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Synergistic effects of climate change and habitat fragmentation on species range shifts and metapopulation persistence

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Abstract. The effects of climate and landscape change on biodiversity are relatively well described. However, there is limited understanding of the interactions between these processes, which generally operate at differing spatial scales. My objective was to evaluate the synergistic effects of climate and landscape changes on persistence and range shift dynamics. The model species was the Cabrera vole, *Microtus cabreræ*, a habitat specialist with limited dispersal ability. The present study demonstrated that, as a result of the combined effects of climate and landscape change, this species' future potential distribution will be considerably reduced. The combined effect of climate change and landscape connectivity was assessed using the software MetaLandSim, a newly developed package, with a good balance between data requirements and output quality, allowing researchers to account for connectivity and dispersal in range forecasting. With this R package, the species' metapopulational dynamics could be simulated at the landscape scale, and range expansion for different connectivity scenarios could be computed.

Keywords. Climate change, ecological niche modelling, landscape change, metapopulation persistence, *Microtus cabreræ*, range shift

Introduction

Climate change raises considerable concerns for biodiversity conservation. The main effects on biodiversity include range shifts and contraction, changes in phenologies, and/or disruptions to ecological networks (Parmesan 2006, Parmesan and Yohe 2003, Walther et al. 2002). In addition, landscape modification by humans is a major factor in biodiversity reduction worldwide (e.g., Fahrig 2003, Lindenmayer and Fischer 2006). Both threats are expected to be particularly damaging for habitat specialists with poor colonization and dispersal abilities (Jiguet et al. 2007, Schloss et al. 2012, Pacifici et al. 2017).

Quantifying the joint impacts of climate and landscape change can be achieved by combining spatially explicit dispersal models (SEDMs) with predictions of future potential distributions ob-

tained from Ecological Niche Models (ENMs; Franklin 2010, Naujokaitis-Lewis et al. 2013). Earlier work looking into the interplay between landscape and climate change by Travis (2003) suggested that there are essentially two distinct thresholds below which species go extinct, one related to habitat availability, and the other related to the rate of climate change. Because the position of the second threshold is influenced by the amount of available habitat, the two processes are connected in the probability of species extinction. Opdam and Wascher (2004) confirmed this idea by also identifying two thresholds: one where the level of fragmentation still allows persistence and range expansion at slow rates, and another above which the expansion of the range is inhibited. Hof et al. (2011) go further, by demonstrating that the crucial difference between current and

past species response to climate change is habitat loss and fragmentation, which reduce landscape connectivity and genetic variability (with negative impacts for phenotypic plasticity), and diminishes the potential for the creation of suitable microclimatic habitat pockets. Clearly, understanding how the interaction of climate and landscape change may impact species requires due consideration of their dispersal and local extinction-colonization dynamics (Parmesan and Yohe 2003, Anderson et al. 2009). However, existing approaches relating these traits with species persistence and expansion potential under climate and landscape change are not straightforward, and usually require considerable biological or ecological data that are not available for most species (Mestre et al. 2016).

Here I have developed a novel approach considering the effect of species dispersal ability and landscape connectivity in the projections of future potential range, which requires less information on the species and landscape traits than previous approaches (see Mestre et al. 2016). However, the methodology still provides a valuable insight into species range expansion. For this, I developed the *MetaLandSim* R package, and illustrate the approach using the 'near-threatened', Iberian endemic Cabrera vole, *Microtus cabreræ*, as a model species. This species is endemic to the Iberian Peninsula (Fig. 1), it is restricted to wet herbaceous habitat patches (Fernandes et al. 2008, Pita et al. 2014) and has limited dispersal ability (Pita et al. 2014). It is an ideal model to evaluate the combined effects of climate and landscape change considering that it is a habitat specialist with presumed low dispersal ability (Pita et al. 2014). The approach is based upon modelling metapopulational dynamics in landscape units, by simulating species extinction and colonization in a patch network. Then, by allowing these landscape units to be sequentially colonized, it effectively upscales processes occurring at the landscape scale to the biogeographical scale (as suggested by Opdam and Wascher 2004).

