Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models

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Species responses to climate change may be influenced by changes in available habitat, as well as population processes, species interactions and interactions between demographic and landscape dynamics. Current methods for assessing these responses fail to provide an integrated view of these influences because they deal with habitat change or population dynamics, but rarely both. In this study, we linked a time series of habitat suitability models with spatially explicit stochastic population models to explore factors that influence the viability of plant species populations under stable and changing climate scenarios in South African fynbos, a global biodiversity hot spot. Results indicate that complex interactions between life history, disturbance regime and distribution patterns mediate species extinction risks under climate change. Our novel mechanistic approach allows more complete and direct appraisal of future biotic responses than do static bioclimatic habitat modelling approaches, and will ultimately support development of more effective conservation strategies to mitigate biodiversity losses due to climate change.

Keywords: population viability analysis; bioclimatic envelope; niche model; uncertainty; fynbos; fire

1. INTRODUCTION

Threats to biodiversity posed by the twenty-first century climate change create an imperative for assessments of extinction risk for planning species-level conservation. Species responses to climate change are likely to depend on interactions between population processes (Maschinski et al. 2006), between species (Araújo & Luoto 2007) and between demographic and landscape dynamics (Wintle et al. 2005). For example, Akçakaya et al. (2004) found that species persistence in a changing landscape depends on the balance between the rate of appearance and spatial arrangement of habitat patches, as well as the species’ capacity for reproduction and dispersal.

A common approach for predicting species’ responses to climate change involves use of habitat suitability (HS) models or ‘bioclimatic envelopes’. These models use present-day species–climate relationships (though they may also include non-climatic habitat predictors) to project potential distributions of species under future climates (Pearson & Dawson 2003). However, the predictions of species responses based solely on projected changes in the availability of suitable habitat are bound to be incomplete because they fail to account for important processes that influence extinction outcomes (Pearson & Dawson 2003; Akçakaya et al. 2006; Thuiller et al. 2008). Furthermore, shifts and contractions of suitable climates do not easily translate into extinction risks (Thuiller et al. 2004). Consequently, methodological problems have been identified in several recent attempts to infer extinction rates or levels of threat based solely on bioclimatic models (Buckley & Roughgarden 2004; Hampe 2004; Akçakaya et al. 2006).

Predictions may be made more accurate by developing models that incorporate interactions among habitat shifts, landscape structure and demography. Population viability models offer an explicit stochastic framework for such analysis (Maschinski et al. 2006; Saltz et al. 2006), yet spatial applications have not been developed to their full potential as a means of seeking generalizations about climate change impacts on large numbers of species. In this study, we developed a novel mechanistic synthesis of spatial dynamics and demographic processes. Our approach links dynamic HS models with spatially explicit stochastic population models to determine how variations in life history, disturbance regime and distribution patterns influence the viability of populations under stable and changing climate scenarios. We applied this approach to predict impacts of climate change on plant population viability in South African fynbos, one of the world’s biodiversity hot spots.

2. MATERIAL AND METHODS

(a) Habitat suitability models

Generalized additive models were constructed for 234 species using spatially explicit presence/absence records (1’ x 1’ spatial resolution) from the Protea Altas (Rebelo 2002) and spatial data for five climate and three substrate variables (see Midgley et al. 2003). Models were calibrated in BIOMOD (Thuiller 2003) using a random sample of the initial data (70%), stepwise variable selection and the Akaike information criterion to select the most parsimonious model. Each model was evaluated on the remaining 30% of the data using the area under the curve of a receiver operating characteristic plot. HS maps for the years 2000, 2030 and 2050 were derived from the models using the projected IS92a climate
A population exceeds the carrying capacity (survival and growth independently for particular life stages whenever dependence (DD) was implemented using a ceiling model to reduce dispersal, and environmental and demographic stochasticity. Density supplementary material). The models included recurring fires, seed studies of Cape Proteaceae and related species (see electronic in the core (Akc¸akaya & Root 2005 ) and parametrized using demographic history, evenness of density-dependence effects across life stages and fire regime (table S3 in the electronic supplementary material). EMA exhibited a similarly complex response (figure 2).

