



Short communication

An R package for simulating metapopulation dynamics and range expansion under environmental change

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ABSTRACT

The metapopulation paradigm is central in ecology and conservation biology to understand the dynamics of spatially-structured populations in fragmented landscapes. Metapopulations are often studied using simulation modelling, and there is an increasing demand of user-friendly software tools to simulate metapopulation responses to environmental change. Here we describe the MetaLandSim R package, which integrates ideas from metapopulation and graph theories to simulate the dynamics of real and virtual metapopulations. The package offers tools to (i) estimate metapopulation parameters from empirical data, (ii) to predict variation in patch occupancy over time in static and dynamic landscapes, either real or virtual, and (iii) to quantify the patterns and speed of metapopulation expansion into empty landscapes. MetaLandSim thus provides detailed information on metapopulation processes, which can be easily combined with land use and climate change scenarios to predict metapopulation dynamics and range expansion for a variety of taxa and ecological systems.

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Software availability

Name of software: MetaLandSim.

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E-mail: mestre.frederico@gmail.com;Availability: <https://cran.r-project.org/web/packages/MetaLandSim/index.html>Installation: Select the repositories CRAN and Bioconductor (BioC software), then type: `install.packages("MetaLandSim", dependencies = TRUE)`.

1. Introduction

The populations of many species are spatially-structured, with subpopulations occupying local habitat patches and interacting via dispersal (Hanski, 1999). Much effort has been devoted to understand and predict the dynamics of such populations, leading to the development of a metapopulation paradigm whereby local subpopulations are subject to chance extinction and the proportion of patches occupied depends on extinction and colonization rates (Armstrong, 2005). Building on this paradigm, a wealth of theoretical and empirical studies have explored how metapopulation dynamics (i.e., temporal variation in patch occupancy) is affected by, for instance, species-specific dispersal and colonization abilities, and landscape-level properties such as the size, number and spatial distribution of patches, as well as matrix permeability (Etienne et al., 2004; Hanski, 1999; MacPherson and Bright, 2011). More recently, studies have addressed the consequences of landscape dynamism (i.e., temporal variation in landscape features), resulting from the destruction and recovery of patches due for instance to land use changes and vegetation succession (Wahlberg et al., 2002; Verheyen et al., 2004; DeWoody et al., 2005). Also, a few studies

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upscaled metapopulation processes to regional and biogeographical scales, thus providing a basis to forecast range shifts in relation to large scale drivers such as climate change (Anderson et al., 2009; Schippers et al., 2011). Overall, this research has greatly increased our understanding of metapopulation ecology, though progress has been slowed by considerable difficulties in collecting empirical data at appropriate spatial (patches to continents) and time (years to decades) scales needed to test theoretical predictions and to develop realistic management and conservation prescriptions (Ims, 2005).

Simulation modelling provides an opportunity to offset the paucity of empirical data, making it possible to explore metapopulation responses to environmental change under fully controlled and replicated conditions (eg. Wahlberg et al., 2002; Blanquart, 2014). Because of this, a large number of simulation models have been developed over the years, encompassing different levels of realism and complexity, some of which including detailed demographic models of each subpopulation (e.g., Hernández-Matías et al., 2013) or even tracking each individual in space and time (Schippers et al., 2011). However, the most popular class of metapopulation models are probably the stochastic patch occupancy models (SPOMs), which achieve a favourable balance between empirical data requirements and the capacity of generalization across a large number of taxa and ecological contexts (e.g. Grimm et al., 2004; Hanski, 1999; MacPherson and Bright, 2011). Starting from a landscape with n habitat-patches that can be either occupied or unoccupied (i.e. 2^n potential occupancy patterns), SPOMs simulate patch occupancy at any time in the future, based on Markov chains, and using a relatively sparse set of parameters affecting the functional forms of local extinction and colonization (e.g. Moilanen, 1999; Etienne et al., 2004; see Supplementary Material #1, Table SM1). SPOM parameters are easily estimated from empirical patch occupancy data (Hanski, 1994; Hanski, 1999). These parameters may then be used to simulate occupancy under any landscape scenario (e.g. Hanski, 1999), and sensitivity analyses

can be performed to evaluate the susceptibility of simulation outputs to variations in model parameters (Moilanen, 2000).