The main objective of this work is to present an approach to assess the combined effects of climate and landscape change on species range,

illustrating the method with the case of the Cabrera vole and describing the main features of the package.

Methods

Range projection for the Cabrera vole

Initially I used the ensemble modelling framework with the BIOMOD R package (Thuiller and Lafourcade 2010) to approximate the realized ecological niche of the Cabrera vole, projecting it into future years (2020, 2050 and 2080) under two IPCC climate change scenarios (A1b and B2). To evaluate the models, I used the standard procedure of splitting each dataset into calibration and evaluation subsets (70–30%) in a multiple cross validation. This data splitting procedure was repeated five times. Projection was done with a four-step process to ensure that the current distribution of the species is the geographic expression of the ecological niche: (a) produce an ENM based on the previously published species occurrences, ENM1; (b) use the output of ENM1 as a guideline for field surveys evaluating the species presence at the potential range margins (defined by the model); (c) confirm the species identity with genetic analysis; and (d) run a second ENM (ENM2) using the dataset in ENM1 and the newly obtained field data. Field sampling, to evaluate species occurrence, was carried out on the Portuguese side of the species range in 40 grid squares (each 100 km²), half from areas given as suitable by ENM1 and the others from areas considered unsuitable. The species occurrence was evaluated in ten sites in each grid square.

The projection of an ENM implicitly assumes infinite dispersal ability and no constraints related with lower landscape connectivity. To account for both climate and landscape connectivity, I developed and used a new simulation tool, the R package *MetaLandSim* (Mestre et al. 2016, Mestre et al. 2017b). This package simulates range expansion, restricting the ENM projections to accessible regions in a given time period. The range expansion of the Cabrera vole was simulated for three landscape connectivity scenarios, each defined by the percentage of habitat in the total landscape: high, medium and low connectivity using as a reference real habitat networks typical of the focal

species (e.g., Pita et al. 2014). The steps followed in MetaLandSim are as follows: the species metapopulation dynamics are simulated in a first landscape unit using the Incidence Function Model (IFM, Hanski 1994) and, when a transition rule is satisfied (see Mestre et al. 2017b for details), the species is allowed to colonize the adjacent landscapes (which is a random realization of the same landscape parameters). In this newly colonized landscape unit the metapopulation dynamics are also simulated using the same IFM, until the species colonizes the next landscape. This process, is repeated until all the time steps in the simulation are consumed. The iteration of the process enables users to combine species colonization distances with the specific probabilities characteristic of that particular landscape, creating a Spatially Explicit Dispersal Model (SEDM). This SEDM is then applied to the current distribution of the species producing a geographic projection of ‘accessibility’.

The IFM parameters for the Cabrera vole were estimated by means of a Bayesian approach (based upon Risk et al. 2011) using a presence/absence dataset from one metapopulation of the

species (see Mestre et al. 2017b for details). Finally, the SEDM was combined with the ENM output. This enables the upscaling of metapopulation landscape-level dynamics to range-scale simulations of range expansion.

The MetaLandSim R Package

The package MetaLandSim was developed to address the challenges of combining large spatial and temporal scales in biogeography and landscape ecology, which rarely allow a traditional experimental approach (Peck 2004, Zurell et al. 2009). It works on two scales: (i) landscape – evaluating species persistence in dynamic landscapes (Fig. 1A,B), and (b) biogeographical – simulating range expansion in a diversity of connectivity scenarios, as describe in Figure 1C,D.

