



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

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Tese apresentada à Universidade de Évora
para obtenção do Grau de Doutor em Biologia

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ÉVORA, JUNHO DE 2017



*The works conducting to this thesis had the financial support of **FCT – Fundação para a Ciência e Tecnologia** (PhD fellowship ref. **SFRH/BD/73768/2010**) through the program **POPH/FSE - Programa Operacional Potencial Humano/Fundo Social Europeu**.*



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MINISTÉRIO DA CIÊNCIA, TECNOLOGIA E ENSINO SUPERIOR

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Agradecimentos

A arte e a ciência advêm de características intrinsecamente humanas, somos um animal curioso, engenhoso e imaginativo. Eu faço parte daqueles que, tentam encontrar respostas através da ciência alimentando esta curiosidade que nos caracteriza. No entanto não faço este caminho sozinho, tenho sempre contado com a ajuda e colaboração de colegas, amigos e família. Não gosto de escrever este tipo de textos, mais pessoais, mas estas pessoas acompanharam-me e contribuíram para que eu trouxesse este trabalho até ao fim, naqueles que foram os anos mais recompensadores a nível profissional até à data.

Contei com a orientação científica dos Drs. António Mira, Pedro Beja e Ricardo Pita. Sem dúvida uma combinação de talentos e conhecimento perfeita para a conclusão com sucesso deste trabalho. O António Mira contribuiu com o seu conhecimento aprofundado da espécie que usei como modelo, o Pedro Beja trouxe uma enorme visão estratégica e um perfeito enquadramento científico das questões tratadas e o Ricardo Pita ajudou-me a estruturar as minhas ideias (e artigos) através do debate constante das várias opções, o que me permitiu progredir. Agradeço também ao ICAAM (Instituto de Ciências Agrárias e Ambientais Mediterrânicas) e ao CIBIO/InBIO - Pólo de Évora (Centro de Investigação em Biodiversidade e Recursos Genéticos), os centros de investigação onde estive inserido durante a realização do doutoramento, e à Fundação para a Ciência e Tecnologia por ter financiado este trabalho ao abrigo de uma bolsa de doutoramento. Estou também grato à Fundação Luso-Americana para o Desenvolvimento pela ajuda financeira para uma deslocação aos Estados Unidos para apresentar uma comunicação que se viria a tornar no quarto capítulo da tese.

Para a elaboração deste trabalho contei com a colaboração das equipas dos projectos PERSIST e NETPERSIST, nomeadamente Helena Marques, Inês Leitão, Pedro Costa, Vânia Salgueiro, Cláudia Encarnação e Paulo Alves (estou particularmente grato à Inês, ao Pedro, à Vânia e ao Paulo que colaboraram no trabalho de campo). Também incluídas nas equipas destes projetos, devem ser mencionadas as colaborações da equipa de genética do CIBIO da Universidade do Porto, particularmente o Paulo Célio Alves, Joana Paupério e Filipa Martins. Ainda no que diz respeito ao primeiro artigo (segundo capítulo), estou também grato aos colegas que me facultaram dados de ocorrência de rato-de-Cabrera nas suas respectivas áreas de estudo.

A elaboração do *software* MetaLandSim (terceiro capítulo) contou com a importante colaboração de Fernando Cánovas Garcia (CCMAR - Universidade do Algarve). Quando me lancei à tarefa de fazer um package para o R não sabia bem o que me esperava. Foram longas horas a escrever código, e a resolver problema atrás de problema e dúvida atrás de dúvida (e várias vezes pensei “Porquê?!”). O Fernando foi importante neste processo contribuindo, sem dúvida, para um melhor resultado final.

Durante a execução das simulações para o terceiro e quarto artigos (quarto e quinto capítulos desta tese, respectivamente) contei com a importante colaboração do Bruno Silva (CIBIO-UE), que facilitou, sem dúvida, o meu trabalho otimizando o processo, tornando-o mais rápido e eficiente.

Agradeço ainda a fugaz, mas importantíssima, colaboração do Benjamim Risk (Statistical and Applied Mathematical Sciences Institute e University of North Carolina) na estimativa de parâmetros que tornaram possíveis as simulações do quarto artigo (quinto capítulo).

A contribuição de colegas e amigos, com quem fui debatendo as minhas ideias, e a quem pedi muitas vezes opiniões foi também um apoio importante (Sérgio Godinho, Diogo Alagador, Márcia Barbosa).

Uma palavra especial à família de onde nasci. Aos meus pais, Lucinda e Manuel, que viram este trabalho avançar, orgulhosos do seu filho e dos seus progressos (como convém a qualquer pai), que me foram aliviando os aborrecimentos e controlando as euforias. O meu pai, em particular, que já não me acompanhou até ao fim deste percurso, foi sempre um apoio incondicional. Aos meus irmãos, Hugo e Guilherme, ambos apaixonados pelas humanidades (o que eu não lhes levo a mal) e que me apoiam com a sua amizade; à minha avó, Lucinda, que nunca fez a mínima ideia qual é o meu trabalho, mas que me apoia sempre e aos restantes avós, Frederico, Luísa e Manuel, que não estão fisicamente presentes, mas que vivem na minha memória, pelo exemplo que foram e a amizade que me deram.

Finalmente, agradeço também à família que ajudei a nascer. À Luísa tenho de reservar um agradecimento muito especial: foi ela a primeira a ouvir-me quando eu me aborrecia ou quando encontrava um novo obstáculo mas (e não é menos maçador) foi ela que me ouviu também quando um artigo era aceite ou quando transpunha um “obstáculo”. Em ambas as situações eu reconheço que sou “intenso”. Sempre, com a paciência possível, foi-me ouvindo divagar sobre modelos, simulações, metapopulações e alterações climáticas. Por fim um agradecimento muito especial a uma menina que, quando comecei o doutoramento, não existia na minha vida: a minha filha Mariana. A nossa vida divide-se em antes e depois de Mariana: ela revolucionou as nossas vidas, tal qual um Che Guevara de fraldas. O apoio da Mariana advém da sua alegria constante, as suas cantigas e danças, talentos que a genética tem dificuldade em explicar, são uma fonte de energia e paz. O amor dela é especial porque é simples, puro e intenso.

Agradeço a todos!

São Bartolomeu de Messines, 6 de Dezembro de 2016



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

Abstract

The effects of climate and landscape change on biodiversity have been widely acknowledged. However, there is still limited understanding on how the interaction among these processes affects species persistence over large spatial scales. This thesis aims to study the synergistic effects of climate and landscape change on species persistence and range shift dynamics. Using the Cabrera vole as model species, and combining ecological niche modeling (ENM), non-invasive genetic analysis and field sampling at predicted range margins, it is shown that forecasting range shifts of metapopulations under climate change, should require detailed sampling at the extremes of the ecological niche and that combining these three techniques allows an effective assessment of the niche. Analysis of metapopulation persistence and range expansion under landscape and climate change involved the development of an R package, 'MetaLandSim'. This package offers a set of simulation tools integrating concepts from metapopulation and graph theories, providing an opportunity for testing ecological theories and evaluating species responses to environmental change. A first example of the package use is demonstrated by combining ENM projections with dispersal models (DM) considering three different connectivity scenarios. It is clearly demonstrated that combining range shift with lower connectivity will result in narrower range sizes for the Cabrera vole, highlighting the relevance of both, climate change and landscape connectivity in range dynamics evaluation. Finally, 'MetaLandSim' was used to test the hypothesis that intermediate levels of landscape disturbance may increase species persistence under certain species and landscape traits. Using a set of 54 virtual species differing in their ecological traits, it is shown that species with mid to higher dispersal and early successional preferences were more likely to benefit from intermediate disturbance. Overall, this study provides important insights for improving predictions on metapopulation persistence and range dynamics under various scenarios of landscape and climate change.

Keywords

Metapopulation persistence, ecological niche modelling, landscape change, climate change, range shift.

Efeitos sinérgicos das alterações climáticas e fragmentação de habitat na distribuição das espécies e persistência metapopulacional

Resumo

Os efeitos das alterações de paisagem e climáticas são reconhecidos na literatura científica. Esta tese tem por objetivo contribuir para a clarificação e compreensão dos efeitos sinérgicos das alterações climáticas e de paisagem na persistência das metapopulações e na alteração das áreas de distribuição das espécies. Usando o rato-de-Cabrera como modelo, e combinando a modelação de nicho ecológico (ENM) com técnicas de genética não-invasiva e amostragens de campo nas margens da área de distribuição, demonstra-se a combinação das três técnicas e a inclusão de amostras nos extremos do nicho ecológico tornam mais eficaz que a previsão das novas áreas de distribuição num contexto de alterações climáticas. A análise da persistência metapopulacional e da expansão da área de distribuição em condições de alterações ambientais envolveu o desenvolvimento do package de R 'MetaLandSim'. Este oferece um conjunto de ferramentas de simulação combinando as teorias dos grafos e metapopulações, o que permite testar teorias ecológicas e avaliar respostas das espécies às alterações ambientais. Usa-se este package para gerar modelos de dispersão (DM) que consideram simultaneamente a conectividade da paisagem e capacidade de dispersão. Estes DM, com três cenários de conectividade, foram projetados para o futuro e combinados com as projeções dos ENM. Demonstra-se que a perda de conectividade, associada à movimentação da janela climática, terá reduzirá a área de distribuição do rato-de-Cabrera. Finalmente, o 'MetaLandSim' é usado para testar a hipótese de que níveis intermédios de perturbação da paisagem podem beneficiar algumas espécies. Foram usadas 54 espécies virtuais com diferentes características ecológicas demonstrando que espécies com dispersões médias a

elevadas e preferência por manchas nos primeiros estados da sucessão beneficiam de níveis intermédios de dinamismo. Este estudo fornece informação relevante para melhorar previsões da persistência das metapopulações e das dinâmicas das áreas de distribuição sob diversos cenários de alterações ambientais.

Palavras-chave

Persistência metapopulacional, modelação de nicho ecológico, alterações de paisagem, alterações climáticas, alteração da área de distribuição.

Chapter 1

General Introduction

Although the effects of landscape and climate change alone have been relatively well studied and modelled, few studies have attempted to test how these processes interact to affect biodiversity. However it has been suggested that synergies emerge from their combined effects, which should be much more severe than the sum of their individual consequences (Hof et al. 2011; Opdam and Wascher, 2004; Travis, 2003). Consequently, it is critical to study the effects of each of these drivers and of their interaction on biodiversity in order to properly forecast conservation constraints and find adequate responses for them.

1. Scientific Background

1.1. *Climate change*

Climate change is a hot topic in many scientific research areas. It is defined as “... *a change in the state of the climate that can be identified (e.g. by using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer.*” (IPCC, 2014). It refers not only to trends in the mean values of the climatic variables, but also to an increase of frequency of extreme climate events. Regarding recent climatic tendencies (IPCC, 2014), it is estimated that the combined land and ocean surface temperature have warmed by about 0.85°C from 1880 to 2012. Besides the increasing average temperature, an increasing variability is also observed. In what concerns the ocean, in the last decades there were changes in i) acidification (decreasing pH by 0.1, since the beginning of the industrial age), ii) mean sea level (increase 1.7 mm/year between 1901 and 2010 and 3.2 mm/year between 1993/2010), and iii) gradual ocean warming (the upper 75 m warmed at a rate of 0.11°C/decade between 1971 and 2010). There has been considerable debate as to whether the causes of climate change are natural or

anthropogenic, or even about the occurrence of a change at all. However, this is currently supported by abundant scientific evidence, showing that, besides external natural drivers such as the solar cycle and volcanic activity, anthropogenic alterations of atmosphere composition and land use are the main driving forces responsible for climate change (Cook et al. 2013; IPCC, 2014).

Climate change has been shown to have relevant impacts on the ecosystems and species (Parmesan, 2006; Parmesan and Yohe, 2003; Walther et al. 2002), including i) shifts in species ranges (an average of 6.1km/decade towards the poles); ii) range contractions, particularly in polar and mountain species; iii) advancement in phenological spring events (ca. 2.3 days/decade for birds, plants, amphibians and insects); iv) evolutionary adaptations (adaptation to higher temperatures in the core of species ranges, broader resource use and the evolution of dispersal propensity at expanding range margins); v) disruption of species interactions (e.g. predator-prey and plant-insect); vi) changes in community composition, and vii) alteration of the structure and dynamics of ecological systems.

Species range shifts and contractions are thought to result mostly from changes in the geographical distribution of bioclimatic niches. In particular, range shifts can be of two main types: in altitude or in the direction of the poles (Walther et al. 2002). A study encompassing all the European Continent and including 120 species of native non-volant mammals Levinsky et al. (2007), predicted that, by considering two climate change scenarios, 1-9% of mammal species are in risk of extinction, while 32-78% will lose more than 30% of their current distribution area. Given the current range shift tendencies (in altitude and poleward), it is expected that the Mediterranean basin will show a greater loss in species richness and diversity, while the northeast and higher altitude regions will show the opposite trends (Levinsky et al. 2007). Other studies (e.g. Maiorano et al. 2013) have agreed that the Mediterranean Europe, which is currently considered a biodiversity hotspot, should suffer a considerable loss in terrestrial vertebrate species, including mammals, birds, reptiles and fishes. In the particular case of amphibians and reptiles, increasing temperature *per se* should not be the main cause for concern; rather, these species are affected by a reduction in water availability (particularly the amphibians) and dispersal limitations (Araújo et al. 2006).

As for plant species, a recent study including 1350 species at the European level has shown that range shifts should occur mostly in altitude (the species' ranges would occupy areas in increasingly higher altitudes than its current distribution), with the consequence that species from mountainous regions (which are already limited by the altitude at their current ranges) are more sensitive to climate change (Thuiller et al. 2005).

Throughout the years several strategies have been proposed to minimize the impact of climate change on ecosystems (Heller and Zavaleta, 2009; Mawdsley et al. 2009). These include: i) increasing the protected area network, as well as creating buffer areas around these areas; ii) promoting large reserves connected by smaller stepping stones (improving connectivity, representation and replication of each habitat); iii) improving management and restoration of current protected areas (boosting resilience); iv) focusing management actions on ecosystem function rather than its components (e.g. species); v) protecting important landscape features promoting range shifts (stepping stones, corridors and *refugia*); vi) increasing landscape connectivity by improving matrix permeability (particularly among protected areas); vii) prioritizing conservation efforts on species prone to extinction; viii) identifying indicator species; ix) translocating populations to facilitate range expansion and avoid range contraction; x) promoting the establishment of captive populations of most sensitive species; xi) reducing other pressures on species (such as the impact of landscape change or invasive species); xii) improving monitoring plans; xiii) incorporating predicted climate change impacts into species conservation plans; xiv) implementing whole landscape conservation plans; and xv) improving the communication amongst public agencies and interdisciplinary collaboration.

There is evidence that existing reserve networks, particularly those first established (such as the national and natural parks networks), are largely ineffective in protecting current biodiversity (e.g. Araújo et al. 2007; Rodrigues et al. 2004). This is probably because, historically, reserve networks were designed with a focus on landscape aesthetic value, competition with other land uses, and ownership structure (Pressey, 1994; Scott et al. 2001). These criteria privileged mountainous regions and larger, flagship species, often disregarding humanized ecosystems, or other areas of highest

conservation value (Rodrigues et al. 2004, Scott et al. 2001). Designing reserve networks should balance several important principles, such as: i) irreplaceability (a measure of how rare and/or irreplaceable are the features of a given site); ii) representativeness (characteristic of a site that specifies how many species and/or habitats are represented); and iii) complementarity (complementary sites have different characteristics, focusing on different natural features) (Cabeza and Moilanen, 2001). Although it is still widely accepted that reserves are the best strategy to cope with future climate changes (Lawler and Hepinstall-Cymerman, 2010), many recent studies have shown that existing reserves do not completely fulfil their function (e.g. Araújo et al. 2004; Araújo et al. 2011a; Hannah et al. 2007), thus suggesting that protecting biodiversity should probably require a reconsideration of the reserve network design. For instance, in a study conducted over three regions (Mexico, South Africa and Western Europe) it was concluded that in none of the areas the reserve networks fulfil their conservation targets, and that there is a need for the establishment of more reserves (Hannah et al. 2007). Another study focusing in protected areas and the Natura 2000 network in Europe, concluded that by 2080 about 58% of the species would evidence a retraction of their distribution on protected areas (Araújo et al. 2011a). This study demonstrated the ineffectiveness of the Natura 2000 network, the largest in the world, in offsetting climate change effects on species distributions. Furthermore, even current reserve selection methods are inadequate to design reserve networks that allow biodiversity conservation under climate change (Araújo et al. 2004). An alternative has been proposed which consists in the implementation of dynamic reserve networks, discarding underperforming protected areas, and considering dispersal ability and dispersal corridors (Alagador et al. 2014).

In summary climate change has important effects on ecosystems, particularly species distribution, phenology and evolution. Reserve networks, a primary tool in species and ecosystem conservation, often do not completely preserve current biodiversity. Given the ongoing trends of climate change, current reserve networks are also inadequate. New reserve design strategies are thus required, in order to cover a greater diversity of ecosystems, and to include dispersal corridors for biodiversity. An accurate knowledge

of the species potential future distribution is needed in order to inform landscape planners of which regions would better serve the connectivity of the landscape and facilitate range shifts.

1.2. Landscape change

Landscape modification by humans is by far the most important cause of landscape change, leading to habitat loss and fragmentation, thus reducing biodiversity worldwide (Fahrig, 2003; Fischer and Lindenmayer, 2007; Haddad et al. 2015; Lindenmayer and Fischer, 2006). Although habitat loss and fragmentation are widely recognised as major factors contributing to the decline of many species, the relative importance of each process is seldom evaluated (Fahrig, 2003). This is probably because habitat loss and fragmentation are often undistinguished concepts in the literature (Fahrig, 2003). Only recently, it was suggested that the term fragmentation should be applied to the separation of habitat, independently of habitat loss (i.e. a landscape might have more, smaller habitat patches, but an equal amount of total habitat than other landscape). Thus, although these are often interconnected processes, it is important to distinguish their separate effects (Fahrig, 2003). Particularly, habitat loss might have a more determinant role in the extinction of species (Fahrig, 2003, 1997).

Several processes describe the way humans can alter landscapes (e.g. Bogaert et al. 2004) including: i) dissection (division of an area of continuous habitat by equal-width lines, e.g. roads); ii) shift (patch relocation); iii) perforation (creation of holes in an area of continuous habitat, e.g. mining sites or other localized disturbance), iv) fragmentation (breaking of an area in smaller, more isolated, areas); v) shrinkage (decrease in patch size) or enlargement (increased patch size). Also, and besides these structural landscape changes, another important process is habitat degradation (e.g. decline in food or shelter) which, in extreme occasions, might lead to habitat loss (Lindenmayer and Fischer, 2006).