Despite their value, existing software packages to implement SPOMs are limited to fully explore the effects of environmental change on metapopulation dynamics (Supplementary Material #1, Table SM2A). A key limitation is the lack of efficient tools to deal with landscape dynamics, though this has been increasingly recognized to significantly affect metapopulations (e.g. Verheyen et al., 2004). Specifically, no package currently available offers the possibility to simultaneously: i) generate random landscapes; ii) simulate landscape change over time; iii) implement patch occupancy models on varying scenarios of landscape change; and iv) compute connectivity metrics at each time step. Another important limitation is that extant packages assume a constant size and geographical position of the landscape occupied by the metapopulation, thereby hindering the possibility of modelling metapopulation expansion to neighbouring landscapes where habitat becomes available due for instance to land use or climate changes. This is an important drawback, because modelling the pattern and speed of expansion would be essential to combine processes occurring at the landscape and regional scales, and thus using the metapopulation paradigm to forecast species range shifts (Wilson et al., 2010; Schippers et al., 2011). For instance, information on expansion speed might be used to evaluate whether metapopulations can track moving windows of climatic favourability through different fragmented landscapes (Schippers et al., 2011), or it might be used to quantify dispersal limitations when predicting species range shifts under future climatic conditions (Barbet-Massin et al., 2012; Lawler et al., 2010; Travis and Dytham, 2012). Although software is available to simulate species range shifts while accounting for dispersal limitations, the packages rarely consider metapopulation processes and often require data that is unavailable for most species (Supplementary Material #1, Table SM2B).

Here we describe the new MetaLandSim R software package,

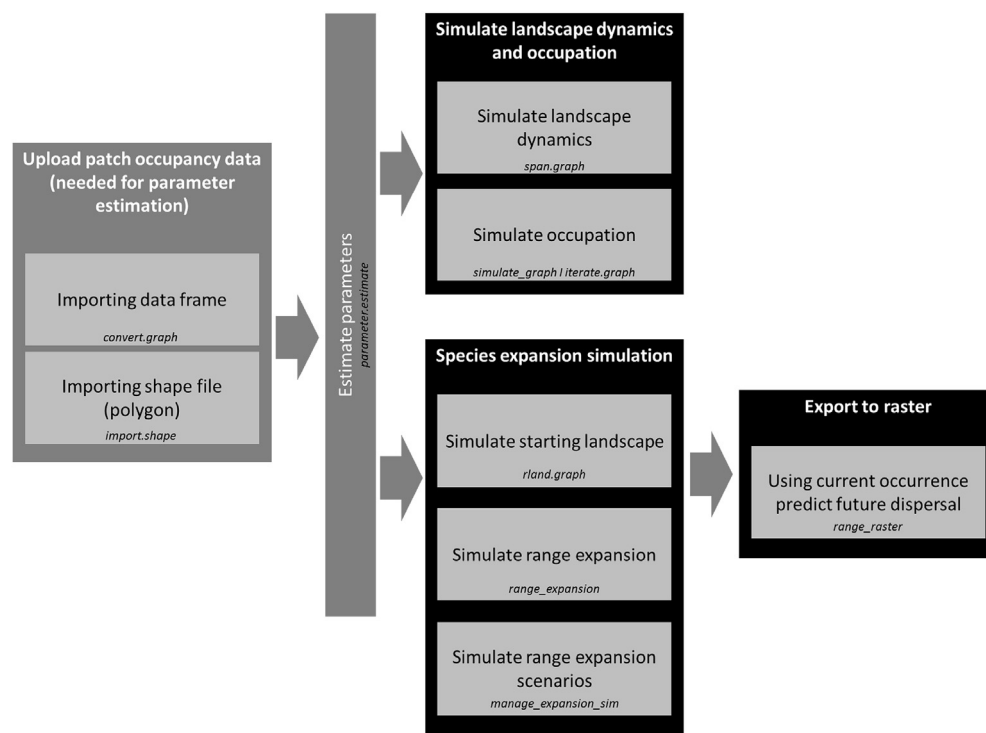


Fig. 1. General workflow of MetaLandSim package. Main functionalities are shown in the grey boxes and functions in italics.

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