The most robust generalization emerging from our simulations was that species populations were more viable under 14-year mean fire intervals than under 8-year intervals. With few exceptions, EMA was approximately double under the less frequent fire regime, irrespective of climate change and other factors (figure 2).

Species with widespread but contracting distributions (pattern A) had the most marked decline in population viability under climate change (figure 2). While viability was reduced under climate change for both life-history types, longer fire intervals mitigated the impact more for the serotinous obligate seeder than for the myrmecochorous resprouter.

For the species exhibiting other patterns of distribution (B and C), complex interactions between life history, fire frequency and the determinants of carrying capacity governed differences in response to stable and changing climate scenarios. Figure 2 illustrates one example of these interactions. Relative to a stable climate scenario, climate change increased population viability under mean fire intervals of 8 years, but reduced viability under 14-year fire intervals. This interaction exists when K depends on HA only but not when it depends on both HS and HA.

The two life histories responded to climate change differently, depending on whether DD acted differentially across life stages. For the serotinous obligate seeder, populations were generally more viable when density-dependent impacts on growth and survival affected life stages evenly than if impacts were greater on seedling, juvenile and senescent stages, although differences were relatively small and there were several exceptions. For the myrmecochorous resprouter, the relationship tended to be reversed, with some exceptions.

3. RESULTS
Species responses to climate change exhibited complex dependencies on all factors examined. Two highly significant fourth-order interactions in the logit-linear model indicated that the probability of population decline under climate change was dependent on distribution pattern, life history, evenness of density-dependence effects across life stages and fire regime (table S3 in the electronic supplementary material). EMA exhibited a similarly complex response (figure 2).

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Responses to climate change were relatively unaffected by alternative models of dispersal for the wind-dispersed serotinous obligate seeder, suggesting that the levels of dispersal required to offset movement of bioclimatic envelopes are beyond the biologically plausible bounds of dispersal for these species. For distribution pattern (C), both long- and short-dispersal models produced zero dispersal probabilities between all present-day populations although viability for the other distributions was marginally improved when probabilities of long-distance movement were increased.

4. DISCUSSION
Our study demonstrates the feasibility of linking spatial and demographic dynamics, for species where both life-history and habitat requirements are well understood. Our population models are detailed, yet generic in the sense that they apply to relatively large groups of functionally similar species. With minor adjustments to parameter estimates, they can offer realistic representations for analysis of large numbers of species. Combined with already well-developed protocols for producing large ensembles of HS models (Araújo & New 2007), they offer a powerful mechanistic approach for assessing extinction risks posed by climate change. By addressing population mechanisms directly, our approach avoids assumptions that oversimplify the relationship between habitat change and extinction processes, such as those inferring rates of species loss from species-area patterns (Buckley & Roughgarden 2004; Thuiller et al. 2004).

Our results indicate that complex interactions between life history, disturbance regime and distribution pattern mediate whether particular species will be exposed to increased extinction risks under future climate scenarios. This underscores the need for methods that link spatial and demographic processes. In isolation, population and habitat models fail to deal with interactions and dependencies between small-scale population processes and landscape-scale habitat change. Coupled together (figure 1), they are more likely to produce projections that are both realistic and robust to uncertainty. This creates an imperative to improve quantitative understanding of

demographic processes in relation to climatic variation. Without reliable primary data, errors in the structure and parametrization of population models could compromise prediction of climate change impacts on species and hence management strategies for their conservation.

Our approach allows incorporation of several factors likely to exacerbate or mitigate the effects of climate change on species viability beyond those predicted by changes in available HA. These factors include spatial heterogeneity in species distributions (Shoo et al. 2005), interaction of range shifts with land-use change, isolation and barriers to dispersal, increased frequency of extreme weather events or fires and increased spatial correlation of population dynamics. In practice, the availability of data will determine which of these factors can be incorporated into extinction risk assessments.

In future work, our approach can be expanded to analyse a broader range of organisms and other climatic regions to seek robust generalizations about the susceptibility of species to global climate change. Our mechanistic approach will ultimately support the development of more effective conservation strategies to mitigate losses of biodiversity from global climate change.

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