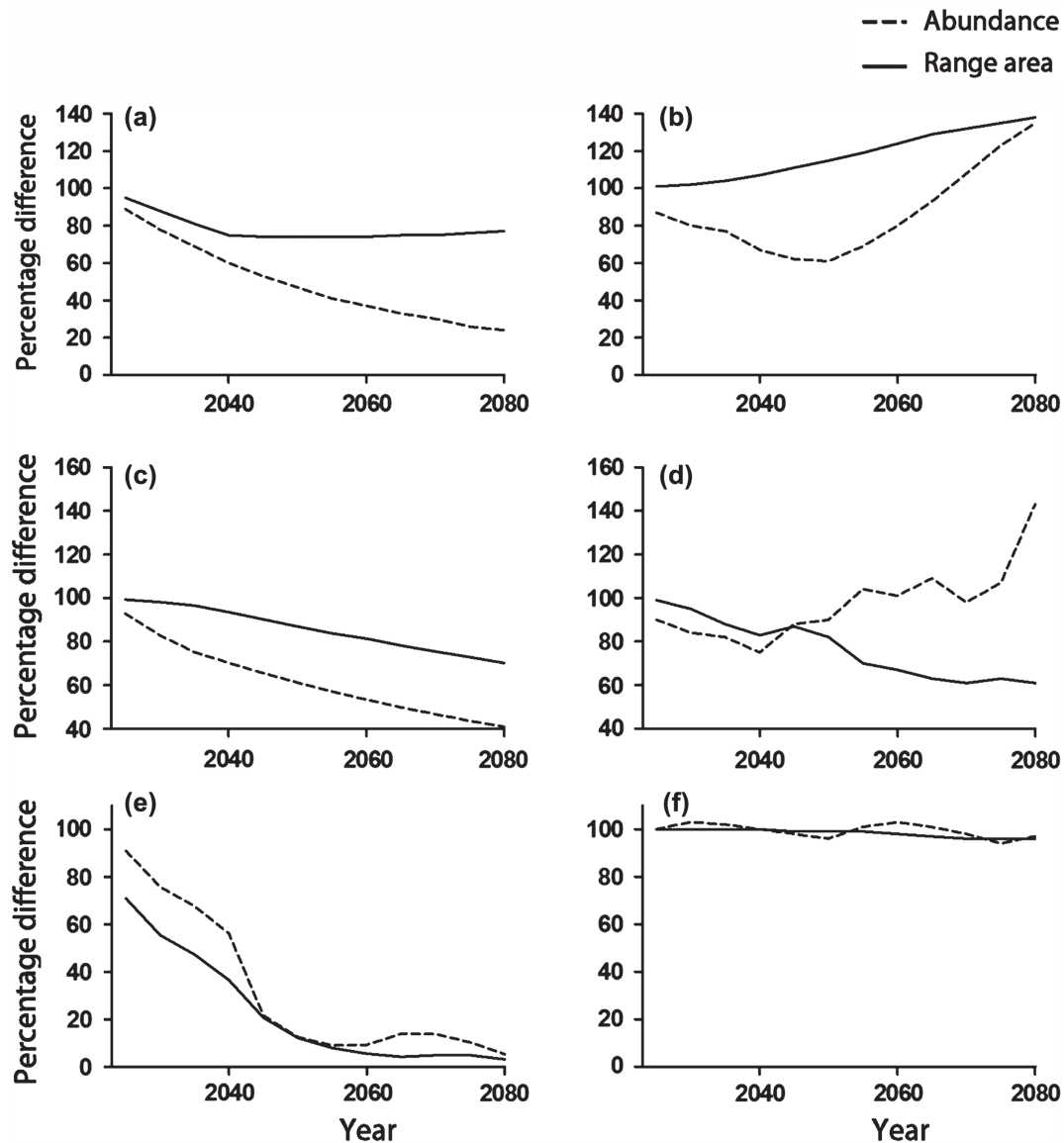
Figure 1. Change in total population abundance and range area between 2020 and 2100 for the Australian plants *Angophora hispida* (a), *Banksia baxteri* (b)*,* and *Xanthorrhoea resinosa* (c), the European rabbit in Australia, *Oryctolagus cuniculus* (d) and a native lizard, *Tiliqua adelaidensis* (e) according to a future typified by high-CO_2 emissions. Trajectories for the mountain hare *Lepus timidus* (f) in Britain assume a lower level of CO_2 mitigation. Note that R_{max} for *O. cuniculus* (and other species) is assumed to be spatially invariant. The model results are the average of 1000 stochastic simulations using the spatially explicit demographic model RAMAS Metapop.