Landscape change impacts on biodiversity might be very diverse, given the different typologies of processes that may be involved, and the multiple ways they can be

combined. One of the frequent consequences of landscape change is the so called edge effect. This refers to the increase in the length of the boundary between habitat and surrounding matrix (Lindenmayer and Fischer, 2006). Increased edge effects magnifies species exposure to other factors that might have negative influence on persistence, either biotic (e.g. increased vulnerability to predators or disease) or abiotic (such as particular microclimatic conditions) (Lindenmayer and Fischer, 2006). Habitat fragmentation also has an effect on extinction threshold (Fahrig, 2002), such that, in more fragmented landscapes the species requires more habitat, effectively affecting the extinction threshold. Besides affecting species persistence and movement among suitable habitat patches, landscape change has also effects at the community level, altering species richness, and mostly, species composition (e.g. Burel and Baudry, 2002; Parody et al. 2001), and often triggering extinction cascades (Fischer and Lindenmayer, 2007). According to the species-area relationship, the number of species increases with habitat area. This is generally mediated by two effects: on one hand, a greater area implies more habitat diversity, thus allowing the occurrence of more species; on the other hand it also minimizes extinction since populations are assumed to be larger (Kallimanis et al. 2008; Rybicki and Hanski, 2013). It is worth noting however, that the effect of habitat diversity on species richness in itself might be stronger than the species-area relationship (Báldi, 2008).

As for habitat degradation, it may reduce abundance or prevent reproduction (Lindenmayer and Fischer, 2006). It can occur gradually (land abandonment or gradual intensification of agricultural practices) or abruptly (replacement of natural habitats or sustainable agricultural practices by urbanized territory, a rapid intensification of agriculture or other infrastructures such as dams).

Several management strategies have been proposed to mitigate the effects of landscape change (Fischer and Lindenmayer, 2007): i) preserve or promote areas of adequate habitat and permeable landscape matrix; ii) protect buffer areas around habitats; iii) promote corridors or stepping stones among habitat core areas; and iv) protect landscape gradients and heterogeneity. Other, more species-centered, management strategies that have been proposed are (Fischer and Lindenmayer, 2007): i) maintain species interactions and functional diversity; ii) focus conservation efforts

on more susceptible species; iii) control invasive or over-abundant species; and iv) minimize other threatening processes.

In summary landscape change may encompass a broad variety of processes that may have important impacts at both the species and the community levels, being recognized as one of the most important threats to biodiversity. In this respect, reserve network design assumes a very important role in landscape management strategies aiming to maintain or increase biodiversity. Since this is a multi-scale process it is important to evaluate its effects on species persistence at different scales.

1.3. Synergies between climate and landscape change

In a study concerning a particular type of landscape change, habitat loss, Travis (2003) concluded that landscape and climate change are interconnected: besides a habitat threshold, under which the species goes extinct, there is a similar threshold for the rate of climate change a species can withstand before extinguishing. Importantly, the position of this threshold is influenced by the amount of habitat and, thus, by habitat loss. Both these effects are particularly damaging for habitat specialist species with poor colonization and dispersal abilities, which are likely less capable of coping with changes. However, there is one major difference in the importance of the colonization and extinction rates of a species facing climate change and habitat loss: in habitat loss, both, colonization (c) and extinction rates (e) are equally important (since patch occupancy is determined by the ratio c/e); for climate change colonization is more relevant, since the species has to be able to follow its climatic niche through the landscape.

Opdam and Wascher (2004) studied the combined effect of climate change and fragmentation. Two thresholds were identified: one where the level of fragmentation still allows persistence and the range expansion is allowed at a slower rate and another one above which, a given level of habitat fragmentation, the expansion of the range is inhibited, thus not allowing species persistence.

A few research priorities have been identified, regarding the study of the combined effects of climate and landscape change on biodiversity. These include: i) assessing whether clumped habitat increase the likelihood of a species to shift its range (Travis, 2003); ii) investigating the underlying effects of landscape patterns on metapopulation dynamics (Opdam and Wascher, 2004); and iii) considering the effect of large scale disturbance on metapopulation persistence (Opdam and Wascher, 2004).

These research priorities highlight the need to consider the interconnection between scales, based on the idea that processes or traits that are relevant at the landscape scale might have an influence at the regional and biogeographical scales. On the other hand, large-scale changes can have an impact at the landscape scale, affecting landscape and metapopulation dynamics.

1.4. Predicting future potential niche distribution

The idea that a species distribution is defined by the values of a given set of environmental variables, or its ecological niche, was first mentioned by Grinnel (1917). Such an apparently simple idea has raised much debate (e.g. McNerny and Etienne, 2012a, 2012b and 2012c) and generated several subsidiary concepts, such as fundamental, realized or potential niches (Hutchinson, 1957; Jackson and Overpeck, 2000). Having had such a long history, many definitions of ecological niche have been presented through the years. In this thesis, the implicit definition of niche, or more specifically *(bio)climatic* niche, is aligned with the definition of the realized niche of Hutchinson (1957). This niche is defined by a set of composed bioclimatic variables (Hijmans et al. 2005) expressing the environmental suitability, defining a n-dimensional space where the species is able to persist, and excluding those areas where the species is absent due to other factors, e.g. competitor species. Ecological niche models (ENM) are a privileged tool in evaluating the relations between the species and the environmental variables (Peterson et al. 2011). Much debate has been produced as to whether the ENM's, output is the geographical expression of a niche (e.g. McNerny and Etienne, 2012a) or which concept of niche is represented in its output (e.g. Sillero, 2011). However, the real niche might never be found since i) it is difficult to evaluate if

the variables considered are the most relevant or are proxies of niche variables; and ii) some important variables might be missed. Nevertheless this does not affect the assumption that, by doing an ENM, the researcher is trying to approach the niche of the species, even if it is incompletely defined.

Furthermore it is important to make a distinction, between environmental and geographical spaces (Peterson et al. 2011). The first is the ecological niche, *sensu* Hutchinson (1957), the second is its geographical expression, i.e. the regions where the environmental conditions have the adequate values for species persistence. Ideally (from the modelling point of view) there would be a direct relation between both. However, some regions with ideal conditions do not have species occurrences (due fundamentally to dispersal constraints, geographical barriers or interspecific interactions) and others without conditions have occurrences (due to source-sink dynamics) (Franklin, 2010a; Peterson et al. 2011; Pulliam, 1988 and 2000).

There is also some debate concerning the designation of these modelling approaches, mainly between “Species Distribution Modelling” (SDM) and “Ecological Niche Modelling”, which is not only a semantic difference (Franklin, 2010a; McInerny and Etienne, 2013; Peterson and Soberón, 2012). As argued by Soberón (2014) and Peterson and Soberón (2012), when the focus is on conditions (rather than species) and when the modelling procedure aims at transferring in time or space the causal factors underlying the species distribution, the designation “Ecological Niche Modelling” should be used. In this case it is assumed that the realized *scenopoetic* niche is being modelled, i.e. the *realized* niche, since it considers the portion of the fundamental niche where the species is allowed to persist, given the presence of other limiting factors (e.g. competing species) and *scenopoetic* since only abiotic and non-interactive variables are considered (e.g. climate) (Hutchinson, 1957, 1978; Soberón, 2014).

Projecting the ecological niche into future climatic scenarios, allows the estimation of the geographic space, where the focal species will have conditions to persist. However, “having conditions” does not mean that the species has the ability to occupy a given area. On the other hand, by implicitly assuming the species will be present in all the areas projected as adequate, it is assumed that the focal species has infinite dispersal

ability, i.e. the individuals will occupy all favourable regions, whatever the distance between them and current occurrences and whatever the available time span (e.g. Bateman et al. 2013). This is not a realistic approach, if the objective is to know where the species will be present. Several alternatives are currently used to account for dispersal in these projections, besides the full dispersal (Bateman et al. 2013): i) No dispersal – assuming that the species will only occupy the areas where the projected niche overlaps current distribution. This is applied generally in conjunction with the full dispersal approach with the argument that these are the two extreme scenarios and that the reality would be somewhere in between. It is, in itself, also a highly unrealistic scenario; ii) Partial dispersal with a buffer – this approach is implemented through the application of a buffer, restraining the full dispersal scenario (assuming that the species would disperse a given distance *per* time interval); iii) Partial dispersal including other more complex approaches using, for instance, demographic, dispersal or habitat selection features for generating predictions on species range expansion.

By incorporating the accessible regions, through any of these approaches (particularly the more complex), and combining this in a GIS with the output of an Ecological Niche Model, a Species Distribution Model is produced (Peterson and Soberón, 2012). This is because the projected distribution, rather than representing the adequate conditions for the species to persist (its realized ecological niche), represents now the potential *species* distribution.

1.5. Landscape-level effects on metapopulation dynamics

The effects of fragmentation in the landscape are frequently addressed resorting to the metapopulation concept (e.g. Ovaskainen and Hanski, 2004; Sawchik et al. 2002; Schnell et al. 2013; Wilson et al. 2010), which was firstly theorized by Levins (1969, 1970). By using the metapopulation approach, it is assumed that “...*local populations, which the metapopulations consist of, are discrete (or relatively discrete) entities in space and that these local populations interact via migration and gene flow*”(Hanski and Gaggiotti, 2004). Levin’s approach is the first to develop a model to study metapopulation persistence in a stochastic equilibrium between extinction and

colonization in habitat patches (Hanski, 1999). This simple model considers an infinitely large habitat network, in which all occupied patches have equal extinction probability, the colonization is proportional to the fraction of occupied patches (sources of colonizers) and the fraction of unoccupied patches (targets for colonization), and all patches are equally connected. It is a spatially implicit model, meaning that the spatial arrangement of habitat patches is either ignored or assumed to be irrelevant (Hanski, 1991; Levins, 1969, 1970).

The commonest approach to the study of metapopulation dynamics, is the incidence function model (IFM), developed by Hanski, (1994). It belongs to another type of models: the spatially realistic models, since it accounts for patch location. It is a discrete time stochastic model, an extension of the first order linear Markov chain model (Hanski, 1999). Using IFM, the extinction is considered to vary with patch area, or quality (where patch area is a proxy of population size) so, smaller patches have greater extinction probability. Colonization depends on the species dispersal ability and patch connectivity to occupied patches (Hanski, 1999). The species is characterized by a set of parameters describing its spatial dynamics. These parameters can be derived using one (ideally more) snapshot of species occupancy in the habitat network, and there are a multitude of methods to parametrize the function (see Etienne et al. 2004 for details). Once parametrized, the IFM can be used to simulate metapopulation dynamics (Hanski, 1999).

Although the metapopulation concept and the IFM have provided important insights on how species may persist in fragmented landscape, there have been few attempts to model and predict metapopulation responses to land use change, and particularly to landscape dynamics (i.e. the rate of both, patch creation and destruction). Unlike habitat loss (which implies a decrease in the total area of habitat) or habitat fragmentation (which refers only to the division of habitat patches on more, smaller patches, not implying habitat loss; Fahrig, 2003), landscape (or habitat) dynamism refers to the relocation of habitat patches. It does not directly suggest habitat loss or fragmentation. Habitat loss and fragmentation have been thoroughly addressed previously and, frequently, the problem posed to the species occupation of a habitat network is not one of fragmentation or loss of habitat, but rather dynamic changes in

patch configuration. Only a few effects of landscape dynamism on metapopulation persistence have been studied (see Van Teeffelen et al. 2012 for a review). Those included the effects of the correlation in disturbance (e.g. Johst and Drechsler, 2003; Vuilleumier et al. 2007), of management options (e.g. Ross et al. 2008; Johst et al. 2011), of patch configuration (Vuilleumier et al. 2007), and of the role of species-specific traits, such as dispersal ability (e.g. Johst et al. 2002). Several conclusions emerged from these works: i) species with greater dispersal ability can sustain higher rate of dynamism (Johst et al. 2002); ii) generally, higher spatial correlation in the disturbance reduces species persistence (Johst and Drechsler 2003; Van Teeffelen et al. 2012; Vuilleumier et al. 2007); iii) more compact habitat networks (with a proportionally lower number of edge patches) have a lower extinction probability (Vuilleumier et al. 2007); iv) higher levels of dynamism, whether in the intensity or frequency, are more detrimental for species persistence and v) higher network area or quality and network connectivity facilitates species persistence (Van Teeffelen et al. 2012).

Regarding the management options of a dynamic landscape, research has shown that patch protection, rather than patch creation, might be a better option (Ross et al. 2009), particularly in highly dynamic landscapes or for species with higher propensity to dispersal, or more sensitive to high environmental stochasticity (Johst et al. 2002, 2011). However, recent research shows that habitat improvement (by means of enhancement in quality, size or stability of habitat patches) might have the unexpected effect of reducing metapopulation persistence. This occurs because, by improving habitat, the species evolves in the direction of less dispersal propensity, with the consequent long term reductions in patch colonization ability and overall network occupation (Poethke et al. 2011). Patch destruction can be compensated by improving other characteristics, such as number of patches or patch connectivity, but these relations are non-linear and the efficiency of such compensatory measures are dependent upon the values of connectivity and number of patches in the landscape. Furthermore, in highly dynamic landscapes such measures are ineffective (Johst et al. 2011). Accordingly, increasing the rate of patch creation, to balance patch destruction, may also fail in very dynamic landscapes (Johst et al. 2011). This happens because,

since these trade-offs are non-linear, the effectiveness of conservations measures is affected by the landscape attributes at the time.

A stimulating, though largely understudied hypothesis, regarding the effects of landscape dynamism on metapopulation dynamics concerns the intermediate disturbance hypothesis (IDH). The IDH has been first proposed by Grime (1973), but it is frequently attributed to Connell (1978). It states that, ecosystems with an intermediate degree of disturbance, can sustain higher species richness. The causes for this effect are: i) intermediate levels of disturbance, allow the coexistence of species that favor early and late successional stages; ii) with lower disturbance, more effective competitors use the resources disproportionally, excluding others (e.g. good dispersers), while at higher disturbance levels only the most resistant species survive (poor competitors which are good dispersers) (Connell, 1978; Roxburgh et al. 2004). Despite this hypothesis being firstly proposed to relate intermediate disturbance with species richness, a few studies have raised the question that intermediate disturbance might also maximize other ecological parameters (see Kun et al. 2009 for references).

Several authors have suggested (although with some nuances) that, since intermediate disturbance maximizes species richness, it might also maximize the persistence of a species in the landscape (Govindan et al. 2015; Govindan and Swihart, 2012; Kun et al. 2009; Stelter et al. 1997; Van Teeffelen et al. 2012; Zeigler and Fagan, 2014).

The reasons for this effect, in the context of species persistence in a landscape are essentially two: i) the species selects early-successional habitat patches (Stelter et al. 1997), with higher dynamism (although producing many new, more adequate, patches) causing the extinction of more subpopulations and lower dynamism not producing enough new, early-successional, patches; ii) the intermediate dynamism favors the establishment of stepping-stone patches, which connect that landscape temporarily. Lower dynamism is insufficient for these to be relevant for the species and higher dynamism promotes species extinction due to patch destruction (Govindan et al. 2015; Van Teeffelen et al. 2012; Zeigler and Fagan, 2014). Furthermore higher migration rates, derived from more connected landscapes, might give rise to the anti-rescue effect, by which the enhancement in migration has negative impacts for persistence,

for example by assisting the spread of a disease or parasite (Harding and McNamara, 2002).

The main conclusion of previous works is that, particularly if the species prefers early successional habitats, a maximum habitat network occupation at intermediate disturbances is observed.

2. Thesis main goals

The general objective of this thesis is to study the synergistic impacts of landscape and climate change on species distributions, linking metapopulation dynamics at the landscape scale and species range shifts at regional and geographical scales.

The thesis seeks to build on the general, though largely understudied, idea that studying processes at both scales should contemplate the reciprocal effects of each scale imposed by landscape and climate change (Opdam and Wascher, 2004).

By focusing on ways to improve either the sampling techniques or the modelling approaches to predict species responses to both climate and landscape change, this thesis aims to provide a contribution to improve conservation prescriptions based on a suite of more realistic scenarios and assumptions. This includes: i) improving the realism of species future potential distributions (which might be important to promote reserves and improve connectivity between reserve networks); ii) evaluating the impact of landscape configuration in the species dispersal (which might be relevant to establish landscape management guidelines promoting corridors or stepping stones or to evaluate dispersal scenarios); and iii) providing tools to improve knowledge of the effect of disturbance on species persistence in the landscape.

3. Model species

Empirical data used in this thesis regard the Cabrera vole (*Microtus cabraerae*, Thomas, 1906) (Fig. 1), which is a “near threatened” rodent (NT) by the IUCN



Figure 1 - Cabrera vole (*Microtus cabraerae*, Thomas, 1906). (F.M.)

criteria (Fernandes et al. 2008). It is endemic to the Iberian Peninsula (Fig. 2), and restricted to wet herbaceous habitat patches that remain green throughout the year (Garrido-García et al. 2013; Luque-Larena and López, 2007; Pita et al. 2006 and 2011; Santos et al. 2005 and 2006). At the regional/geographic scale, the species occurrence is sensitive to rainfall and humidity, being promoted in areas characterized by moderate values of these climatic traits (Mira et al, 2008).

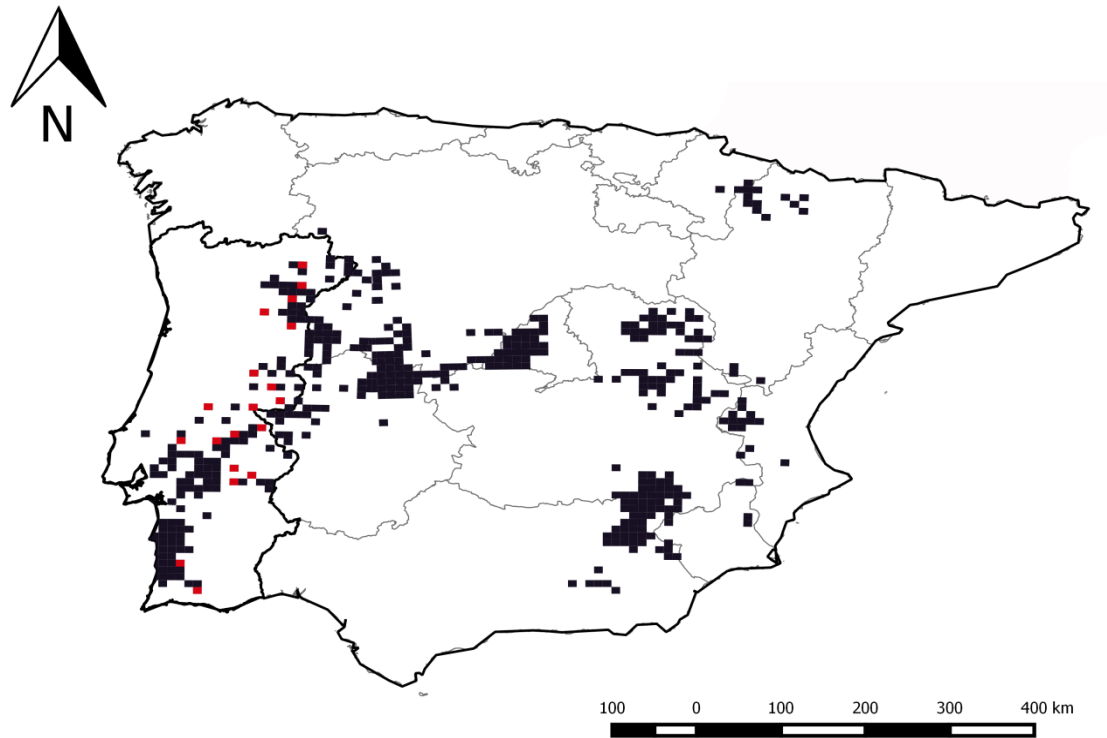


Figure 2 - Cabrera vole distribution. Dark blue - previously known distribution; Red - Data collected during the current thesis.

