

A metapopulation approach to predict species range shifts under different climate change and landscape connectivity scenarios



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ABSTRACT

Forecasting future species distributions under climate change scenarios using Ecological Niche Models (ENM) is common practice. Typically, these projections do not account for landscape connectivity and species dispersal abilities. When they do account for these factors, they are based on either rather simplistic or overly complex and data-hungry approaches. Here we apply a new approach for predicting species range shifts under different climate change and landscape connectivity scenarios that balances data requirements and output quality. The approach builds on the metapopulation concept to produce a dispersal model based on repeated simulations of stochastic extinction-colonization dynamics across multiple landscapes of variable connectivity. The model is then combined with an ENM to produce more realistic predictions of species range shifts under environmental change. Using the near-threatened *Cabrera vole* (*Microtus cabrerae*) as a model species and considering two contrasting climate change scenarios (B2 and A1b) and three scenarios of increasing landscape connectivity, we confirmed that model predictions based solely on ENM overestimated future range sizes (2050 and 2080) in relation to predictions incorporating both future climates and landscape connectivity constraints. This supports the idea that landscape change critically affects species range shifts in addition to climate change, and that models disregarding landscape connectivity tend to produce overly optimistic predictions, particularly for species with low dispersal abilities. We suggest that our empirically-based simulation modelling approach provides a useful framework to improve range shift predictions for a broad range of species, which is essential for the conservation planning of metapopulations under climate and landscape change.

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1. Introduction

Ecological niche models (ENMs) based on climate envelopes are widely used to predict species' current geographical ranges and their potential shifts in response to climate change. These models provide useful information for assessing the overall conservation status of a species and for supporting conservation decision making (Peterson et al., 2011). However, a range of uncertainties related to the choice of the statistical model, variable selection,

model range and emissions scenarios may influence the results of ENMs (Araújo and Guisan, 2006; Heikkinen et al., 2006; Pearson et al., 2006; Beaumont et al., 2008; Synes and Osborne, 2011). While increased emphasis has been given to the validation of statistical models and the development of ensemble approaches to account for such uncertainties (Araújo and New, 2007), ENM forecasts are still criticized for the assumptions made about dispersal, which range from unlimited to no dispersal (Heikkinen et al., 2006; Sinclair et al., 2010; Travis and Dytham, 2012). A further limitation of most ENM-based projections is that they generally ignore how landscape connectivity within climatically suitable areas may affect the way species modify their distribution ranges (Opdam and Wascher, 2004). It is thus likely that ENMs incorporating both dispersal limitation and landscape connectivity should provide more

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accurate and realistic predictions of species range shifts under both climate and landscape change. However, illustrative examples integrating these two factors are still largely lacking (e.g. Wilson et al., 2010; Bennie et al., 2013), probably because there is still no solid conceptual framework for linking processes operating at the landscape scale with distribution patterns over large (geographical) spatial scales.

Dispersal is a critical process determining species' spatial dynamics, which restricts species ranges to at least some extent by preventing individuals from colonizing suitable climate spaces, particularly in the case of species with metapopulation dynamics in landscapes with low connectivity (Opdam and Wascher, 2004; Anderson et al., 2009). However, evaluating how species track changes in climatic suitability is challenging because of species traits and landscape complexity and variability (Synes et al., 2016). There are a number of approaches of variable complexity and specific data requirements to account for limited dispersal in ENMs. The simplest and most straightforward approaches assume a fixed migration rate for the focal species, often based on expert opinion and literature (e.g. Williams et al., 2005). Although these approaches are easy to implement, they generally disregard the spatial processes that drive real dispersal patterns. To solve this problem, alternative approximations involve species-specific dispersal kernels, which imply more intensive experimental and/or field work (Barbet-Massin et al., 2011). However, most illustrative examples combining ENMs with dispersal models still ignore landscape connectivity, though dispersal is known to depend strongly on landscape configuration and composition (Travis and Dytham, 2012). More complex models incorporating connectivity metrics together with local demography in an individual-based framework have also been proposed (e.g. Engler et al., 2012; Bocedi et al., 2014), but they typically require a large amount of data that are not available for most species. There is therefore a need for practical solutions that efficiently combine spatially explicit dispersal models (SEDMs), integrating information on landscape connectivity with ENM-based predictions of species ranges under future climates (Franklin, 2010; Naujokaitis-Lewis et al., 2013).