Under the high emission scenario these patches of habitat for invasive rabbits are lost quickly, minimizing their impact on metapopulation processes at the northern range margin.

Population abundance is forecast to increase either substantially or marginally under the emissions-intensive scenario, depending on whether or not the relationship between R_{max} and climate change is modelled explicitly. We predict a similar, but less pronounced, relationship for the low-emission scenario. This is because a greater number of habitat patches with below average R_{max} are forecast for the future. Thus, modelling patterns of variation in R_{max} (and potentially other vital rates) has important implications for tools for informing pest and conservation management. In the case of *O. cuniculus*, failing to do so could result in misleading model results, leading to policy decisions that provide financial burden to agriculture and negatively influence

biodiversity conservation. It is important, however, to note that the methods by which environmental conditions influence demographic rates are complex, being influenced by evolutionary processes, such as local adaptation and phenotypic plasticity, as well as ecological limitations.

Assessing regional conservation alternatives

NPMs, with structures that characterise the uncertainties underlying biological mechanisms driving species distribution and population persistence, can be used by conservation practitioners to develop strategic responses to multiple (often reinforcing or synergistic) drivers of global change (Fordham and Brook 2010). For instance, a richer variety of management scenarios can be modelled and their

Table 1. Change in the range and abundance of the introduced European rabbit *Oryctolagus cuniculus* along the northern extent of its distribution in Australia between 2020 and 2100 according to two climate change scenarios.

Emission scenario	R_{max}	EMA	Change N (%)	Range movement (km)
High	constant	568958	+90	286
High	variable	866497	+6	203
Low	constant	581694	+35	76
Low	variable	1034755	+25	159

Maximum annual finite rate of population increase was modelled as spatially invariant (constant) or as a function of bioclimatic region (variable). Climate change was modelled according to two greenhouse gas emission scenarios: high-CO_2 concentration stabilising scenario (High) and an alternative scenario that assumes strong mitigation (Low). We report expected minimum abundance (EMA) and change in mean abundance (N) between 2020 and 2100 and movement of the northern range margin (most northern 10%-centroid of the metapopulation) in southerly direction. The model results are the average of 1000 stochastic simulations using RAMAS Metapop. Modelling focused on the northern Australian range boundary north of $-25.5°$ latitude.

efficacy assessed, compared to correlative ENMs, including: 1) translocating animals from captive bred populations to climatically favourable areas of their historical range (i.e. managed relocation) and/or regions where vital demographic rates are high, ensuring establishment; 2) increasing the carrying capacity of occupied areas; and 3) dampening negative anthropogenic influences (e.g. harvesting or predation by alien species) in areas of the range where vital rates are most sensitive. For example, NPMs for a set of South African plants (Keith et al. 2008) showed that the viability of these species is most sensitive to climate change through changes in fire regimes, suggesting fire management as

a potential conservation measure. Fire regime changes have large effects on demographic processes (such as seed production and germination) that are not, and cannot, be predicted by ENMs alone.

Our third case study (Methods) shows that reintroductions are the best management approach for mitigating the influence of anticipated climate change on the long-term persistence of *T. adelaidensis* (Fig. 2). Stopping reintroduction after 2070, in conjunction with an increased rate of habitat loss, resulted in substantial population decline (Fig. 2c). Similarly, NPMs were used to conclude that managed relocations provide an appropriate climate adaptation strategy for a rare fire-dependent plant (Regan et al. 2012). While the underlying correlative ENM can be used to guide management intervention (by detecting sites for translocations and increasing carrying capacity), an approach based on ENM alone does not allow for the potential efficacy of management responses to be evaluated. This requires an NPM approach.