The species has been referred to be highly influenced by landscape configuration, being susceptible to disturbance. In fact, recent studies have shown that the structural characteristics of the landscape are key to the species persistence (Pita et al. 2007). It is frequently found in highly fragmented agricultural ecosystems (Pita et al. 2007), but also in other more neglected habitats, such as road verges and field margins (Pita et al. 2006; Santos et al. 2007) where it is subjected to lower disturbance (e.g. cattle grazing). Cabrera voles typically occur at very low densities (Fernández-Salvador et al. 2005), persisting as metapopulations in highly fragmented agricultural and pastoral landscapes, a phenomenon common to other species subjected to habitat disturbance

(Ross et al. 2008; Sjögren-Gulve and Hanski, 2000). It has been suggested that the Cabrera vole is a climate-sensitive species, responding to climate change with a change in its distribution (Araújo et al. 2011b and 2012; Laplana and Sevilla, 2013).

Habitat specialists, particularly those with lower colonization and dispersal ability, such as Cabrera voles, are particularly exposed to the synergistic effects of climate and landscape change (Travis, 2003), making this a good model species. Ecological traits that make the species less resilient to climate change are similar to those that make it less resilient to landscape change. In particular, the degree of specialization relative to climate variables (homologous of the degree of habitat specialization); and the rate of climate change it can sustain (homologous of the degree of landscape change sustained) are fundamental characteristics explaining species responses (Travis, 2003).

In addition to Cabrera vole, a set of virtual species were also used for conducting detailed analysis based on simulation modeling. Specifically, 54 virtual species were considered based on different combinations of metapopulation parameters used in the Stochastic Patch Occupancy Model (SPOM), characterizing different metapopulational dynamics. The creation of virtual species is not new to ecological works (e.g. Hirzel et al. 2001) and the value of this approach to forecast conservation measures has been previously acknowledged (Peck, 2004; Zurell et al. 2009). A traditional experimental approach implies repeatability, different treatments and comparative evaluation of outputs. In landscape ecology, given the temporal and spatial scale of the phenomena and study objects, and the complexity of the systems, simulation is a particularly adequate approach (Ims, 2005).

4. Study area

Since the model species used in the empirically based sections of this thesis is an Iberian endemism occurring in different regions of the peninsula, the study area consists on the whole Iberian Peninsula (Fig. 3), which is the westernmost portion of Continental Europe connected to the Eurasian continent by an isthmus dominated by the Pyrenees. This region is strongly influenced by the Mediterranean and the Atlantic, with a climatic gradient from costal to inland (Rivas-Martinez and Rivas-Saenz, 2015). Average monthly temperature ranges from $<0.0^{\circ}\text{C}$ (during December to February in

high altitude regions) to $>27^{\circ}\text{C}$ (during July and August in some areas of the Spanish provinces of Caceres, Badajoz, Toledo, Seville, Cordoba and Jaen). Average annual maximum temperature ranges between $<10.0^{\circ}\text{C}$ (in areas of high altitude) and $>22.0^{\circ}\text{C}$ (in inland southern Portugal

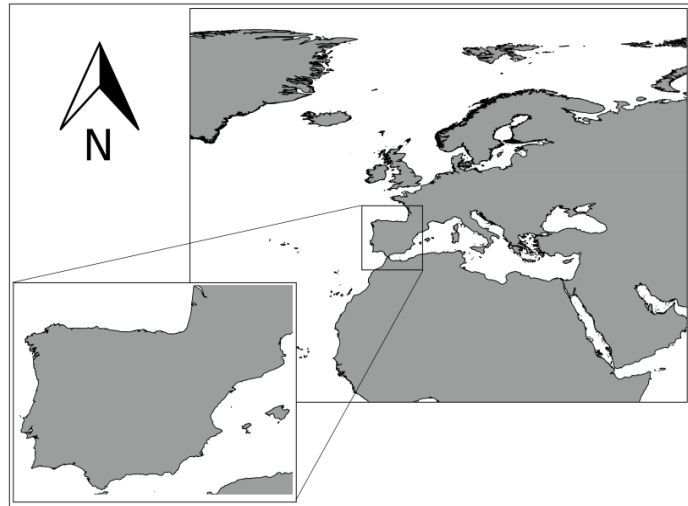


Figure 3 – The Iberian Peninsula.

and the Spanish provinces of Caceres, Badajoz, Huelva, Seville, Cadiz, Cordoba, Jaen, Almeria, Murcia and Alicante). Average annual minimum temperature ranges between $<0.0^{\circ}\text{C}$ (in regions of high altitude in Spain) and $>15.0^{\circ}\text{C}$ (in the region of Algarve, Portugal, and in the coastal Spain between the provinces of Cadiz and Alicante). Lowest monthly average minimum temperature ranges between values $<2.5^{\circ}\text{C}$ (between December and February in high altitudes) and $>17.0^{\circ}\text{C}$ (between July and August on Algarve, southern Portugal, on the majority of the coastline of Extremadura, Andalusia, western Castile-La Mancha, southern Madrid and the Balearic Islands) (AEMET and IM, 2011) (Fig. 4).

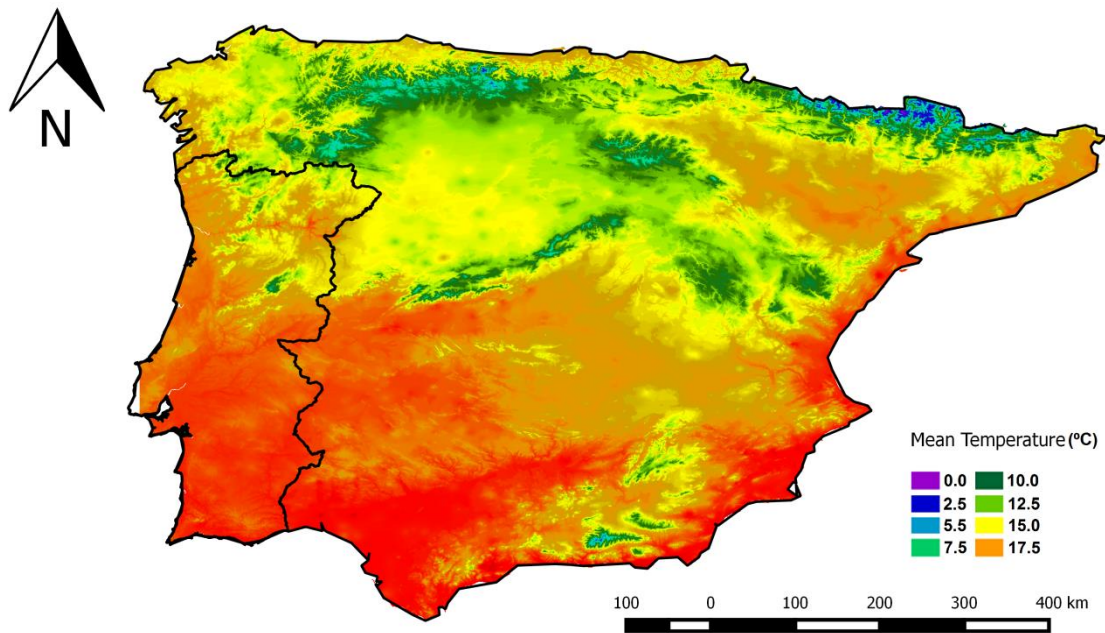


Figure 4 - Mean temperature (°C) (Ninyerola et al. 2005).

As for precipitation, the Iberian Peninsula is marked by a strong seasonality, particularly in the southern portion of the territory, which is less intense in north-eastern Spain. December is the month with higher precipitation (>300 mm), particularly in northeast Portugal and southwest Galicia. Lower rainfall (10-20 mm) occurs in southeast Spain (provinces of Almeria, Murcia and Alicante) and areas of Teruel. July is the month with lower precipitation; during this month the lower values (<5 mm) occur in southern Baixo Alentejo, Algarve (Portugal) and in Andalusia, southern Extremadura, Murcia and southern Valencia (Spain). The highest values for average monthly rainfall (>150 mm) are in the north of Catalonia, north of Navarra and scattered areas of the Basque Country (Spain); (AEMET and IM, 2011) (Fig. 5).

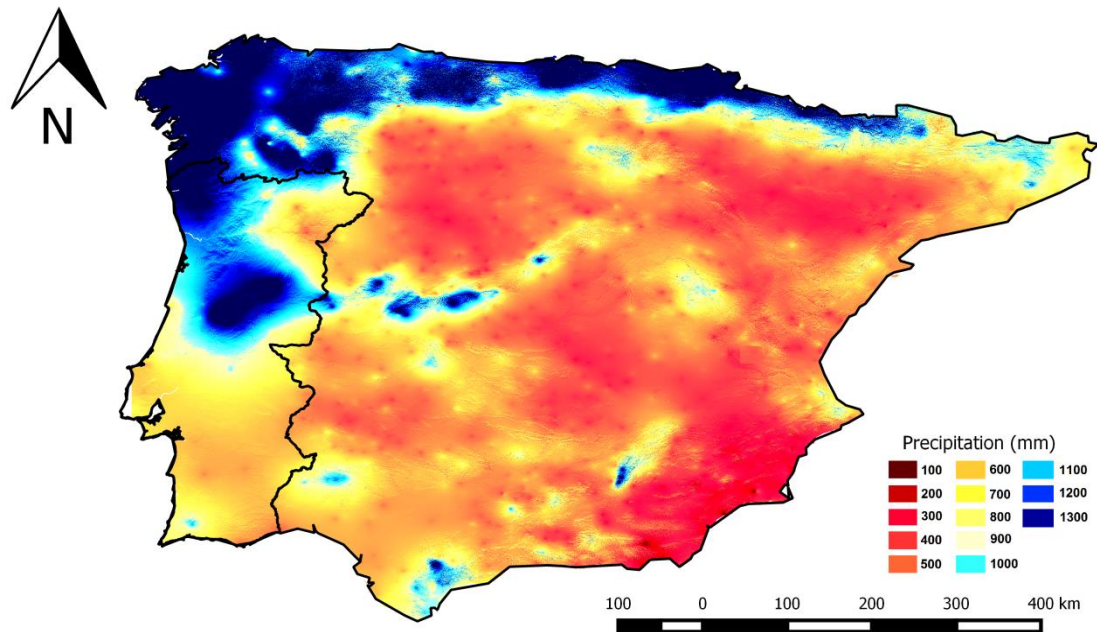


Figure 5 - Mean Precipitation (mm) (Ninyerola et al. 2005).

The major Iberian rivers are the Guadalquivir, Ebro, Douro, Tagus and Guadiana. These rivers have an eastern/western orientation (with the exception of the Ebro, which runs northwest to southeast). In what concerns orography the Iberian Peninsula is very diverse. The central region is dominated by the Iberian Central Plateau, the Toledo Mountains (separating the Tagus and Guadiana Basins), the Iberian Mountain Range (isolating the Tagus, Douro and Ebro basins) and the Sierra de Gredos and Guadarrama. To the north, the Cantabrian Range borders the coastline of the Cantabric Sea. In the southern portion the Iberian Peninsula the most relevant mountain systems are the Sierra Morena, between the Guadiana and Guadalquivir basins, and the Baetic System along the southern coastline. In the west are prominent the Catalan Coastal Range and the Pyrenees (connecting the peninsula to the rest of Europe). The southwestern portion of the Peninsula (the Portuguese regions of Alentejo and Algarve and parts of the Spanish regions of Andalusia and Extremadura) presents smoother topographies (Fig. 6).

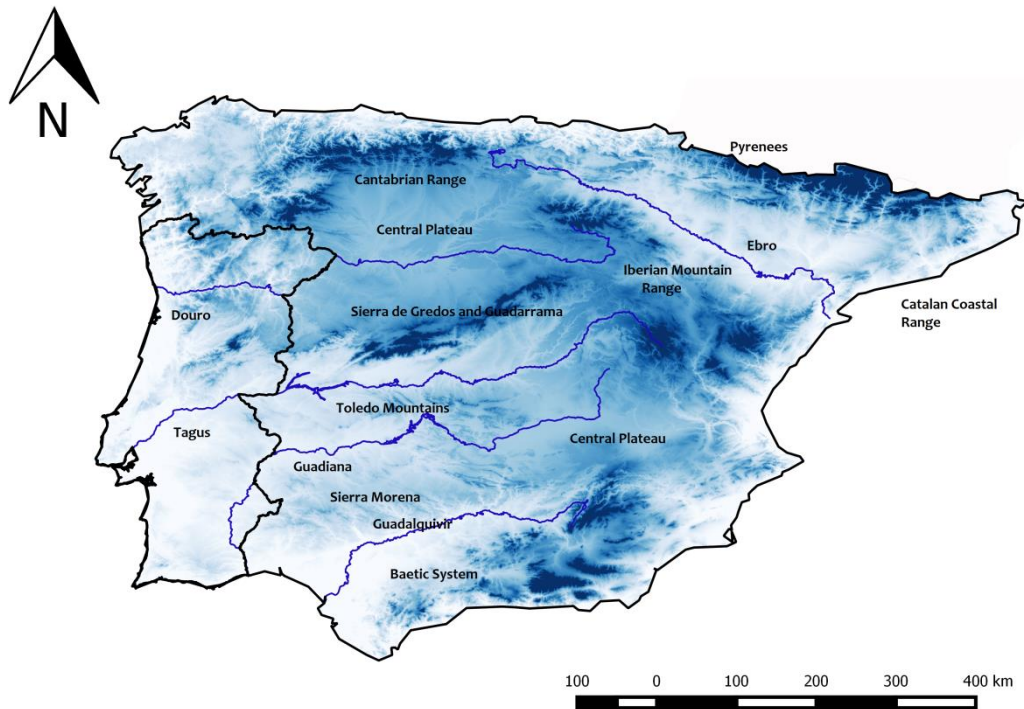


Figure 6 - Geography of the Iberian Peninsula.

Concerning soil type, and according with the World Reference Base (IUSS Working Group WRB, 2014), the Iberian Peninsula presents a few particularities, such as some soil types which are uncommon throughout Europe, as solonchak and gypsisols. Cambisols (present in a diversity of climates, altitudes and vegetation types) are the commonest soil type in the region, followed by regosols (present in very diverse areas, but mostly in arid regions and mountain ranges). Luvisols, with high nutrient content, are present in the western portion of the peninsula (particularly southern Portugal). This type of soil is typical of flat landscapes in cool temperate to warm Mediterranean climates, in regions with well-defined dry-wet seasons. The Ebro region and parts of south-eastern Spain have areas of calcisols, typical of flat to undulating landscapes of arid and semi-arid regions dominated by xerophytic shrubs/trees and herbs or ephemeral grasses, with patches of leptosols (typical of mountains regions) in mountainous regions of eastern and northern Spain. (Fig. 7).

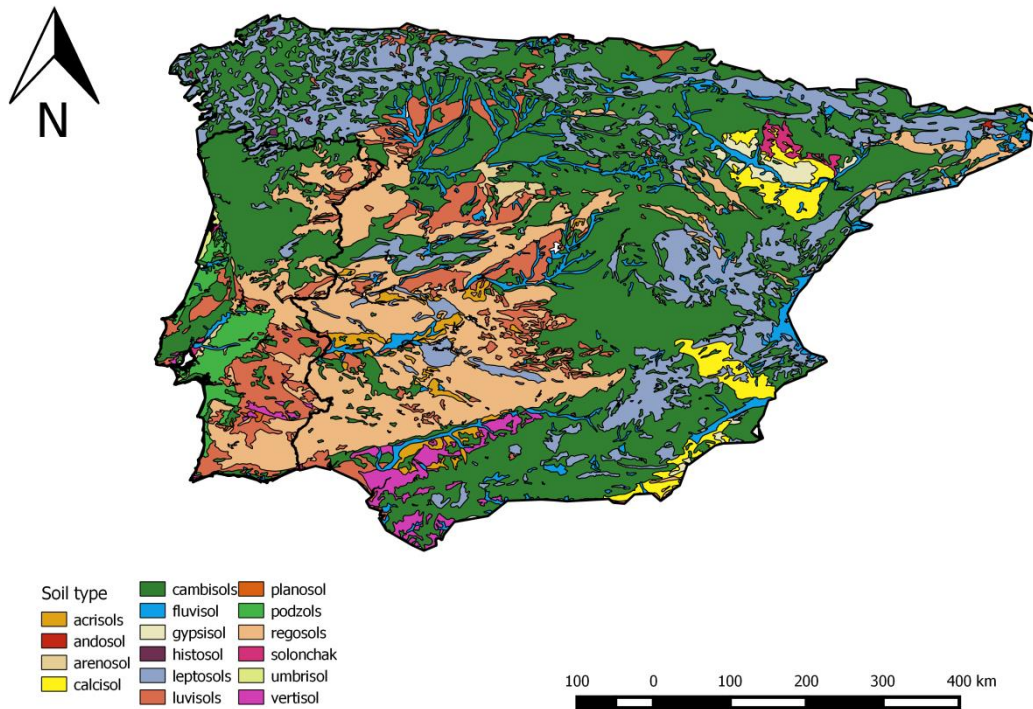


Figure 7 - Soil type (Panagos et al. 2012).

According to the Corine Land Cover 2006, the land use in the Iberian Peninsula is dominated by scrub and herbaceous associations, arable lands, forests and heterogeneous agricultural areas. In the central, south-western regions of Portugal there is some dominance of forests and arable land. In the north-eastern Portugal and Algarve Mountains scrub and herbaceous associations are prevalent. In Spain, in the Central Plateau and in the Guadalquivir basin, arable land is dominant. Spanish mountainous regions are dominated by both, scrub and herbaceous associations and forests (EEA, 2014) (Fig. 8).