Here we introduce a novel approach to achieve this goal, which is based on simulations of metapopulation dynamics and does not require detailed demographic data. The metapopulation concept provides a useful framework for testing how the effects of local extinction-colonization dynamics along species' range margins may influence the rates of species range expansion into suitable climate spaces over large spatial scales (Anderson et al., 2009; Wilson et al., 2010). Although the assumption of stochastic quasi-equilibrium dynamics may not hold in the range margins of a metapopulation, metapopulation models can still have considerable predictive power in non-equilibrium systems, and may be particularly useful in understanding species responses to climate and landscape change (Thomas and Hanski, 2004). Even species that do not form recognizable metapopulations may show metapopulation-like features along range margins, and consequently the metapopulation framework can be used to assess how quickly species track their changing environment, and thus be used to scale up landscape-level dynamics to geographic distributions and range dynamics (Thomas and Hanski, 2004; Anderson et al., 2009). In particular, stochastic patch occupancy models (SPOMs), such as the Incidence Function Model (IFM), provide an excellent opportunity for generating SEDMs from observed patterns of occupancy, which may then be coupled with correlative models of climate suitability (Wilson et al., 2010).

Based on these ideas, our approach involves a three-step procedure (see Fig. 1): i) develop an SEDM derived from IFM simulations of metapopulation dynamics under plausible scenarios of landscape connectivity; ii) build an ENM based on climate variables and ensemble forecasting; and iii) combine these two models to

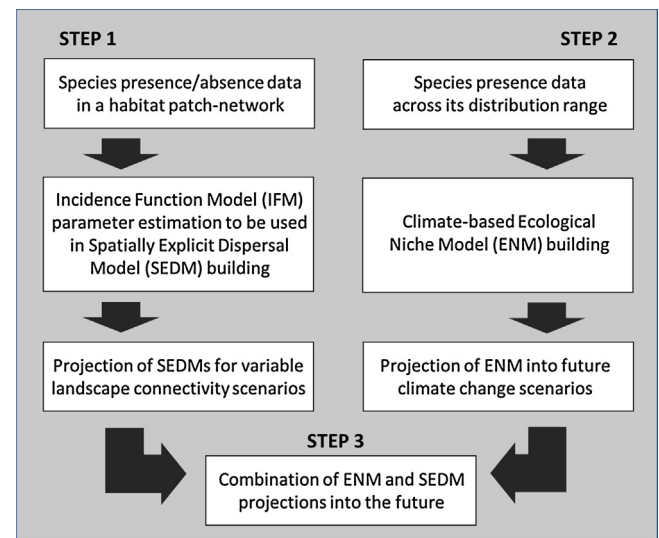


Fig. 1. General framework describing the three main steps of our approach for predicting the future geographic distribution ranges of metapopulations under alternative climate and landscape connectivity scenarios.

forecast species distribution ranges while accounting for both climate and landscape effects (Mestre et al., 2016). We describe the innovative nature and outputs of our framework by modelling range shifts of the globally near-threatened Cabrera vole (*Microtus cabreræ*), a species confined at present to four geographical regions within the Iberian Peninsula (Fig. 2) (Garrido-García et al., 2013). The Cabrera vole was considered a suitable model because it has metapopulation-like structure and dynamics, with individuals occupying patches of tall wet herbaceous habitats surrounded by a largely unsuitable matrix (Pita et al., 2007). Habitat loss and fragmentation due to agricultural intensification have been identified as main threats to extant populations, compromising landscape connectivity for the species (Pita et al., 2014). On the other hand, previous research has shown that Cabrera voles have been highly sensitive to climate variations in the past (Laplana and Sevilla, 2013; Barbosa et al., 2017), while preliminary niche modelling pointed out a strong vulnerability to future climate changes (Araújo et al., 2012; Mestre et al., 2015).

2. Methods

2.1. Metapopulation model

The metapopulation dynamics of the Cabrera vole were specified using the IFM (Hanski, 1994). The IFM describes the processes of occupancy of a patch as a first-order Markov chain with two possible states (occupied or empty), producing changes in local populations at discrete time intervals as the result of colonization and extinction events (Hanski, 1999). The probability of a patch being occupied is given by $J_{i,t} = C_{i,t} / (C_{i,t} + E_i)$, where $C_{i,t}$ is the colonization probability at time t when patch i is empty, and E_i is the constant extinction probability per unit time when patch i is occupied (Hanski, 1994). In our study these probabilities were given as, respectively:

$$C_{i,t} = S_{i,t}^2 / (S_{i,t}^2 + y^2)$$

$$\begin{cases} E_{i,t} = e/A_i^\alpha \text{ if } A_i > e^{1/\alpha} \\ E_{i,t} = 1 \text{ if } A_i \leq e^{1/\alpha} \end{cases}$$

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