Sensitivity analysis for population viability analysis is often used to compare the relative worth of different management actions (and levels of intervention), directly informing conservation decision-making (Kuemmerle et al. 2011). Furthermore, a capacity to assess conservation alternatives enables NPMs to be couched in an economic optimization framework, whereby the cost effectiveness of climate change investments in biodiversity can be measured according to economic constraints. For example, potential management strategies to reduce forecast extinction risk amongst plants in the South African fynbos were ranked according to unit cost by integrating NPM predictions into an economic decision framework, allowing the optimal investment strategy to be identified for different fixed budgets (Wintle et al. 2011).
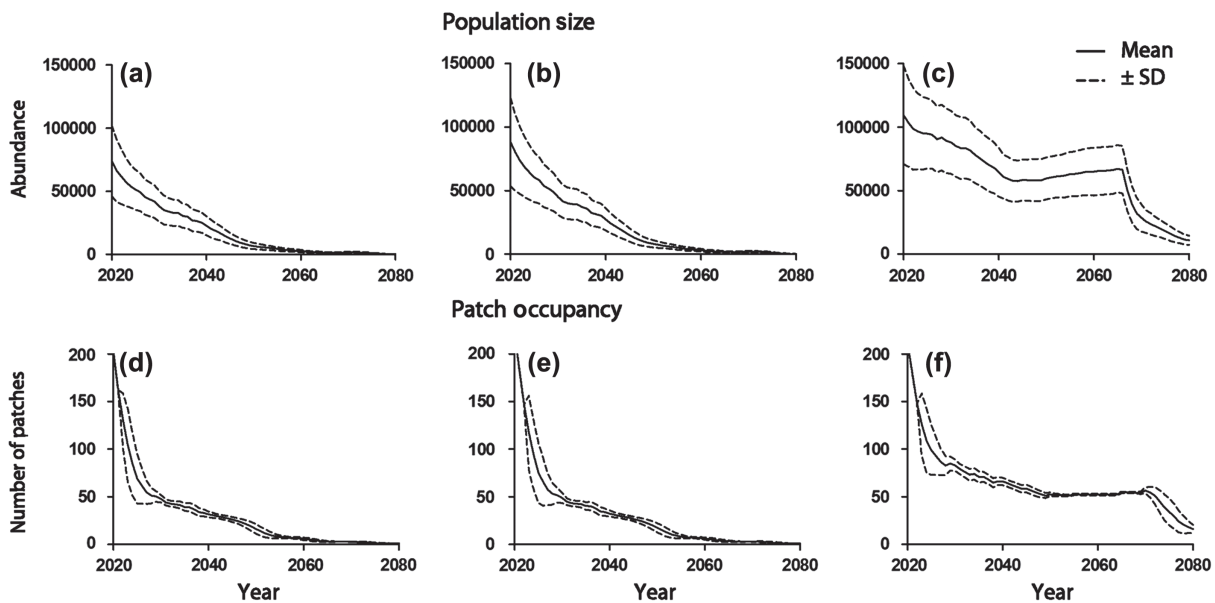

Figure 2. Population size and patch occupancy for pygmy bluetongue lizards *Tiliqua adelaidensis* between 2020 and 2080 according to a no-climate-policy emissions future without management intervention (a, d), with increasing the carrying capacity of all patches in all years 2020–2070 by 20% (through the creation of artificial burrows) (b, e), and by translocating captive-bred animals to five patches of habitat every five years at a rate of 5% of the breeding population per patch between 2020 and 2070 (c, f). Broken lines show ± one standard deviation around the mean. Species–habitat model results were used to rank suitable relocation sites according to the forecast habitat area. The model results are the average of 1000 stochastic simulations using RAMAS Metapop.

Model verification and validation

Since NPMs require a strong understanding of the population dynamics of the focal species as well as distributional data, uncertainty in estimates of important demographic parameters could potentially amplify model uncertainty in forecast species range movements under climate change. To address this issue, we recommend always undertaking a global sensitivity analysis to determine the relative influence of spatial and non-spatial parameters on model predictions. Latin-hypercube-sampling methods (Iman et al. 1981) can be used to ensure that sampled values cover the entire parameter space (Fordham et al. 2012c, Harris et al. 2012). Parameters identified as having a strong influence on forecast spatial distribution and total abundance (and underlying uncertainties in their estimate) can be used to evaluate whether the inclusion of a demographic component in the modelling process strengthens model predictions. If demographic parameters with high levels of uncertainty are primarily driving model predictions, it may be more parsimonious to opt for an ENM only approach (because model limitations will be more transparent) or to explore Bayesian approaches.

Although the importance of life-history traits on forecasts of species' range and abundance is often assumed on a priori grounds (Fordham et al. 2012b), external validation is still required to definitively know whether the inclusion of population dynamics information using NPMs helps improve the predictions of climate change effects on biodiversity. We suggest that this could be done by using historical distributions of well-studied taxa and comparing the ability of standard ENMs and NPMs to predict historical changes in range area and spatial pattern. The efficacy of ENMs have already been examined using this sort of approach (Araujo et al. 2005, Green et al. 2008, Macias-Fauria and Willis 2012). An alternative approach is space-for-time substitution, whereby models are developed in one region and projections are tested against data from another region (Randin et al. 2006, Segurado et al. 2006). Again, examples of such validation strategy can only be found for ENM.

Synthesis and conclusion

There are now a variety of approaches that incorporate demographic information into ENM output. The coupling of both approaches can be done either as a two-step process (Methods) or simultaneously (Pagel and Schurr 2012), with varying levels of complexity, ranging from simple dispersion models (Engler et al. 2009) to more complex models that include spatiotemporal demographic and physiological details (Anderson et al. 2009, Fordham et al. 2012a, Schurr et al. 2012) and, in some cases, one-way species interactions (Harris et al. 2012). Existing commercial (RAMAS GIS; Akcakaya 2005) and open source software (Nenzén et al. 2012) allows such type of analysis to be undertaken with relative simplicity.