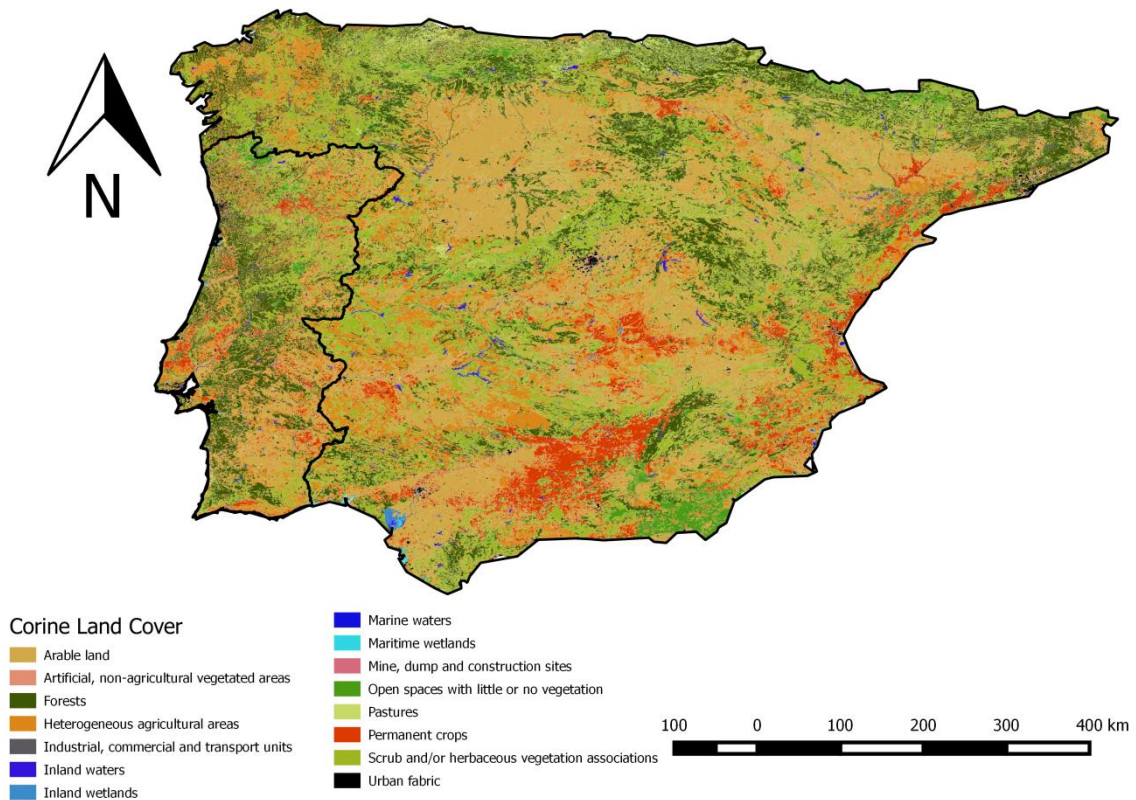


Figure 8 - Corine Land Cover 2006 (EEA, 2014).

4.1. Climate change and its impacts on the Iberian Peninsula

Predicted climate change scenarios in the Iberian Peninsula indicate a decreasing precipitation (Rodríguez-Puebla and Nieto, 2010), which will lead to an increasing frequency of average and longer dry spells, with a north-south growing gradient intensifying the current latitudinal dissimilarities. As such, hydrological stresses, which are already important in some areas of the Iberian Peninsula, will tend to be intensified (Sánchez et al. 2011). In particular, in Portugal, an increase of mean temperature, predominantly in the summer and autumn, as well as an increase in the frequency of daily extremes, chiefly in the maximum temperatures in the summer, is expected to occur (Andrade et al. 2014).

The impact of such changes has been assessed in previous studies for vertebrates and vascular plants, in Spain. For the vertebrate species there will be no taxonomically-based differences, i.e. the different taxonomic groups do not show discernible differences amongst them in what concerns range shifts and contractions. Overall, for

these species, a range contraction is observable (southwest/northeast and south/north) which is consistent with an increase in aridity in the south/southwest Iberian Peninsula (decreased rainfall and increased temperature) (Araújo et al. 2011b). The tendency for an increase in aridity in Mediterranean Europe will have a particular impact on mammal species richness (Levinsky et al. 2007). Iberia, together with the Italian Peninsula, shows the highest values of vertebrate species richness (Maiorano et al. 2013). Regarding the vascular plants the main tendency shown in continental Spain is the loss of species in mountainous regions, mainly in the center and northern Spain (Felicísimo et al. 2011) in line with studies made for Europe (Benito Garzón et al. 2008; Thuiller et al. 2005). In fact, these studies mention that central/northern Spain should show the highest rates of species loss, more than 80% (Thuiller et al. 2005) and that Mediterranean tree species appear prone to migrate north and upward and persist in climate change scenarios (Benito-Garzón et al. 2008).

Given that about 80% of the Iberian vertebrate species, tend to retract in protected areas in Spain (Araújo et al. 2011b), addressing climate change, and its ecological consequences is essential to preserve biodiversity.

4.2 Landscape change and its impacts on the Iberian Peninsula

As in other regions across Europe, current landscape changes in the Iberian Peninsula are largely related to the development of the road networks and land cover modification. These trends in landscape change are driven by changes in agricultural practices which are a consequence of the European Union agricultural policy and its constant evolution (Selva et al. 2011; Stoate et al. 2001, 2009). The intensification of agricultural practices in Iberia (often with irrigation) has created a more uniform landscape (Stoate et al. 2001, 2009). Traditional land uses like the *montado* ecosystem (similar to the Spanish *dehesa*), which is very characteristic of the southern Iberian Peninsula, are generally associated with high biodiversity levels (Pinto-Correia and Mascarenhas, 1999), but these traditional systems are currently suffering contrasting modifications: extensification (leading to a more forest-like landscape) or

intensification (leading to a more intense agriculture/forestry) (Pinto-Correia and Mascarenhas, 1999; Stoate et al. 2001, 2009).

In the case of the empirical model species used in this thesis (the Cabrera vole), the more prevalent and potentially damaging landscape changes are those related with the reconversion of traditional agriculture to other, more lucrative, crop plants, the effect of cattle grazing intensification and the road-derived dissection of habitats (Fernández-Salvador, 2007; Pita et al. 2007). These might cause habitat loss (decreasing the mean area or the number of patches available by, shrinkage or attrition, respectively) and fragmentation (dissection of otherwise continuous habitat) and a reduction in matrix permeability which decreases landscape connectivity.

5. Specific objectives and thesis structure

In order to address the general purpose of this thesis, i.e. evaluate the synergistic effects of landscape and climate change on species persistence and distribution range, three main specific objectives were outlined:

1. Optimizing the modelling procedure by improving the apprehension of the ecological niche combining ecological niche modelling, sampling at the range margins and genetic analysis, improving range shift projections.
2. Producing a tool to enable the inclusion of landscape effects on range expansion, providing an ideal way to relate both scales, biogeographical and landscape. This tool would allow considering landscape effects in range expansion modelling in a species with a metapopulational distribution in the landscape.
3. Evaluating the Intermediate Disturbance Hypothesis in the context of species persistence in a dynamic landscape.

Each of these objectives was divided by the chapters of the thesis.

Firstly, the thesis aimed to show how forecasting species future range shifts under different climate change scenarios may be affected by inaccurate estimates of the species ecological niche, due for instance to incomplete occurrence data on locations where species are at low densities. Using the Cabrera vole as model species, and non-

invasive genetic sampling along the species range margins, it was aimed to i) generate more accurate projections of future ecological niche; and ii) optimize the modelling procedure and data collection. This was done by calibrating an ENM with the known occurrence of Cabrera vole and current climatic conditions. The output of the ENM was used to define areas for field sampling, at the range margins determined by the model. One important feature of this chapter is the link between geographical space and ecological space, since the sampling at the species distribution margins was also intended to capture the conditions of the *ecological* margin. The data collected in the field sampling were joined to the previous data and a second model was calibrated. Both these models were then projected into future climatic conditions. The main goal was to evaluate the differences between the two models, assessing the impact of the new data on the ecological niche projections. This first study is presented in Chapter 2.

A further objective was to develop a new modeling tool to predict metapopulation persistence in dynamic landscapes that simultaneously allows the scaling-up to regional and biogeographical scales. By simulating metapopulation dynamics in landscape units that are sequentially occupied, a dispersal kernel is produced, generating the probability of occupation of areas at a given distance to the closest current species occurrence. This kernel is applied to a raster map of current distribution, generating a Dispersal Model, which can be later combined with an Ecological Niche Model using any GIS software. The main idea was to connect both the landscape and biogeographical scales, providing the necessary link between metapopulation and range dynamics, as claimed by Opdam and Wascher (2004). This study is presented in Chapter 3.

Then, aiming to answer the main research question of this thesis regarding the synergies between climate and landscape change, the information from the projection of Ecological Niche Models (ENM) into the future was combined with that generated by Dispersal Models (DM) in several landscape fragmentation scenarios. This chapter profits from the outputs of preceding chapters, namely, the ENM (chapter 2) and the tool developed to produce the DM (chapter 3). By analyzing the several climate-based and landscape-based scenarios as well as the combination of both it is possible to evaluate the effects of climate and landscape change on the future distribution of

Microtus cabreræ. This study, recently submitted for publication, is presented in Chapter 4.

Finally it aimed to assess the support of the Intermediate Disturbance Hypothesis (IDH) in explaining metapopulation persistence in dynamic landscapes. Specifically, the IDH was tested for 81 virtual species with different spatial and ecological traits, in order to assess whether there are any species benefiting from an intermediate level of disturbance in the landscape. Here, besides the different spatial dynamics, different species preferences regarding succession stage of the patches (early, mid and late-successional species) were considered, a factor which has been studied previously (Stelter et al. 1997; Wahlberg et al. 2002). It builds on previous works using particular species (Govindan and Swihart, 2012; Govindan et al. 2015; Stelter et al. 1997), and achieves generalizations regarding the relations between IDH and metapopulation persistence. The approach described here aims to identify species characteristics that are prone to behave accordingly with the IDH. This objective is addressed in Chapter 5 (manuscript in preparation to be submitted).

The sixth chapter summarizes the main findings and contributions of the study, framing these in the current research agenda and providing guidelines for further development.

Chapter 2

Combining distribution modelling and non-invasive genetics to improve range shift forecasting

Published on Ecological Modelling as:

Mestre, F.; Pita, R.; Paupério, J.; Martins, F.M.S.; Alves, P.C.; Mira, A. & Beja, P. (2015). "Combining distribution modelling and non-invasive genetics to improve range shift forecasting". *Ecological Modelling*, 297: 171-179. Doi: 10.1016/j.ecolmodel.2014.11.018.

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Abstract

Forecasting species range shifts under climate change is critical to adapt conservation strategies to future environmental conditions. Ecological niche models (ENM) are often used to achieve this goal, but their accuracy is limited when species niches are inadequately sampled. This problem may be tackled by combining ENM with field validation to fine-tune current species distribution, though the traditional methods are often time-consuming and the species ID inaccurate. Here we combine ENM with novel field validation methods based in non-invasive genetic sampling to forecast range shifts in the threatened Cabrera vole (*Microtus cabreræ*). Using occurrence records mapped at 10x10km resolution, we built a first ENM (ENM1) to estimate the current species distribution. We then selected 40 grids with no previous data along the predicted range margins, and surveyed suitable habitats through presence-sign searches. Fecal samples visually assigned to the species were collected for genetic identification based on the mitochondrial cytochrome-b gene, which resulted in 19 new grids with confirmed presence records. A second model (ENM2) was built by adding the new data, and species distribution maps predicted by each model under current and future climate change scenarios were compared. Both models had high predictive ability, with strong influence of temperature and precipitation. Although current distribution ranges predicted by each model were quite similar, the range shifts predicted under climate change differed greatly when using additional field data. In particular, ENM1 overlooked areas identified as important by ENM2 for species conservation in the future. Overall, results suggest that combining ENM with non-invasive genetics may provide a cost-effective approach in studies regarding species conservation under environmental change.

Keywords

Climate change, ecological niche, *Microtus cabreræ*, range margins, range shift, conservation genetics.

1. Introduction

There is growing evidence that many species will change their current ranges in response to climate change. These range shifts, may have multiple conservation implications on, for instance, the design of reserve networks (Hannah, 2008; Hannah et al. 2002), assisted colonization approaches (Hoegh-Guldberg et al. 2008), and habitat restoration priorities (Mawdsley et al. 2009). Species range shifts are caused by the expansion or contraction of favourable climatic conditions, and typically emerge from extinction/colonization processes mostly driven by the species physiological tolerances, dispersal abilities, and habitat availability along their distribution limits (Anderson et al. 2009; Thomas, 2010; Walther et al. 2002). Generally, species tend to occupy newly available patches at their expanding margins, being more likely to become locally extinct at the retracting margin (Anderson et al. 2009). Support for such climate-induced range dynamics in many plants and animals has led to the recognition that effective conservation planning should move from a static to a dynamic approach. Accurate projections on potential species distribution ranges, should allow the conservation of both present-day and future biodiversity (Fuller et al. 2011; Hannah et al. 2002; Peterson et al. 2011).

Ecological Niche Models (ENM) are commonly used to assess the relation between the species and the environment (Guisan and Zimmermann, 2000), evaluating the existing fundamental niche of the species (Peterson et al. 2011). While these models provide a valuable tool for designing policies to lessen the effects of climate change on biodiversity (e.g. Peterson et al. 2011), they are not impervious to some potential biases and uncertainties (Beale and Lennon, 2012; Hanspach et al. 2011; Rocchini et al. 2011). A primary source of uncertainty underlying ENM is related to the quality and quantity of species occurrence data. Small sample sizes or inadequate spatial coverage decreases the statistical confidence of correlations underlying niche models (Wiens et al. 2009, and references therein). Uncertainties in occurrence information may be particularly common along range margins, where the species might occur at lower densities (Hengeveld and Haack, 1982), increasing the risk of erroneous results and predictions (Hanspach et al. 2011). Thus, these uncertainties may have important implications for the evaluation of the ecological niche, and for the computation of

accurate projections of current and future distributions, particularly in rare or elusive species which are difficult to sample.

Although interactive modelling and ground validation sampling can provide a useful method to fine-tune current species distribution ranges, its implications in forecasting species range shifts are still largely unexplored, often because field surveys are logistically difficult, costly, inaccurate and time-consuming. In this context, novel genetic techniques (non-invasive genetic sampling) may provide a fast and effective solution to assess the impact of combining ENM and post-modelling sampling on species range shift forecasting. The combination of non-invasive genetic sampling with DNA-based tests for species identification, highly improved the efficiency in using field signs (faeces, hair, feathers, etc.) for determining species presence and distribution (see e.g. Beja-Pereira et al. 2009; Waits, 2004). In what concerns small mammals, for instance, reliable occurrence data typically require relatively demanding field sampling efforts, often involving intensive capture campaigns, or owl pellet dissection (e.g. Landete-Castillejos, 2000; Mira et al. 2008; Pita et al. 2006, 2007 and 2011). Recently, it has been shown that non-invasive genetic sampling of small mammals (e.g. using faecal samples) may provide a promising alternative to monitor populations, by allowing the indirect identification of species (Alasaad et al. 2011; Barbosa et al. 2013). However, to the best of our knowledge, no study has yet combined ENM and non-invasive genetics to refine range shifts estimates, and so the potential value of this approach remains untested.

Here, we evaluate the impact of combining ENMs with non-invasive genetic sampling at the range margins in forecasting range shifts of a threatened species, for which range margins are incompletely surveyed or poorly defined. Specifically, we focus on a threatened rodent endemic to the Iberian Peninsula, the Cabrera vole *Microtus cabrae*, which is restricted to wet herbaceous habitats (Luque-Larena and López, 2007; Pita et al. 2006 and 2011; Santos et al. 2005 and 2006). This species typically occurs at very low densities (Fernández-Salvador et al. 2005), and often persists as metapopulations in highly fragmented agricultural and pastoral landscapes, where patch-level extinction-colonization events are relatively common (Pita et al. 2007). Recent studies suggested that the Cabrera vole is a climate-sensitive species (Araújo et

al. 2011b and 2012; Laplana and Sevilla, 2013), implying that its conservation should consider the dynamic and uncertain effects of climate change. Identification of effective conservation actions for the Cabrera vole is, however, hindered by the difficulty to survey the species using traditional sampling approaches such as live-trapping (e.g. Fernández-Salvador et al. 2005; Pita et al. 2007). Although presence signs (e.g. runways on grasses, faeces) have been successfully used to survey this vole (e.g. Garrido-García et al. 2009; Pita et al. 2006 and 2007), the approach may be limited in situations of sympatry with other vole species producing similar signs (e.g. *M. agrestis* in Northern Iberia). Here we combine ecological niche modelling and recent DNA-based tests for species ID using faecal samples to forecast range shifts of rare and illusive species. In particular we aimed to i) fine-tune the distribution limits of a threatened and endemic rodent (Cabrera vole) in Iberia, using non-invasive genetic sampling at the range margins; ii) predict the species range shifts under future climate conditions, and evaluate the effect of the new occurrence records on such forecasts; iii) assess the impacts of climate change on the conservation of the Cabrera vole, in the light of the new distribution model predictions. Results of the study are then used to discuss the potential of non-invasive genetics to improve the value of ENM in guiding conservation action.

2. Material and Methods

2.1. Study design

We followed an approach similar to Guisan et al. (2006), which consisted in modelling the ecological niche using all previously known location records of Cabrera voles (henceforth ENM1), and then using the model output to select a set of sites at the predicted range margins for surveying the species (Figure 1). Considering that previously known occurrences of the species in Portugal were obtained mostly by owl pellet analysis (Mira et al. 2008), contrasting with the higher sampling effort applied in Spain (e.g. Fernández-Salvador, 2007; Garrido-Garcia et al. 2013) and that Portugal encompasses a significant proportion of the global species range, surveys were conducted on the range margins in Portugal, where the species may be undersampled.

By concentrating surveys at the range margins we aimed to maximize the ecological niche apprehension, while refining the knowledge about the species distribution. Surveys were based on the detection of the characteristic faeces of the species, which were collected and identified unequivocally using molecular techniques (see below). Afterwards, the model was re-run, including the new occurrences (henceforth ENM2), and predictions from ENM1 and ENM2 were projected and compared under current and future climatic scenarios.