At the landscape scale all the simulations are run within a graph-like landscape unit with characteristics (structure and dynamics) defined previously by the user. IFM species parameters should also be estimated in order to derive the species persistence in a series of landscape scenarios. The user can choose the dispersal kernel, connectivity, colonization and extinction functions

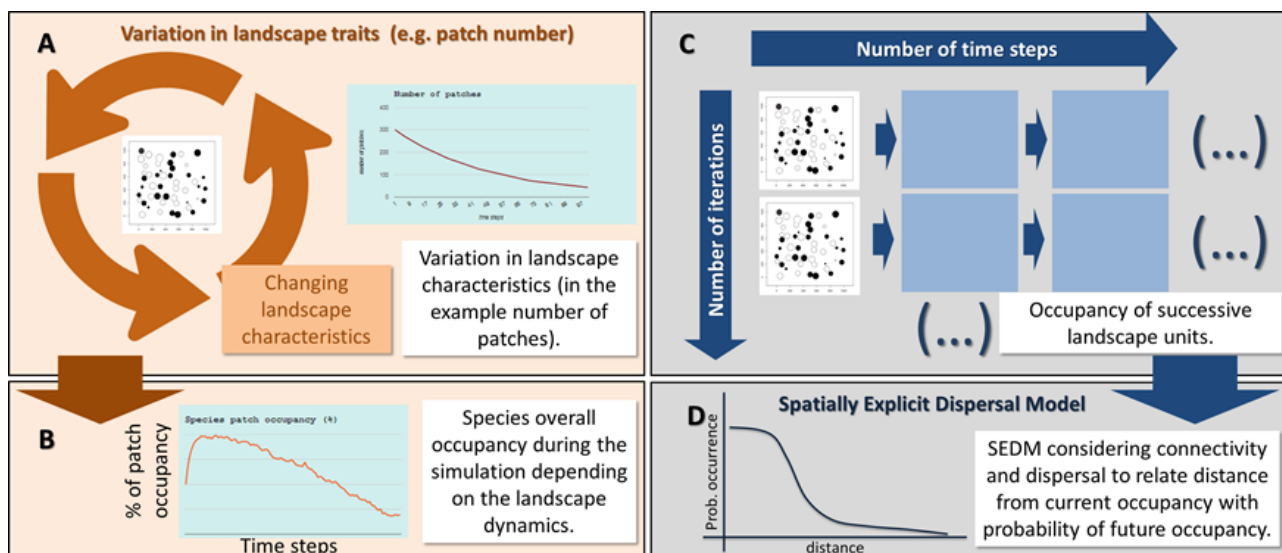


Figure 1. MetaLandSim simulations: At the landscape scale (panels **A** and **B**) the software resorts to the IFM to simulate metapopulation dynamics in a landscape unit (**A**) with changing characteristics (in this case a decreasing number of habitat patches at each time step as shown in the graph). As output MetaLandSim provides the species occupancy throughout the simulation. In this case, the occupancy as the landscape loses a given percentage of its habitat patches at each time step (**B**). At the biogeographical scale (panels **C** and **D**), MetaLandSim simulates the dynamics of the metapopulation inside each landscape unit and allows the colonization of the next landscape unit until all the time steps are spent. This process that should be repeated (**C**) producing an output, the Spatially Explicit Dispersal Model (SEDM), that relates species probability of occurrence with distance from nearest current presence (**D**).

that are best suited to each case (see user manual, Mestre et al. 2017a).

Results and discussion

The fieldwork identified 19 new presences, increasing the global range of the Cabrera vole by 4.84% and its Portuguese range by 15%. These new occurrence data in conjunction with the dataset from ENM1 were used to calibrate ENM2. Both models, ENM1 and ENM2, revealed a tendency for reduced suitability and future fragmentation of the range and became more different as the projections advanced into the future (Fig. 2).

However, these projections assumed infinite dispersal, a common simplifying approach in many modelling studies despite evidence that accessibility can reduce the potential future distribution of a species (Mestre et al. 2017b for details and discussion). Species dispersal ability and landscape connectivity are also relevant considering that range shifts are mediated by dispersal to new areas and extinctions occur in 'unsuitable' areas (Anderson et al. 2009). After accounting for dispersal and connectivity (Mestre et al. 2017b), the results showed that landscape connectivity, combined with the species reduced dispersal ability, as given by the SEDM, would further limit the potential range in the future (Fig. 3).