There are also mechanistic biophysical models that either do not require any information about a species' distribution, or use this information for parameter calibration (Kearney and Porter 2009). Yet, a demographic model is needed to properly account for important metapopulation processes such as source-sink and density-feedback dynamics, extinction lags, and interacting effects of habitat fragmentation and demographic stochasticity (Dullinger et al. 2012, Fordham et al. 2012b). Predictions from ENMs provide a surrogate for species' carrying capacity (VanDerWal et al. 2009) which can then be used in NPMs. However, if biophysical responses between key demographic rates and spatiotemporally variant environmental drivers can be established explicitly, NPMs could, in theory, be generated without the correlative ENM component. For example forest landscape models, such as TreeMig, provide estimates of species biomass and patch structure from endogenous dynamics conditioned by exogenous drivers studies (Lischke et al. 2006). By removing the ENM component, uncertainties in ENM projections arising from statistical modelling technique and point location data (Peterson et al. 2011) are avoided. Nevertheless, more realistic results will only be produced if the functions linking survival and fecundity to environmental conditions are estimated from field data, thus incorporating the effect of species interactions in mediating these biophysical responses.

The usefulness of a given modelling approach is specific to the research question being asked (Dormann et al. 2012) and/or the species being modelled. For example, ENMs can be used to address the extinction of endangered species by identifying potentially suitable habitats for translocation (Fordham et al. 2012c). However, if the issue is to estimate future extinction risk for species in the face of changing climates, NPMs are need. This is because ENMs only estimate the empirical relationships between species' present-day distribution and environmental variables, and use the inferred relationships to identify potential distributional areas of the species under future climate scenarios (Araujo and Peterson 2012). Likewise, simple dispersal models (Engler et al. 2012) can reduce uncertainties in projections of species distributions under climate change scenarios (Engler and Guisan 2009), but they ignore the important effect of population size and trend in determining the actual number of emigrants and the probability of successful colonization of unoccupied patches. For situations that allow more incorporation of field data or life-history information, Bayesian 'range dynamics models' with priors derived from related species are a promising development that could help improve our theoretical understanding of range dynamics for species' with simple demographic characteristics (Schurr et al. 2012).

A strong driving motivation behind the development of NPMs has been to provide general guidelines for assessing the IUCN Red-List status of species potentially at risk (based on aggregations of many individual case studies), to better reflect the interactions of climate change with other threats such as habitat destruction, overexploitation and invasive species (Brook et al. 2009). NPMs are also strongly suited to management applications that seek to evaluate alternative management options under climate change, in terms of how effectively each one reduces extinction risks. Recent uses include developing optimal climate adaptation strategies focused on managed relocations (Fordham et al. 2012c, Regan et al. 2012), habitat restoration (Harris et al. 2012), responses to sea-level rise (Aiello-Lammens et al. 2011) and minimizing catastrophic events (Keith et al. 2008, Wintle et al. 2011). NPMs are also very useful for exploring the metapopulation processes underlying edge-of-the range shifts (Anderson et al. 2009) and within range spatial abundance patterns.

The drawbacks are that NPMs: 1) are more data intensive, requiring a robust understanding of the population dynamics of the focal species (as well as distributional data) for effective parameterization, so they will not be possible for the majority of the world's species; 2) are constrained, at least partially, by the predictive strengths of the underlying suitability model; and 3) generate predictions that will only be better than those from correlative ENMs if the demographic (or physiological) component of the model appropriately captures the ecology of the species. Thus, correlative ENMs, which are much simpler to parameterize and computationally less intensive than coupled approaches, might be better suited to some circumstances (see also Araujo and Peterson 2012).

Previously, descriptions of the merits of linking ENMs with population modelling have focused on the fundamental step of integrating dispersal and metapopulation dynamics into forecasts of species geographic range (Brook et al. 2009, Franklin 2010, Huntley et al. 2010). Here, we highlight three additional advantages of coupled ecological niche population models. We argue that these coupled methods should be used preferentially by conservationists and resource managers, where data availability permits, and conservation decisions require intervention, prioritization, or direct estimates of extinction risk. Moreover, a targeted approach, focused on case studies with extensive cross-system and cross-taxa contrast, should be used to develop general guidelines that better describe traits and conditions that make some species more vulnerable to climate change than others, and to identify management actions that best mitigate the influence of global warming.

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Supplementary material (Appendix ECOG-00147 at <www.oikosoffice.lu.se/appendix>). Appendix 1.