2.2. Data sources

Presence data of Cabrera vole across its entire current range (the Iberian Peninsula) were obtained from all available literature sources documenting the occurrence of the species between 1970 and 2011 (Figure 1a; Table A1 in Supplementary information) and recorded in 10 km² UTM grids. Variables of current climatic conditions obtained from the Worldclim website (<http://www.worldclim.org/> and Hijmans et al. 2005) consisted of interpolations of observed data, for the time period between 1950 and 2000. Variables of future climatic conditions were derived from the Hadley Centre Coupled Model, version 3 (HadCM3), which is a coupled atmosphere-ocean general circulation model, available at the CCAFS GCM Data Portal (<http://www.ccafs-climate.org> and Ramirez and Jarvis, 2008). Bioclimatic variables were averaged for the 10 km² UTM grids encompassing the Iberian Peninsula. Future niche projections of both ENM1 and ENM2 were carried out for the A1b and B2 scenarios. The A1b storyline describes a world with fast economic growth with balanced use of fossil/non-fossil energy resources, while the B2 storyline describes a world of local environmental sustainability (see IPCC, 2000 for details).

2.3. Field surveys and genetic analysis

A total of 40 UTM 10 km² grid cells, located along the Portuguese range margins predicted by ENM1, were randomly selected for field sampling. From these, 20 were located in the northern margin and another 20 were located in the southern margin. In each case, 10 cells were located up to 30 km into the core of the predicted distribution, and the other 10 were located up to 30 km outwards of the predicted distribution (see Figure A1 in Supplementary information).

Surveys were conducted in December 2012 by a team of one or two experienced researchers, and involved a two-step hierarchical procedure. First, we identified 10 sites with potential habitat conditions for the Cabrera vole, based on vegetation characteristics and a searching image developed from previous studies (Pita et al. 2006 and 2007). Sites were spread as much as possible throughout each cell, using a combination of 1:25 000 cartographic maps, aerial photograph interpretation, and field checking. Second, at each site a thorough survey was undertaken to detect the characteristic signs of the species, including faeces, grass clippings and runways (e.g. Garrido-García et al. 2009; Pita et al. 2006 and 2007). A particular effort was made to detect fresh faeces that could be visually assigned to the species, since these were the only signs amenable for genetic analysis.

Faecal samples were collected using sterilized tweezers to avoid contamination, and stored in 95% ethanol until analysis. In each cell, a maximum of 13 samples from different sites were selected for DNA extraction (Table A2 in Supplementary information). DNA extraction was performed with three to five faecal pellets per sample according to the procedures described in Barbosa et al. (2013). Species identification was performed by amplification and sequencing of one fragment of the cytochrome *b* mitochondrial gene (Barbosa et al. 2013). This gene fragment was selected because it allows the successful identification of all Iberian rodent species, although it is unable to separate the pine voles *Microtus lusitanicus* from *M. duodecimcostatus*. Genetic analysis of the samples collected in each cell was performed until Cabrera vole presence was identified or until species identification was obtained for up to 10 faecal samples. Cabrera vole was considered to be absent from the cell if no presence signs were detected in the 10 sampling sites or if none of the faecal samples analysed was genetically identified as belonging to the species.

2.4. Modelling procedures

Pre-selection of bioclimatic variables for modelling purposes was conducted using a two-step process. We first fitted logistic regression models relating presence/absence of the Cabrera vole and each individual variable, and retained only those predictors that were significant at $p < 0.05$. Then, we computed the pairwise Spearman correlation coefficients (r_s) among variables (see Table A3 in Supplementary

information), and for each pair of highly correlated variables ($|r_s| > 0.7$) we retained the one with higher biological meaning (Tabachnik and Fidell, 1996).

The current and future distributions of the Cabrera vole were modelled through the ensemble forecasting approach (Araújo and New, 2007), using the BIOMOD package (Thuiller et al. 2009b; Thuiller and Lafourcade, 2010) implemented in R, version 3.0.2 (R Core Team, 2013). Ensemble forecasting was used, because it is recognized to provide more robust predictions than single models (Araújo and New, 2007). Eight of the nine algorithms available in the package were run in order to build the ensemble (generalized linear model, generalised boosting model, generalised additive model, classification tree analysis, artificial neural network, flexible discriminant analysis, multivariate adaptive regression spline, and random forest). In order to evaluate the models, each dataset was randomly split in calibration and evaluation subsets (70-30%) in a multiple cross validation procedure, replicating the data splitting procedure five times. Overall, this procedure produced 96 models, of which only those with a good fit were selected and weighted by accuracy to generate an ensemble model.

Selection of the best models and posterior weighting was made using the True Skill Statistics (TSS), as recommended by Allouche et al. (2006). The relative weight of the contribution of each model was calculated using a decay of 1.6, the BIOMOD default weighting value (Thuiller et al. 2009a). TSS ranges from -1 to +1, where +1 indicates perfect agreement, while $TSS \leq 0$ are indicative of a performance no better than random. Only the models with $TSS > 0.5$ were kept in the final ensemble. The contribution of each variable to the final ensemble was evaluated through the variable importance metric (Thuiller et al. 2009a), which is independent of the modelling technique used, and it is given as one minus the correlation score between the prediction of each model and the prediction using a permuted variable. The final value ranges between zero (no importance) to one (high importance) (Thuiller et al. 2009a). This was computed using five permutations to each variable.

BIOMOD classifies each grid cell between 0 and 1000, according to its suitability. In order to convert this continuous value in a potential presence/absence value, the Minimal Predicted Area (MPA, Engler et al. 2004) was used. This approach predicts the

smaller possible area while keeping 90% (in this case) of the presences correctly classified (thus keeping sensitivity equal to 0.9 and fixing the omission error). The method is particularly adequate to choose the threshold when the available data are presence-only, as threshold methods that consider commission error (proportion of absences predicted as presences) should not be used when there are no true absences available (Peterson et al. 2011). The PresenceAbsence package (Freeman and Moisen, 2008) was used to compute the threshold.

The Area Under the receiver operator Curve (AUC) was designed to be used with binary presence/absence data, equally weighting omission and commission errors. However, considering that absences are rarely available, the use of pseudo-absence and background data is common practice. In such cases, commission errors are expected to be overestimated, as predicted presences on pseudo-absences will be considered an error (Peterson et al. 2011) and the AUC must be interpreted in a different manner, since the question is not the ability to distinguish between presence and absence but to distinguish between presence and randomness (Phillips et al. 2006). Furthermore, the maximum AUC possible in such conditions is <1 , because it depends on the predicted area (being “a” the proportion of predicted presence by the model $AUC_{max} = 1-a/2$) (Phillips et al. 2006; Wiley et al. 2003).

2.5. Range map comparisons

Pairwise comparisons between potential range maps produced by ENM1 and ENM2 at each time step (current, 2020, 2050 and 2080, under both scenarios considered) were made using the improved fuzzy Kappa algorithm for categorical maps, implemented in the Map Comparison Kit, version 3.2.3 (Visser and Nijs, 2006). Two geographic extents were considered, the Iberian Peninsula and Portugal, totalling 14 range map comparisons. In each case, the outputs of BIOMOD were first reclassified from 0 to 4, with all square grids with predicted absence classified as zero, and all above the presence threshold classified from 1 to 4, according to the quantile. Similarly to the traditional Kappa statistics, the improved fuzzy Kappa algorithm expresses the mean agreement between two maps, relative to the expected agreement from random relocation of all cells in both maps, ranging between 0 (different maps) and 1 (identical maps). However, contrary to the Kappa, it does not account for cell-by-cell agreement;

instead it considers the fuzziness of the location, for near cell-by-cell agreement, while also accounting for autocorrelation in the changes amongst maps (Hagen-Zanker, 2009; Visser and Nijs, 2006). All geographic information was stored and managed using QGIS, version 2.0.1 Dufour (QGIS Development Team, 2013).

3. Results

Following the pre-selection procedure of the most influential, uncorrelated variables, five bioclimatic variables were retained for subsequent analysis: Mean Diurnal Range (MDR), Minimum Temperature of Coldest Month (MTCM), Mean Temperature of Wettest Quarter (MTWQ), Precipitation of Wettest Month (PWM) and Precipitation of Warmest Quarter (PWQ). Importance scores derived from models developed using the original dataset (ENM1) suggested that PWQ was by far the most influential variable, while the PWM was the least important. The importance of the remaining variables was relatively low and similar to each other (Table 1).

Table 1 - BIOMOD variable ranking of predicted ecological niche of the Cabrera vole, according to ENM1 and ENM2.

Variable	Code	Variable Importance	
		ENM1	ENM2
Mean Diurnal Range (°C)	MDR	0.176	0.200
Minimum Temperature of Coldest Month (°C)	MTCM	0.177	0.168
Mean Temperature of Wettest Quarter (°C)	MTWQ	0.216	0.184
Precipitation of Wettest Month (mm)	PWM	0.128	0.100
Precipitation of Warmest Quarter (mm)	PWQ	0.441	0.496

In general, ENM1 pointed out that the ecological niche of the Cabrera vole was associated to intermediate levels of PWQ and PWM, moderate MTWQ, relatively high MDR and MTCM (Table2). The model AUCs suggested that ENM1 showed a good predictive ability of the potential distribution of the Cabrera vole ecological niche, with mean (AUC_{mean}) and maximum (AUC_{max}) values amongst all models in the ensemble of 0.881 and 0.911, respectively.

From the 40 grid cells selected along the range margins defined by ENM1, a total of 351 fresh faecal samples potentially belonging to Cabrera voles were collected in 110 sites located in 30 grid cells (Figure 1c; Table A3). In the remaining 10 squares, we either did not find suitable potential habitat patches, or there were no faeces or other indirect signs that could be identified as belonging to Cabrera vole or in the patches surveyed. In total, DNA extraction was performed on 115 faecal samples from 69 sites, and a 90% amplification success rate was obtained. From 104 faecal samples amplified, 37 were identified as Cabrera vole, confirming its presence in 19 new grid cells (47.5% of the total sampled). From these, 14 were located in the 30 km within the core of the predicted range, and 5 were located up to 30 km outwards (Table A3). Other small mammals were identified in 14 grid cells, namely, the European field vole (*Microtus agrestis*), the western Mediterranean mouse (*Mus spretus*), the southern water vole (*Arvicola sapidus*), the wood mouse (*Apodemus sylvaticus*) and the Lusitanian/Mediterranean pine vole (*Microtus lusitanicus/duodecimcostatus*). The non-invasive sampling approach resulted in an increase of the known occurrences of the Cabrera vole of about 4.84% squares (15.97% for the distribution in Portugal) (Figure 1d).

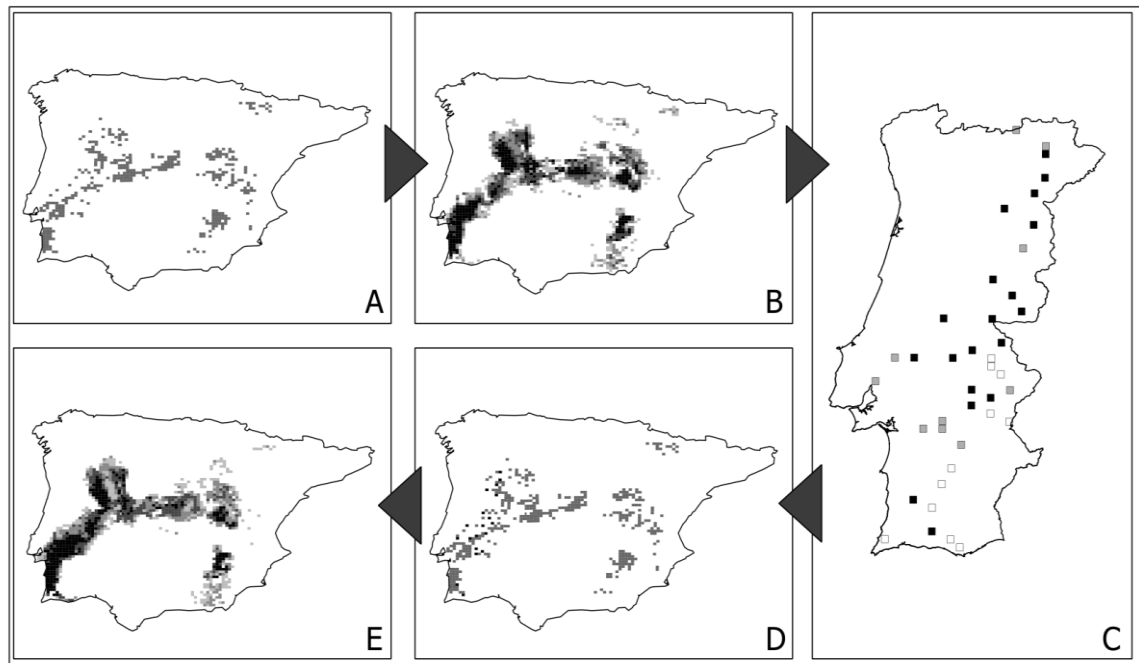


Figure 1 - a) Map of Cabrera vole occurrence records at a 10 km² cell grid resolution, which were used to build the initial Ecological Niche Model (ENM1) (records extracted

from literature published between 1970 and 2011, see Table A1 in Supplementary information); b) Potential range map predicted by ENM1; c) cells selected for field survey (black – confirmed presence; grey – collected samples, presence not confirmed; white – no samples collected); d) Refined map of Cabrera vole distribution (new field data in black) used to build the improved Ecological Niche Model (ENM2); e) Potential range map predicted by ENM2.

The model produced using the improved dataset (ENM2) showed a ranking of variables importance very similar to that obtained using ENM1, though there was a larger difference in the scores of the most and the least important variables. The ecological niche of the Cabrera vole defined by both models was also very similar, though ENM2 produced slightly wider amplitudes of adequate values for the species (Table 2). The predictive ability of ENM2 (AUC= 0.885 and AUC_{max} = 0.908) was similar to that of ENM1.

Table 2 - Minimum and maximum values of each variable, for all the square grids in the study area (study area), and for the square grids with confirmed occurrences (Occ. data) before and after non-invasive sampling at range margins, and for the models ENM1 and ENM2. See Table 1 for variable codes.

Variable	Study area		Occ. Data(initial)		ENM1		Occ. Data (final)		ENM2	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
MDR	5.312	12.869	8.265	12.410	8.406	12.410	8.265	12.410	8.122	12.410
MTCM	-8.796	9.032	-4.714	8.304	-4.777	8.304	-4.144	8.304	-4.777	8.409
MTWQ	0.272	19.974	1.256	15.360	1.256	12.900	1.256	15.360	1.256	14.303
PWM	31.750	246.070	41.540	178.753	41.540	132.480	41.539	178.753	41.540	145.090
PWQ	15.000	314.010	19.395	180.110	18.310	180.110	19.395	180.108	17.910	163.200

The modelling projections of ENM1 and ENM2 for 2020, 2050 and 2080 revealed considerable reduction in the potential distribution of the Cabrera vole under both climate change scenarios considered, although according to expectations, the B2 scenario had less dramatic effects than the A1b scenario (Figures 2 and A2). Pairwise comparisons between predicted range maps generated by ENM1 and ENM2 from the

present up to 2080 indicated that there was a general tendency for a decrease in map similarity, showing that the further in the future the projection is made more dissimilar outputs are produced (Table 3, and Figure 2). Differences between maps were largest in Portugal, where the supplementary field data were collected. In general, the predictions of ENM1 for future conditions failed to identify potentially suitable areas that were identified using ENM2. For instance, under scenario B2 the ENM2 predicts that the Cabrera vole will maintain a considerable range in south-western Portugal, while this area is deemed largely unsuitable by ENM1.

Table - 3 Results of range map comparison of models ENM1 and ENM2 using fuzzy Kappa index, implemented with the Map Comparison Kit, at the scale of both the Iberian Peninsula and Portugal. Current: model projected to the current climatic conditions; A1 and B2: IPCC climatic storyline with the respective years.

Climate Scenario/Time step	Portugal	Iberian Peninsula
Current	0.579	0.635
A1b-2020	0.553	0.559
A1b-2050	0.291	0.449
A1b-2080	0.149	0.337
B2-2020	0.433	0.509
B2-2050	0.464	0.500
B2-2080	0.260	0.326

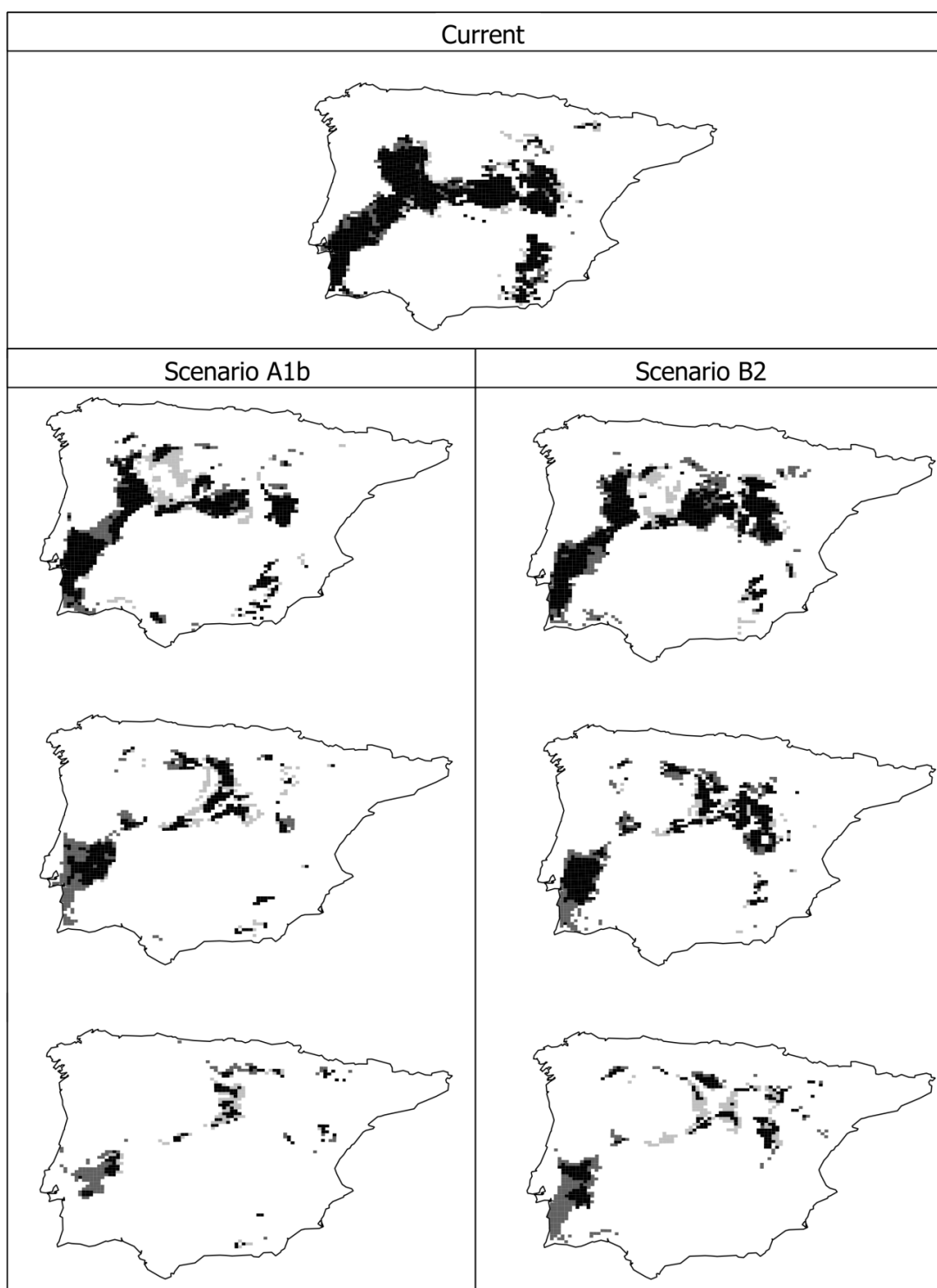


Figure 2 - Model comparisons for the studied time steps and climate scenarios. Current – top; Scenario A1b (left column): from 2020 (top) to 2080 (bottom); Scenario B2 (right column): from 2020 (top) to 2080 (bottom). Light grey – only ENM1 predicts presence; Dark grey - only ENM2 predicts presence; Black – both models predict presence.