The ability to spatially upscale the landscape metapopulation dynamics to the biogeographic scale, allows the user to evaluate how habitat fragmentation and climate change affect species range. By using MetaLandSim, I showed that the future potential range of the Cabrera vole will be more restricted and fragmented than its current range. Furthermore, I only detected a negligible northward shift, unlike that reported for most species in the literature so far (Walther et al. 2002).

In addition to providing concrete information concerning the effect of climate change and landscape connectivity on the future range of a particular species, this work provided an innovative methodology to combine the effects of landscape connectivity and ecological niche more effectively. It is an explicit approach concordant with the view that methods should be kept as sim-

ple as possible in order to better understand the underlying effects. Often, if the model is too complex, there is the risk of multiplying uncertainties and not identifying the underlying process. Furthermore, this approach provides a good balance between data requirements and robustness of the method, while giving the user more explicit control.

Thesis and software availability

Thesis: <https://dspace.uevora.pt/rdpc/handle/10174/21118>

MetaLandSim: <https://cran.r-project.org/web/packages/MetaLandSim/index.html>

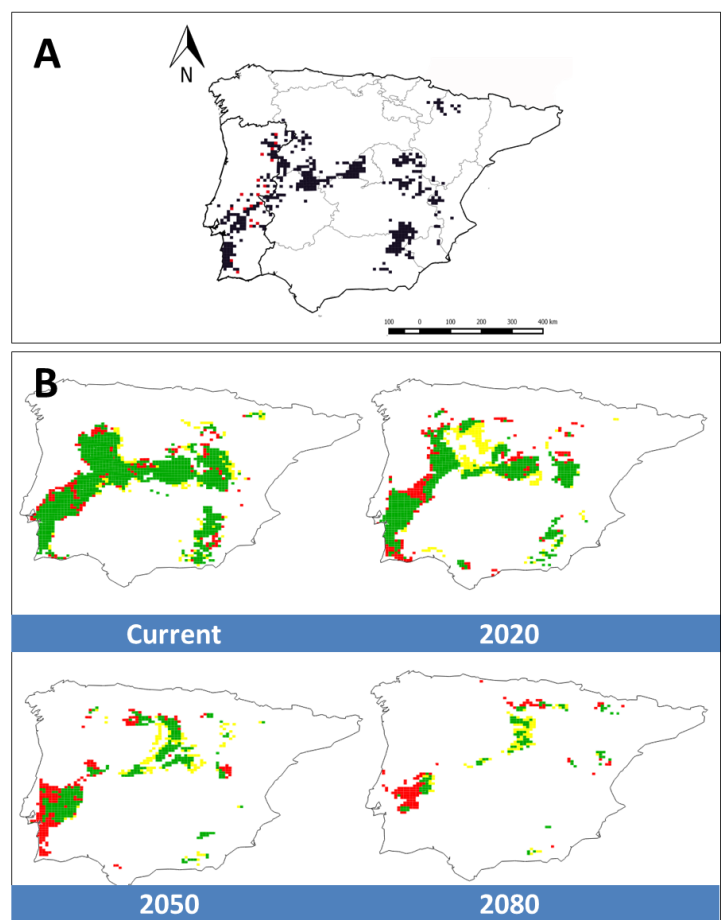


Figure 2. (A) The range of the Cabrera vole (black: previously published dataset; red: new occurrences resulting from field work). (B) Comparison of the results for ENM1 (based on published data only) and ENM2 (which includes the published and new occurrences) under the climate change scenarios A1b (scenario B2 in Mestre et al. 2015 and Mestre 2017). Light grey square grids: potential presence given only by ENM1. Medium grey square grids: potential presence given by ENM1 and ENM2. Dark grey square grids: potential presence given only by ENM2.