4. Discussion

Our empirical example focusing on the Cabrera vole supports the view that a combination of ENM modelling and field surveys based on non-invasive genetic sampling provides a relatively simple, accurate and effective approach to refine estimates of species ranges in poorly surveyed areas, thus contributing to improve predictions of current and future species ranges. This is in line with research pointing out the value of non-invasive genetics to describe species distribution patterns (e.g. Waits, 2004) but, to our knowledge, this method had not been used before in combination with ENM to improve the forecast of range shifts under climate change. This approach may be particularly useful for rare, elusive, and patchily distributed habitat specialist species, such as the Cabrera vole in the Iberian Peninsula, which are difficult to sample using traditional methods (e.g. direct counts, camera or live trapping, etc.). Our study also suggested that the combination of ENM and non-invasive genetic sampling in poorly surveyed areas may be particularly useful to clarify range edges, where species often occur at low density and are difficult to detect. Field surveys at range edges may provide a major contribution to improve estimates of species niche breadth, which may then have major consequences for predictions based on ENMs (Gaston, 2003; Hanspach et al. 2011).

Although field surveys carried out in this study to refine range margins covered only a part of the species distribution where it is presumably under sampled, this is unlikely to have affected our key results in a significant way. In particular, this constraint is unlikely to undermine the contention that even relatively modest refinements in current range margin delimitation, may generate highly divergent predictions of species range shift. We recognise, however, that concentrating new surveys in a part of the species' range likely resulted in an incomplete coverage of the species ecological niche, which might have translated in an ecological bias (Peterson et al. 2011). This probably explains why differences between ENM1 and ENM2 predictions were much larger in Portugal than in Spain, as the new surveys were only carried out in the former. Results thus suggest that future studies refining the range margins of the Cabrera vole in Spain could strongly improve predictions regarding range shifts under

climate change. Another potential problem was that field surveys were focused exclusively on range margins, and so likely false negatives within the core range were not corrected. However, this is somewhat less problematic, since the environmental conditions within the core distribution are already sufficiently represented by the high number of occurrence records registered in this area.

The modelling results obtained with either ENM1 or ENM2 highlighted the small current range of the Cabrera vole within the Iberian Peninsula and confirmed the predicted northward range shift in response to future climate change (Araújo et al. 2011b). This suggests distinct population dynamics, and thus distinct conservation needs, between potentially expanding and contracting edges, with higher extinction rates in the southern rear edge, and higher colonization rates in the northern front range. In addition, results also suggest that the overall balance between predicted extinctions and colonisations up to the year of 2080, should in general favour extinction events, as evidenced by the strong decrease in the overall potential range size of the species for both climate change scenarios considered. Projections of the ecological niche of the Cabrera voles further highlighted the importance of the central region of Portugal for the species, particularly after considering the new localities identified by combining ENM and non-invasive genetic sampling along the range margins in Portugal. Thus, because this region is likely to retain the climatic conditions necessary for the long term persistence of the Cabrera vole, it may be particularly important in terms of conservation planning.

Differences between ENM1 and ENM2 in current and future range predictions were significant, mostly in Portugal, despite the relatively modest increase in the number of new occurrences obtained through non-invasive genetic sampling. In general, environmental characteristics at the range margins of a species are different from those in the core range (Sexton et al. 2009). Local populations at range margins are often restricted to sub-optimal habitats (Gaston, 2003) which, although representing a minor part of the species' environmental ranges, should be essential to assess fine-scale distributional details and to produce more realistic predictions regarding species responses to climate change (Sexton et al. 2009). Our study thus supports the view

that undetected presences along species range margins may have particular impact on the predicted range shifts of patchily distributed species (Hanspach et al. 2011). Fine-scale evaluation of species distribution in the range margins should thus be critical to properly assess species ecological niche, project species range shifts, and define specific conservation measures for different parts of the species range. In this context, non-invasive genetic sampling along the areas where species are poorly sampled and where most suitable environmental conditions become scarcer (e.g. range margins, distributional gaps), seems to provide a very useful approach to detect species at low densities. In particular, for species difficult to survey using standard sampling approaches, model-guided non-invasive genetic sampling provides a reliable and readily usable approach to detect marginal populations that otherwise would remain unknown, and hence, to identifying highly suitable regions for habitat restoration, preservation, or species translocations (Peterson et al. 2011).

Overall, the additional data provided by the non-invasive genetic sampling at range margins produced important differences in the predicted distribution of the species under both future climate change scenarios considered. In each case, the central/southwestern portion of Portugal assumed an increased importance for the Cabrera vole when predictions were based on ENM2, particularly under the scenario B2 for 2080. These differences in predicted range shifts between models may have important consequences for scheduling conservation actions, particularly for identifying and selecting priority areas where local- and landscape-level management prescriptions are to be implemented. Proper allocation of conservation efforts aiming the long-term conservation of the species should be particularly critical, given the considerable reduction of the distribution range of the species, consistently predicted across climate change scenarios and models considered. Thus, our results strengthen the idea that predicting species range shifts for conservation purposes should require an accurate assessment of the species' niche, which in many cases may be incorrectly estimated when species range margins are poorly defined.

Obtaining accurate and reliable predictions of current and future species ranges based on ENM should be best supported when the actual known geographical distribution of

the species cover their full ecological niche (e.g. Araújo and Guisan, 2006). Undetected presences in areas where species are actually present may have a strong impact on ENM results, particularly when local environmental conditions include possible extremes of species ecological niches (Comte and Grenouillet, 2013; Hanspach et al. 2011). In this context, non-invasive genetic sampling has shown to provide a reliable and often readily usable approach for detecting species in poorly surveyed areas and hence improve estimates of species distribution ranges. In particular, model-guided genetic sampling along species range margins should allow effective identification of new occurrences in areas where most suitable environmental conditions usually found in core ranges become scarcer (Oliver et al. 2009), and in turn may have great implications in the estimated ecological niche and thus in the predicted distributional ranges. Combining species distribution modelling with non-invasive genetic sampling along species range margins should thus be highly recommended to improve range shift forecasting and required conservation planning, based on incomplete datasets of species occurrences.

Acknowledgments

This study was funded by European Social Funds and the Portuguese Foundation for Science and Technology through the fellowships to FM (SFRH/BD/73768/2010), and RP (SFRH/BPD/73478/2010). It was also partially supported by the European Regional Development Fund (ERDF) through COMPETE program and Portuguese national funds through FCT (PTDC/BIA-BEC/105110/2008 and PTDC/AAG-MAA/3227/2012). JP has a post-doctoral grant funded by the project “Genomics and Evolutionary Biology” co-financed by North Portugal Regional Operational Programme 2007/2013 (ON.2 – O Novo Norte), under the National Strategic Reference Framework (NSRF), through the ERDF. The EDP Biodiversity Chair supported PB. We are grateful to Inês Leitão, Paulo Alves, Pedro Costa and Vânia Salgueiro for their collaboration in the field work, to Soraia Barbosa and Clara Ferreira for collaboration in genetic analyses, and to Robert P. Anderson for early discussions and revision of the manuscript.

Supplementary Material #1

Table A1 – Data sources for the Cabrera vole occurrences across Iberian Peninsula. Some square grids have the occurrence of the species confirmed by more than one reference. Therefore the sum of occurrences is not the same as the total number of occurrences (this dataset includes occurrences gathered from 1970 until 2011).

Source	Geographical range covered	Nr. grids
Published		
<i>Inventario Nacional de Biodiversidad. Vertebrados.</i> url: http://www.marm.es/es/biodiversidad/temas/inventarios-nacionales/inventario-nacional-debiodiversidad/mamiferos_m.aspx .	Continental Spain	276
<i>Conservation Biology Unit Database</i> (Universidade de Évora, Portugal)	Continental Portugal	51
Mira, A.; Marques, C.C.; Santos, S.; Rosário, I.T.; & Mathias, M.L. (2008). Environmental determinants of the distribution of the Cabrera vole (<i>Microtus cabreræ</i>) in Portugal: Implications for conservation. <i>Mammalian Biology - Zeitschrift für Säugetierkunde</i> , 73(2), pp.: 102-110.	Continental Portugal	35
Santos, S. M., Mathias, M., Mira, A., & Simões, M. P. (2007). Vegetation structure and composition of road verge and meadow sites colonized by Cabrera vole (<i>Microtus cabreræ</i> Thomas). <i>Polish Journal of Ecology</i> , 55(3), 481. Santos, S. M., Simões, M. P., Mathias, M. D. L., & Mira, A. (2006). Vegetation analysis in colonies of an endangered rodent. <i>Ecological Research</i> , 21(2): 197-207.	Central Portugal	25
Rosário, I. T., Cardoso, P. E., & Mathias, M. D. L. (2008). Is habitat selection by the Cabrera vole (<i>Microtus cabreræ</i>) related to food preferences? <i>Mammalian Biology-Zeitschrift für Säugetierkunde</i> , 73(6), 423-429. Rosário, I.T. <i>Towards a conservation strategy for na endangered rodent, the Cabrera vole (Microtus cabreræ Thomas) insights from ecological data.</i> PhD Thesis. Faculdade de Ciências, Departamento de Biologia Animal, Universidade de Lisboa. Lisboa, Portugal.	Southern Portugal	15
Pita, R. (2010). <i>Persistence and coexistence of spatially structured populations in heterogeneous environments: The case of Cabrera and water voles in Mediterranean farmland.</i> PhD Thesis, Universidade de Évora. Évora, Portugal.	Southern Portugal	10
Mira, A.; Ascensão, F. & Alcobia, S. (2003). <i>Distribuição das espécies de roedores e insectívoros - Relatório final</i> , Unidade de Biologia da Conservação, Universidade de Évora.	Southern Portugal	6
Gonçalves P., Alcobia S. & Santos-Reis M., Eds. (2013). <i>Atlas dos Mamíferos na Charneca do Infatado</i> . Companhia das Lezírias S.A. / Centro de Biologia Ambiental (FCUL), Benavente e Lisboa, 92 pp.	Central Portugal	3
Ortuño, A. (2009). Nuevos datos sobre la distribución del Topillo de Cabrera <i>Microtus cabreræ</i> Thomas, 1906 en Murcia. <i>Galemys</i> , 21(2): 71-72.	South-eastern Spain	3
Profico Ambiente (2009). <i>RECAPE do Aproveitamento Hidroelétrico de Foz Tua; Anexo Y - Estudo Complementar Sobre o Rato-de-Cabrera; Relatório de Conformidade Ambiental do Projecto de Execução do Aproveitamento Hidroelétrico de Foz Tua.</i>	North-eastern Portugal	2
Mathias, M.L.; Mira, A.; Pereira, M.; Pereira, P.; Nunes, A.C.; Marques, C.C.; Figueiredo, C.; Carvalho, F.N.; Sousa, I.; Perestrello, M.; Santos, M.J.; Santos, S. & Oliveira, V. (2004). <i>Programa de monitorização do património natural (Área do regolfo de Alqueva e Pedrógão) - Projecto Pmo 6.2 - Monitorização de roedores - Relatório Final</i> , Centro de Biologia Ambiental (Faculdade de Ciências da Universidade de Lisboa) e Centro de Ecologia Aplicada (Universidade de Évora).	Southern Portugal	1
Anonym (2008). <i>Estudo de Impacte Ambiental do Estudo Prévio da Ocupação Turística da UNOP 4 DE Tróia</i> , Resumo Não Técnico.	Southern Portugal	1
Unpublished		
Frederico Mestre (own data).	Southern Portugal	3
Célia Gomes unpublished data.	North-eastern Portugal	3

Table A2 - Summary results of non-invasive genetic analysis; Grid location: RE – Rear edge, out of the predicted potential niche; RI - Rear edge, inside the predicted potential niche; FE – Front edge, out of the predicted potential niche; FI - Front edge, inside the predicted potential niche.

UTM code	Sample group	Sample collection		Genetic analysis		Cabrera vole		Other species		Genetic ID failed
		Sites	Samples	Sites	Samples	Sites	Samples	Sites	Samples	
29SNB11	RE	0	0	-	-	-	-	-	-	-
29SNB46	RI	1	1	1	1	1	1	0	0	0
29SNB62	RI	1	2	1	1	1	1	0	0	0
29SNB65	RE	0	0	-	-	-	-	-	-	-
29SNB78	RE	0	0	-	-	-	-	-	-	-
29SNB81	RE	0	0	-	-	-	-	-	-	-
29SNB90	RI	0	0	-	-	-	-	-	-	-
29SNC55	RI	1	1	1	1	0	0	0	0	1
29SNC75	RE	1	1	1	1	0	0	1	1	0
29SNC76	RI	1	1	1	1	0	0	0	0	1
29SNC80	RE	0	0	-	-	-	-	-	-	-
29SNC93	RE	1	1	1	1	0	0	1	1	0
29SND01	FE	2	6	2	6	0	0	2	6	0
29SND24	FE	5	12	5	10	0	0	5	10	0
29SND44	FI	2	10	2	6	1	3	1	2	1
29SND79	FE	9	27	6	8	3	3	4	5	0
29SND84	FI	1	2	1	2	1	2	0	0	0
29SPC08	RI	1	1	1	1	1	1	0	0	0
29SPC27	RE	0	0	-	-	-	-	-	-	-
29SPC29	RI	1	2	1	2	1	2	0	0	0
29SPC46	RE	0	0	-	-	-	-	-	-	-
29SPD00	RI	1	2	1	2	1	2	0	0	0
29SPD05	FI	1	3	1	2	1	2	0	0	0
29SPD23	RI	0	0	-	-	-	-	-	-	-
29SPD24	FI	1	3	1	3	0	0	1	3	0
29SPD29	FE	8	22	2	2	2	2	0	0	0
29SPD32	RI	0	0	-	-	-	-	-	-	-
29SPD36	FE	2	5	1	2	1	2	0	0	0
29SPD40	RE	1	1	1	1	0	0	1	1	0
29SPE42	FI	2	11	1	3	1	3	0	0	0
29SPE50	FI	4	12	1	2	1	2	0	0	0
29TPE24	FE	6	18	5	8	2	2	3	5	1
29TPE58	FE	10	46	10	12	0	0	9	10	2
29TPF33	FE	9	44	2	3	1	1	1	1	1
29TPF61	FI	5	20	1	3	1	3	0	0	0
29TPF65	FI	3	12	1	2	1	2	0	0	0
29TPF77	FI	7	13	2	2	2	2	0	0	0
29TPG43	FE	8	33	7	12	0	0	7	11	1
29TPG70	FI	7	20	1	2	1	1	1	1	0
29TPG71	FE	8	19	7	13	0	0	6	10	3

Table A3 – Summary results of correlation analysis (in grey - Spearman $|r| > 0.7$).

	bio1	bio2	bio3	bio5	bio4	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio1		0.068	0.162	0.695	-0.050	0.881	0.008	0.426	0.814	0.894	0.938	-0.222	-0.037	-0.833	0.785	-0.004	-0.798	-0.756	0.066
bio2			-0.042	0.715	0.848	-0.334	0.954	-0.043	0.478	0.431	-0.207	-0.594	-0.631	-0.377	0.066	-0.588	-0.427	-0.467	-0.427
bio3				-0.101	-0.515	0.307	-0.316	-0.100	0.048	-0.084	0.323	0.208	0.284	-0.123	0.276	0.306	-0.094	-0.097	0.353
bio5					0.627	0.323	0.699	0.211	0.886	0.923	0.434	-0.571	-0.488	-0.822	0.557	-0.429	-0.834	-0.839	-0.264
bio4						-0.447	0.962	0.026	0.343	0.375	-0.355	-0.606	-0.674	-0.233	-0.100	-0.650	-0.291	-0.324	-0.544
bio6							-0.407	0.304	0.552	0.601	0.982	0.130	0.308	-0.600	0.743	0.333	-0.538	-0.497	0.361
bio7								-0.030	0.432	0.419	-0.295	-0.617	-0.676	-0.317	-0.015	-0.638	-0.375	-0.414	-0.492
bio8									0.165	0.382	0.382	-0.499	-0.398	-0.206	0.008	-0.458	-0.216	-0.137	-0.571
bio9										0.914	0.637	-0.375	-0.250	-0.867	0.699	-0.193	-0.854	-0.852	-0.021
bio10											0.694	-0.476	-0.336	-0.869	0.671	-0.295	-0.861	-0.835	-0.187
bio11												0.004	0.194	-0.679	0.765	0.219	-0.626	-0.579	0.254
bio12													0.953	0.370	0.045	0.952	0.448	0.418	0.875
bio13														0.210	0.241	0.986	0.291	0.281	0.892
bio14															-0.862	0.143	0.987	0.978	-0.018
bio15																0.301	-0.816	-0.806	0.412
bio16																	0.227	0.208	0.939
bio17																		0.988	0.059
bio18																			0.011
bio19																			

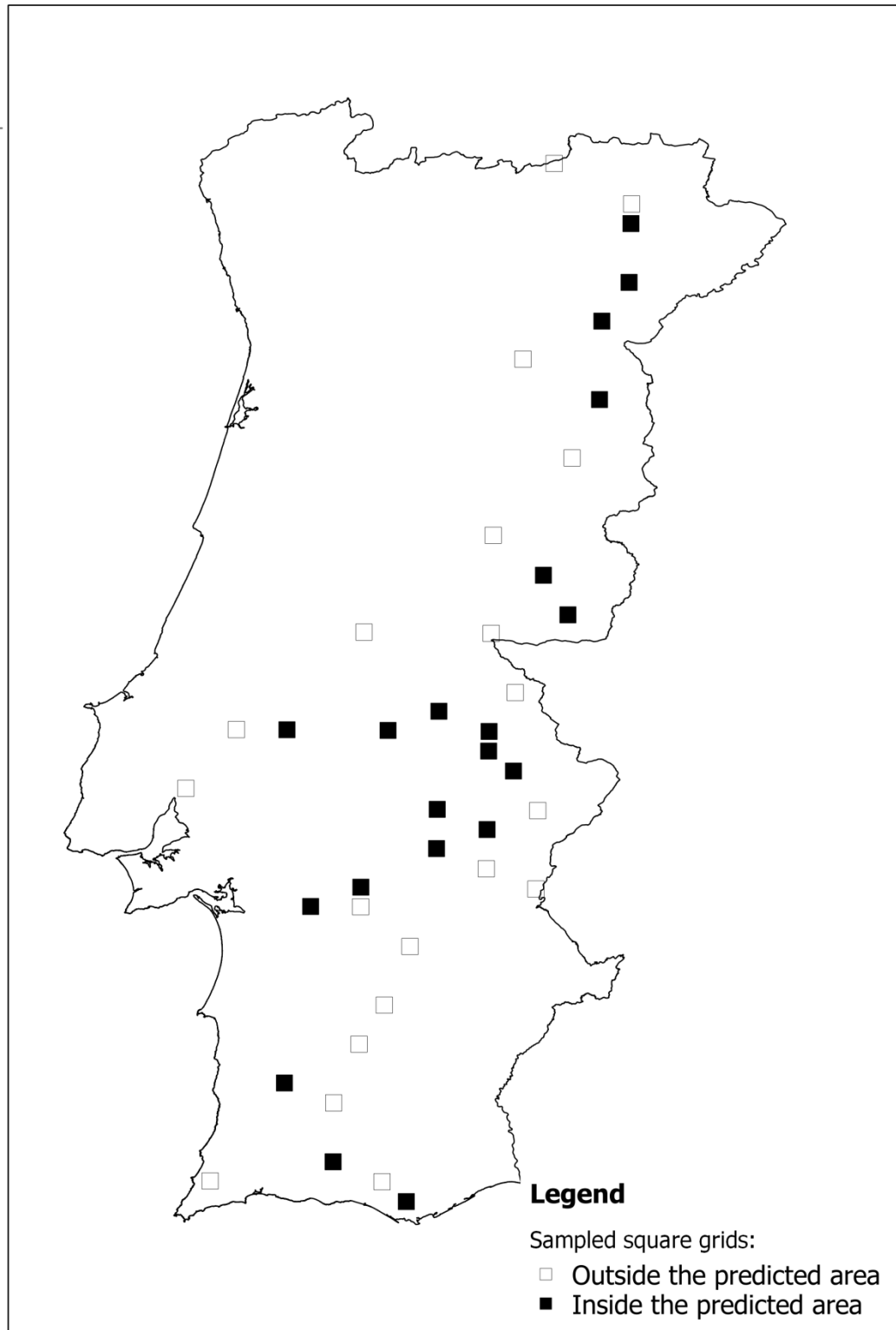


Figure A1 – Sampled 10x10 km UTM grids. Inside the potential niche, as given by ENM1 (black) and outside the potential niche, as given by ENM1 (white).

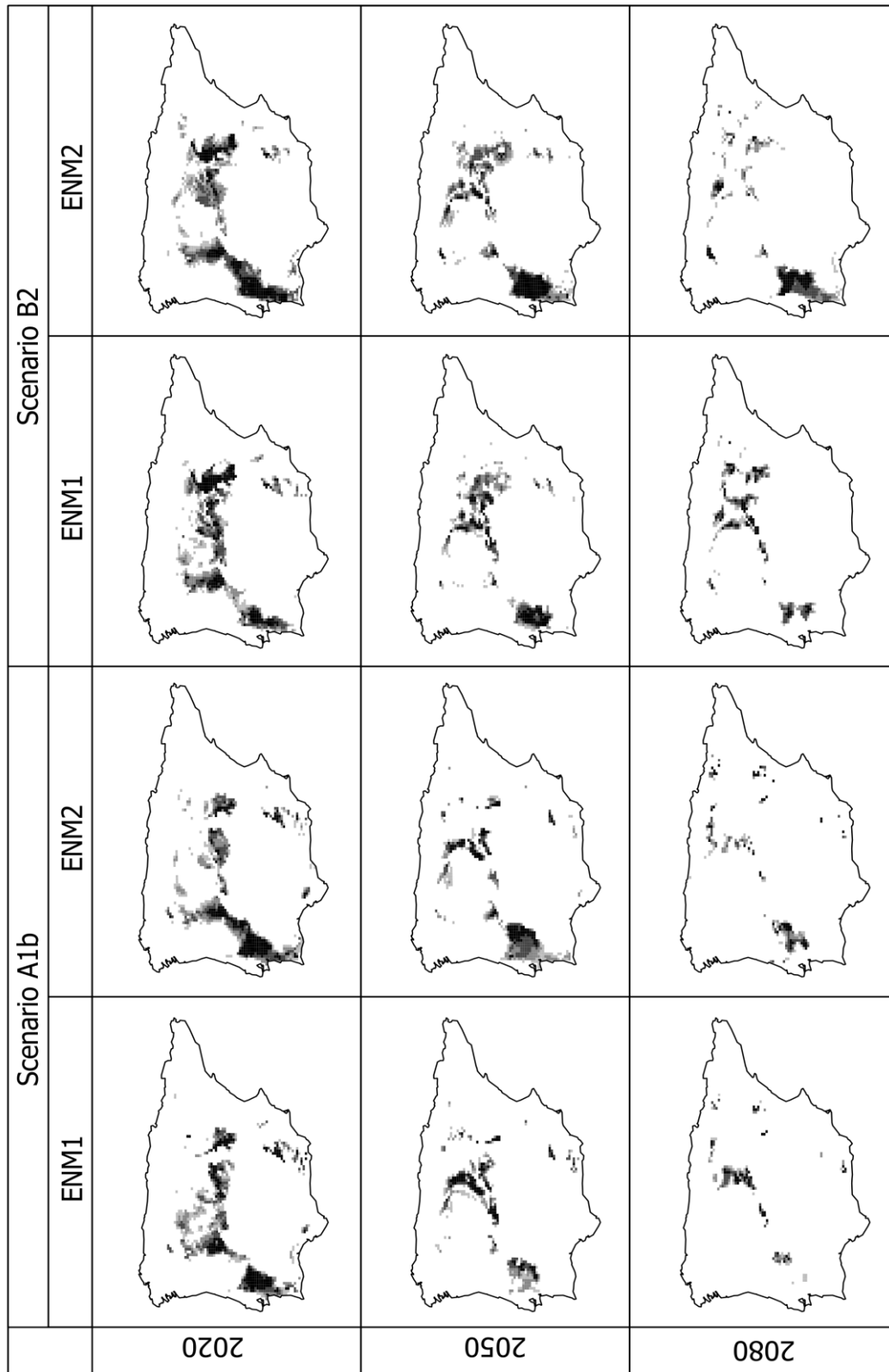


Figure A2 – Maps of predicted distribution of the Cabrera vole in 2020, 2050, and 2080 (IPCC Scenarios B2 and A1b), based on the projection of models developed considering the original dataset (ENM1) and the dataset including additional field data (ENM2).

Chapter 3

An R Package for simulating metapopulation persistence and range expansion under environmental change

Published on Environmental Modelling & Software as:

Mestre, F.; Cánovas, F.; Pita, R.; Mira, A. & Beja, P. (2016). "An R Package for simulating metapopulation persistence and range expansion under environmental change". *Environmental Modelling & Software*, 81: 40-44.

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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.

Keywords

Occupancy-extinction dynamics, landscape dynamics, incidence function model, climate change, range shift.

Software availability

Name of software: MetaLandSim

Developers: Mestre, F.; Cánovas, F.; Pita, R; Mira, A. and Beja, P.

Contact address: CIBIO/InBio, Centro de Investigação em Biodiversidade e Recursos Genéticos, Pólo de Évora, Universidade de Évora, Núcleo da Mitra, Apartado 94, 7002-554, Évora, PORTUGAL. +351 282338232

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 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, which provides a set of user-friendly tools to simulate metapopulation dynamics and range expansion, integrating and enhancing considerably the functionalities available in other software (Supplementary Material #1, Table SM2). MetaLandSim represents virtual and real landscapes as graphs, and it uses SPOMs to simulate metapopulation dynamics. Graph-based techniques were used because they effectively summarize spatial relationships between patches, facilitate multi-scale analysis, and avoid technical restrictions due to computational constraints (Bergerot et al., 2013; Fortin et al., 2012; Galpern et al., 2011). Simulations can be carried out either in dynamic or static landscapes, with the level of dynamism specified by the user. Finally, MetaLandSim simulates metapopulation expansion into empty landscapes, and uses these simulations to compute dispersal models whereby the probability of landscape occupancy during a given time window in the future is specified as a function of geographical distance to currently occupied landscapes. The dispersal model can be combined with ecological niche models to estimate future species ranges under the constraint of dispersal limitations (e.g. Barbet-Massin et al. 2012), thus providing a mechanism to upscale metapopulation processes from the landscape to the regional and biogeographical scales. Hereinafter we summarise the main components, functions, and technical features of MetaLandSim (Figure 1). See Supplementary material #1 for a detailed description.

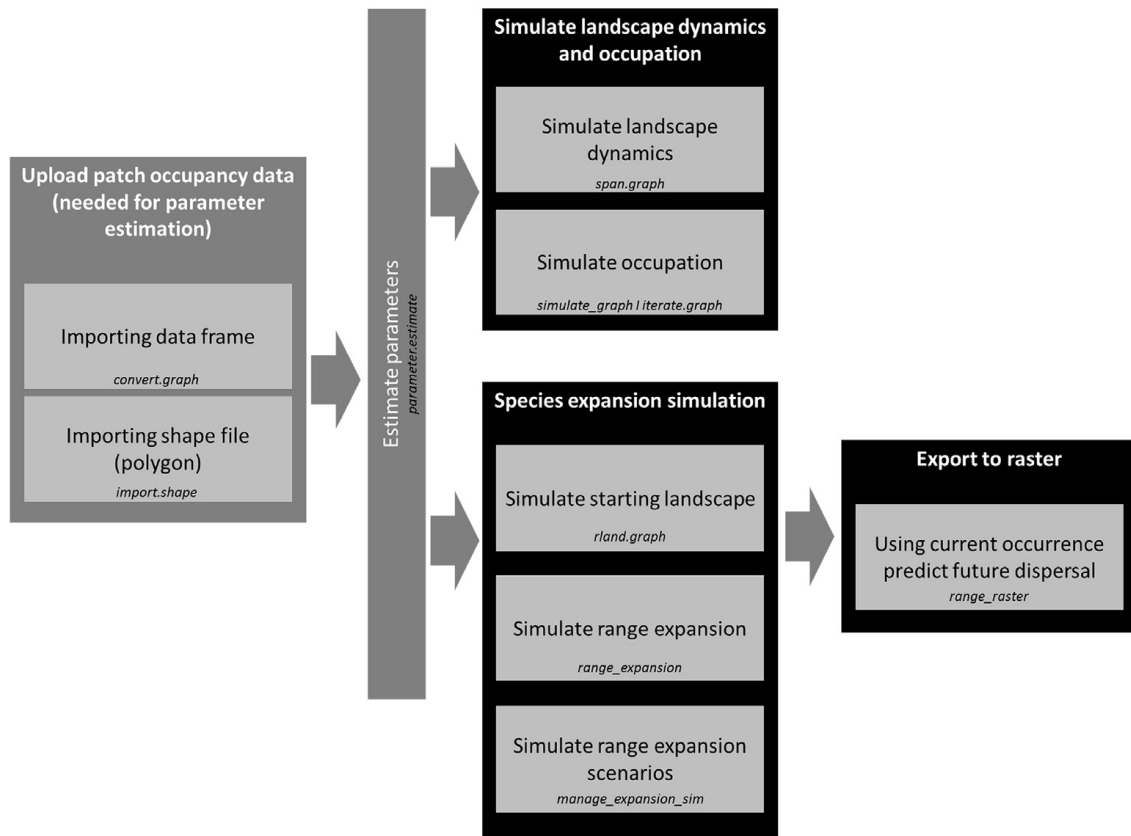


Figure 1 - General workflow of MetaLandSim package. Main functionalities are shown in the grey boxes and functions in italics.

2. Landscapes and metapopulations

Simulation in MetaLandSim requires specification of the initial landscape features and patch occupancy patterns, and the metapopulation parameters (Figure 1). MetaLandSim creates random landscapes (function “*rland.graph*”), or loads real ones from a data frame (“*convert.graph*”) or a polygon shapefile (“*import.shape*”) (Figure 2A). Landscapes are represented as graphs, where nodes correspond to habitat patches surrounded by an inhospitable matrix, which may be scored according to patch size (Hanski, 1994; Moilanen and Hanski, 1998). Landscape dynamism may be specified through temporal variations in the number, sizes and spatial distribution of patches (“*iterate.graph*”). MetaLandSim produces maps of the graph-like landscapes, with node sizes and colour corresponding for instance to patch size and occupancy status, respectively (Fig 2A). Each pair of nodes is linked by an edge, with the probability of dispersal specified as a decreasing function of inter-node distance (e.g. Saura and Pascual-Hortal, 2007). For graphical purposes MetaLandSim only represents

edges when internode distances are shorter than the species mean dispersal ability (Fig 2A). MetaLandSim computes 15 landscape connectivity metrics (“metrics_graph”), mostly derived from graph theory or assuming a graph representation of the landscape (Table SM4 in Supplementary Material #1).

The metapopulation parameters used in simulations may be specified by the user to describe a virtual species, or they may be estimated from empirical data. Because simulations are based in SPOMs, the parameters required are: “a”, the reciprocal of the species mean dispersal ability ($a = 1/\text{dispersal ability}$); “x”, describing the strength of the relation between extinction risk and patch area, with lower values corresponding to higher extinction risk due to increased environmental stochasticity; “y”, which affects colonization efficiency; and “e”, the extinction probability in a patch of unit area (Hanski, 1999; Etienne et al., 2004). MetaLandSim estimates these parameters from snapshot surveys of patch occupancy (“parameter.estimate”), which assume that metapopulations are in equilibrium (Hanski, 1994; Ter Braak et al., 1998; Moilanen, 2000). Alternatively, MetaLandSim generates input files for external software applications, which estimate metapopulation parameters from occupancy turnover observed in consecutive surveys (Moilanen, 2000), using Monte Carlo simulation (Moilanen, 1999) or Bayesian MCMC (Ter Braak and Etienne, 2003).

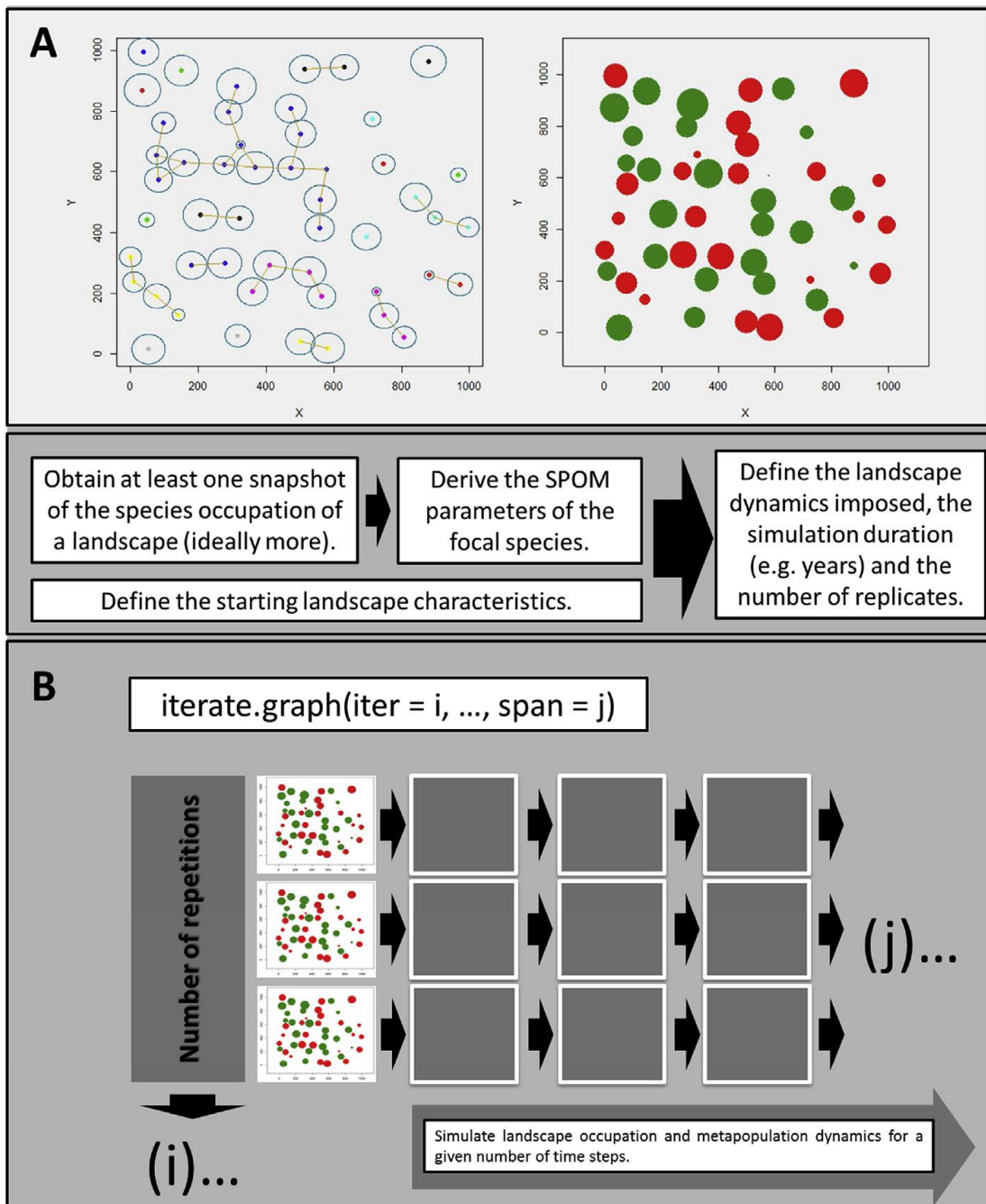


Figure 2 - (A) Empty (left) and occupied (right) graph-like landscapes represented by MetaLandSim, with nodes corresponding to either occupied (green) or unoccupied (red) patches. In the left panel, the edges (links) correspond to interpatch distances shorter than the mean dispersal ability of the focal species. (B) Simplified scheme of MetaLandSim simulations of metapopulation dynamics (SPOM) during “j” time steps, and with “i” iterations.