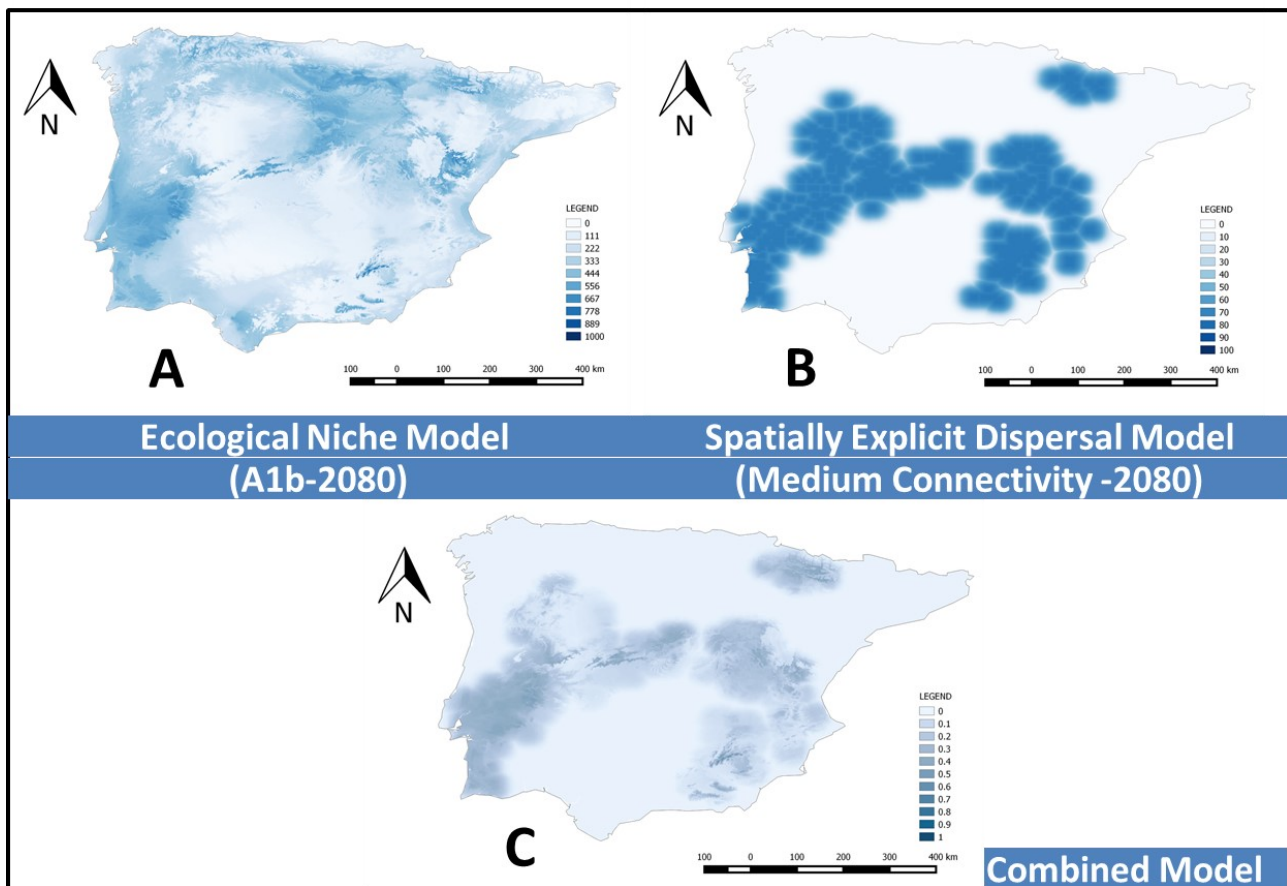


Figure 3. Example of the integration of Ecological Niche Models (ENMs) with Spatially Explicit Dispersal Models (SEDMs) to project the potential future distribution of the Cabrera vole. (A) ENM of the climate change scenario A1b in 2080, which considers ecological niche requirements only. (B) SEDM of medium connectivity in 2080, which incorporates dispersal limitations and landscape characteristics. (C) Combined Model. Additional results in Mestre et al. (2017b) and Mestre (2017).

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