3. Metapopulation dynamics

MetaLandSim uses Markov chain-based SPOMs (“spom”) to simulate metapopulation dynamics multiple times (“iterate.graph”) in static or dynamic landscapes, either real or virtual. After input of the parameters for a real or virtual species, the user can specify two alternative kernel functions describing distance dependent dispersal, two connectivity functions describing the probability of dispersal between any two patches, and three functions each for the colonization and extinction rates (Table SM1 in Supplementary Material #1). Irrespective of the options chosen, simulations start with an occupied landscape at time t , and then estimate the occupancy status of each patch at each of n successive time steps ($t + 1, t + 2, \dots, t + n$)(Figure 2B). At each step, MetaLandSim computes a number of parameters describing landscape (e.g., mean patch area, number of patches, mean nearest-neighbour distance between patches) and metapopulation (e.g., percentage of patches occupied, occupancy turnover) characteristics. Results can be viewed in HTML format, using an interface with Google Chart Tools API through googleVis package (Gesmann and Castillo, 2011). See Supplementary Material #2, for a worked example.

4. Range expansion

To simulate metapopulation expansion into empty landscapes (“range_expansion”), MetaLandSim starts with an occupied landscape with a given set of patch characteristics, where metapopulation dynamics is simulated using SPOMs as described in section 3 (Figure 3). A spurious node is set at each of the cardinal margins (i.e., north, south, east, and west) of the landscape, which is used to detect when the metapopulation reaches that margin. When a spurious node is occupied, the algorithm assumes the transition to an empty landscape in the corresponding cardinal direction. This new landscape is generated randomly, with characteristics similar to that of the initial occupied landscape. Metapopulation dynamics is then simulated in this new landscape starting from the newly occupied margin. The process is repeated across landscapes that become progressively available to the metapopulation until it hits the

time steps defined, producing a map of the total area and number of landscapes occupied at the end of simulation. Future versions of MetaLandSim will allow direct dispersal in diagonal directions, which at present are mimicked through rook-like movements in a chessboard. Also, they will include the possibility of metapopulation and landscape characteristics varying spatially, thereby accounting for instance for geographic changes in land uses or habitat fragmentation patterns. See Supplementary Material #2, for further discussion on MetaLandSim limitations. After “m” iterations of the metapopulation expansion simulation (defined by the argument “iter”), MetaLandSim computes the proportion of times each new landscape was occupied (i.e., probability of landscape occupancy; Figure 3). These data are then used for estimating a dispersal model for a given species and simulation conditions, which involves fitting a sigmoid curve relating the probability of landscape occupancy during the simulation period to the nearest distance to landscapes occupied at the beginning of the simulation (Figure 3). Different dispersal scenarios may be obtained by specifying metapopulation expansion into landscapes with different characteristics (“manage_expansion_sim”), thereby estimating how the speed and spatial pattern of expansion may be affected, for instance, by habitat fragmentation and dynamism. Dispersal models may also be combined with maps of current species distributions (“range_raster”), generating maps of occupancy probabilities resulting exclusively from metapopulation expansion into empty landscapes during a given time frame. Externally to MetaLandSim, these maps can be combined with projections from Ecological Niche Models to estimate species distributions accounting for both future environmental conditions, and species and landscape-specific dispersal limitations. See Supplementary Material #2 for a worked example.

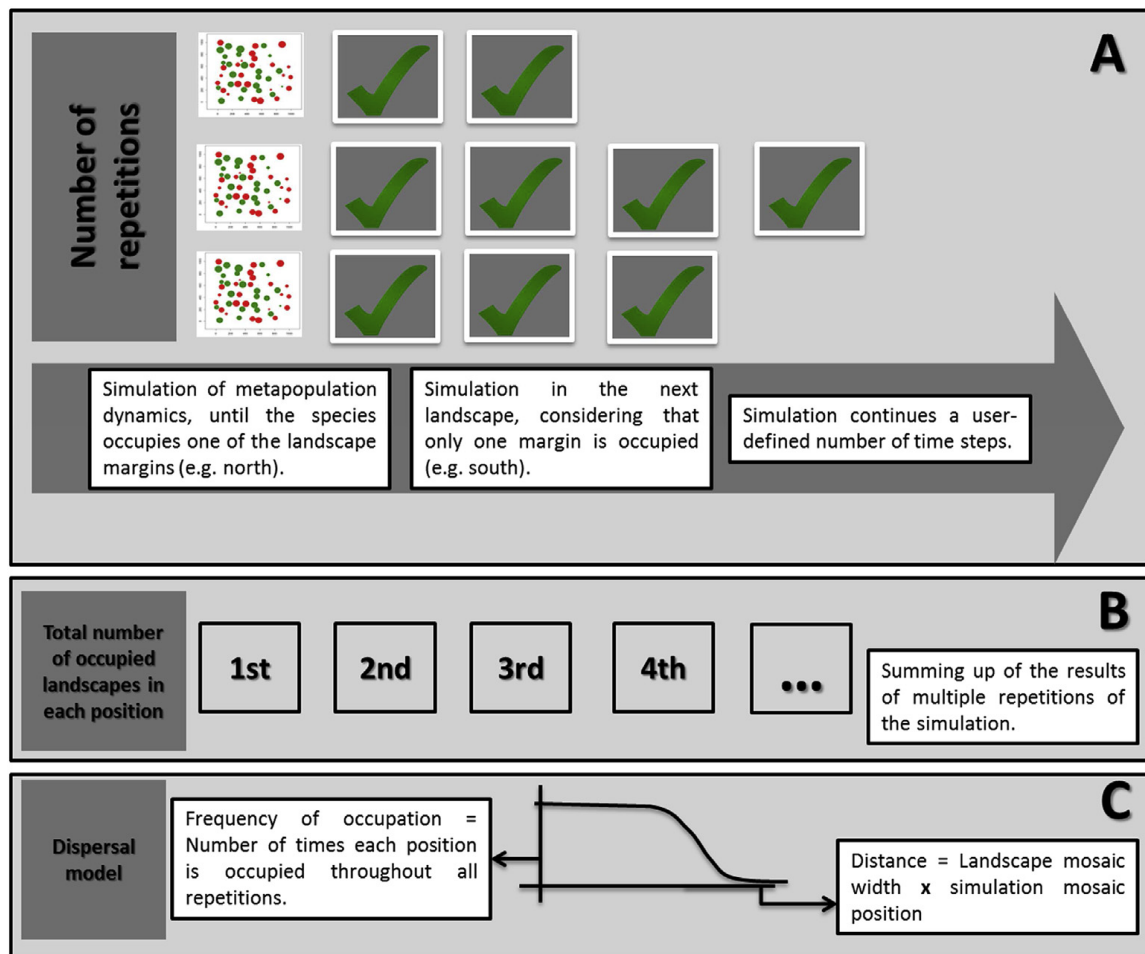


Figure 3 - Simplified scheme of MetaLandSim simulation of metapopulation range expansion and the estimation of a dispersal model. (A) Sequential colonization of empty landscapes, based on simulations of metapopulation dynamics (SPOM) during “j” time steps, and with “i” repetitions. (B) Number of occupied landscapes in all positions during the simulations. (C) Sigmoid curve (dispersal model) specifying the probability of patch occupancy in relation to the nearest distance to occupied landscapes at time step $j = 0$.

Acknowledgements

This study was funded by the Portuguese Foundation for Science and Technology through the fellowships to FM (SFRH/BD/73768/2010), RP (SFRH/BPD/73478/2010) and FC (SFRH/BPD/38665/2007) and the project NETPERSIST (PTDC/AAG-MAA/3227/2012). The EDP Biodiversity Chair supported PB. We thank the thoughtful revision of the manuscript by two anonymous reviewers.

Supplementary Material #1

Review of Software and MetaLandSim Structure

Frederico Mestre, Fernando Cánovas, Ricardo Pita, António Mira, and Pedro Beja

- Table SM1. Equations describing alternative functions available in MetaLandSim.
- Table SM2. Comparison of the functionalities and data requirements of MetaLandSim (MLS) and other software packages.
- Tables SM3. Main functions and object classes in MetaLandSim.
- Table SM4. Landscape connectivity metrics computed by MetaLandSim.

Table SM1. Equations describing the alternative functions available in MetaLandSim to model the dispersal kernel, the connectivity among patches, and the colonization and extinction rates. Users should select options according to the specific research questions and characteristics of the focal metapopulations (see also the “user’s manual”).

Dispersal kernel	Connectivity	Colonization	Extinction
$D(D_{ij}, \alpha) = \exp(-\alpha \cdot d_{ij})$ Hanski (1994, 1999)	$S_i = \sum p_j \cdot D \cdot A_j^b$ Moilanen (2004)	$C_i = \frac{S_i^2}{S_i^2 + y^2}$ Hanski (1994, 1999)	$E_i = \min\left(1, \frac{e}{A_i^x}\right)$ Hanski (1994, 1999)
$D(D_{ij}, \alpha, \beta) = \frac{1}{1 + \alpha \cdot d_{ij}^\beta}$ Shaw (1995)	$S_i = A_i^c \sum p_j \cdot D \cdot A_j^b$ Moilanen & Nieminen (2002)	$C_i = 1 - \exp(-y \cdot S_i)$ Moilanen (2004)	$E_i = 1 - \left(\frac{-e}{A_i^x}\right)$ Hanski & Ovaskainen (2000); Ovaskainen & Hanski (2002)
		$C_i = \frac{S_i^z}{S_i^z + \frac{1}{c}}$ Ovaskainen (2002a)	$E_i = \min\left[1, \frac{e}{A_i^x} \cdot (1 - C_i)^R\right]$ Ovaskainen (2002a)

Parameters in dispersal kernel (DK), connectivity (Cn), colonization (Cl) and extinction (E):

α (DK) – Parameter describing survival while crossing the matrix (1/ mean dispersal distance).

β (DK) – Parameter related with the shape of the dispersal kernel.

d_{ij} (DK) – Interpatch distance between the focal patch (i) and patch j.

A_j ; p_j (Cn) – Area and occupation state of the other patch (j).

c , b (Cn) – Parameters scaling focal patch (i) area and other patch area (j).

y , c (Cl) – Parameters regulating efficiency of colonization.

z (Cl) – Parameter regulating Allee effect (with value 2 in the option 1).

e (Ex) – Extinction probability in patch of unitarian area.

x (Ex) – Parameter scaling extinction risk with focal patch area.

R (Ex) – Parameter regulating Rescue effect.

Table SM2A. Comparison of MetaLandSim (MLS) with other software packages available for running metapopulation simulations, regarding data requirements (landscape and metapopulation parameters), main uses and outputs produced.

Software	Data requirements	Main uses/features	Comparison with MLS	References
SIMMAP	<ul style="list-style-type: none"> • Landscape configuration: <ul style="list-style-type: none"> - initial probability - classes - pattern - minimum mapped unit - neighborhood criteria. 	<ul style="list-style-type: none"> • Spatial simulation. 	<ul style="list-style-type: none"> • Provides categorical raster maps. • Species occupancy not considered. • Temporal variation not considered. 	Saura & Martínez-Millán (2000)
Graphab	<ul style="list-style-type: none"> • Landscape map. • Species dispersal ability. 	<ul style="list-style-type: none"> • Landscape connectivity. • Integration with SDMs. • Connectivity metrics. 	<ul style="list-style-type: none"> • Random landscapes not generated. • Metapopulation simulation on a dynamic landscape not implemented. 	Foltête et al. (2012)
Conefor Sensinode	<ul style="list-style-type: none"> • Landscape map. • Species dispersal ability. 	<ul style="list-style-type: none"> • Connectivity analysis. • Patch and link importance. • Allows prioritization. 	<ul style="list-style-type: none"> • Random landscapes not generated. • Simulation of Landscape dynamics not implemented. • Metapopulation simulation on a dynamic landscape not implemented. 	Saura & Torné (2009)
Spomsim	<ul style="list-style-type: none"> • Metapopulation occupancy. • Species dispersal ability. 	<ul style="list-style-type: none"> • SPOM definition. • Metapopulation simulation. • Parameter estimation. • Reserve network design. 	<ul style="list-style-type: none"> • MLS is more effective in setting up the landscape dynamism. • Connectivity metrics not computed. • Simulation of landscape dynamics and occupation is much more straightforward in MLS. 	Molilanen (2004)
RAMAS Landscape	<ul style="list-style-type: none"> • Population-level demography. 	<ul style="list-style-type: none"> • Integrates LANDIS for simulating landscape change, with population-based simulation models generated in RAMAS GIS. 	<ul style="list-style-type: none"> • Requires far more detailed information for parametrization. 	Akçakaya et al. (1996, 2003); He et al. (1996)

Software	Data requirements	Main uses/features	Comparison with MLS	References
demoniche	<ul style="list-style-type: none"> • Requires detailed geographic and demographic information for the focal species. • Locations and areas of the species population (either metapopulation patches or grids). • Details on species dispersal and some demographic parameters (life stages information, vital rates, density, carrying capacity). 	<ul style="list-style-type: none"> • Enables the simulation of scenarios by creating demographic models with populations connected by dispersal with different habitat suitability. • Provides population estimates, considering environmental scenarios. 	<ul style="list-style-type: none"> • Requires much more information on demographic parameters. • Metapopulation simulation on a dynamic landscape not explicitly implemented. • Similarly to MLS, evaluates different scenarios, although MLS is based on the SPOM framework, deeply rooted in metapopulation ecology. 	Nenzén et al. (2012)

Table SM2B – Comparison of MetaLandSim (MLS) with other software packages available for simulating species range expansion, regarding data requirements (habitat and species parameters), main uses, and outputs produced.

Software	Data requirements	Main uses	Comparison with MLS	Reference
MIGCLIM	<ul style="list-style-type: none"> Suitability maps. Dispersal kernel. Reclassification threshold. Barrier effect and type. Propagule production. Long distance dispersal frequency. Minimum distance dispersal. Maximum distance dispersal. 	<ul style="list-style-type: none"> Projection of future distributions, considering the species dispersal ability and habitat suitability in different time steps. 	<ul style="list-style-type: none"> In MIGCLIM the dispersal kernel must be obtained elsewhere. The long distance dispersal parameters must be carefully considered as the barrier effect (since inaccurate values might produce incorrect results). MIGCLIM requires information on propagule production. MIGCLIM has the advantage of considering barrier effect (however in a simplified version). MLS allows the building of the dispersal model (equivalent to the kernel) through a simple approach, its projection into a map (provided the user as the current species range), and the evaluation of dispersal scenarios. MLS does not require demographic data. 	Engler et al. (2012)
BioMove	<ul style="list-style-type: none"> Semi-quantitative: <ul style="list-style-type: none"> Competitive capacity at different life-stages Dispersal ability Mortality rate Regeneration after fire Relevant disturbances Biological: <ul style="list-style-type: none"> Age-specific mortality and fecundity Age at maturity Disturbance response Mean dispersal distance Seed dispersal data. 	<ul style="list-style-type: none"> Simulation of plant species' geographic range shifts in response to climate, habitat structure and disturbance, at annual time steps. Simulation of a plant species dynamics within dynamic landscapes. 	<ul style="list-style-type: none"> BioMove was designed for plant species. BioMove considers species dispersal, inter-species competition and disturbance. It also requires much more data to parametrize the simulations (demographic, disturbance, etc) than MLS. 	Midgley et al. (2010)

Software	Data requirements	Main uses	Comparison with MLS	Reference
RangeShifter	<ul style="list-style-type: none"> Requires a large amount of parameters regarding species biological and ecological traits, habitat suitability and population dynamics. 	<ul style="list-style-type: none"> Integrate of complex population dynamics and dispersal behavior, include plastic and evolutionary processes and simulate scenarios on spatially explicit landscapes. 	<ul style="list-style-type: none"> The package may produce more realistic results than MLS because it integrates a large number of parameters from species and habitats, but it may be difficult to apply in most cases due to lack of the data required. MLS requires fewer assumptions, its implications are easier to understand and they potentially have less impact on the final output. 	Bocedi et al. (2014)

Table SM2C. Summary of comparisons between MetaLandSim and other software packages regarding data requirements, computation of connectivity metrics, generation of artificial landscapes, simulation of metapopulation dynamics in static and dynamic landscapes, production of range shift model and range shift scenario building. (*) Experimental feature, to be further developed.

Software	Data requirements	Connectivity metrics	Artificial landscapes	Metapopulation dynamics		Range shift model	Range shift scenario evaluation
				Static landscapes	Dynamic landscapes		
MetaLandSim	Low	X	X	X	X	X	X(c)
SIMMAP	Low	X	X				
Graphab	Moderate	X		X			
Conefor Sensinode	Low	X					
Spomsim	Low		X	X	X		
demoniche	Moderate			X		(b)	(b)
RAMAS Landscape	High						
MIGCLIM	Moderate					X	
BioMove	High					X	
RangeShifter	High		X	(a)		X	

(a) Simulates species spatial dynamics and landscape occupation (not metapopulation dynamics) in real or artificial landscapes, providing the possibility to simulate environmental gradients and environmental stochasticity.

(b) Although demoniche evaluates the species persistence under different environmental scenarios, it does not produce a spatial explicit dispersal model at the biogeographical scale.

(c) Experimental feature, to be further developed.

Table SM3A – Description of main function implemented in MetaLandSim (see details in the user manual and vignettes).

Function	Title	Description
convert.graph	Convert data frame to landscape	Converts a given data frame in a list which can be used in the following functions, an object of class 'metapopulation'.
import.shape	Import a shapefile	Imports a shapefile, converting it to an object of class 'metapopulation'.
iterate.graph	Simulate landscape series occupation	Repeats the process of simulation through <code>simulate_graph</code> as many times as required.
manage_landscape_sim	Manage landscape simulations	Runs a series of simulations allowing the change in simulation parameters in several sequential simulations.
manage_expansion_sim	Manage range expansion simulations	Runs a batch of range expansion simulations, allowing the evaluation of simulation parameters in the expansion.
MetaLandSim.GUI	Graphic User Interface	User-friendly graphic user interface that allows running the main functions of the package.
metrics.graph	Computes landscape connectivity metrics	Computes several landscape metrics, mostly derived from graph theory or assuming a graph representation of the landscape.
parameter.estimate	Estimate parameters	Estimates the parameters of the Stochastic Patch Occupancy Model with the following approaches. Uses regression of snapshot data and produces files to facilitate the use of external software applications which use Monte Carlo simulation and Bayesian MCMC on the full dataset.
plot_expansion	Graphical display of the expansion	Plots the expansion object.
plot_graph	Graphical display of the landscape	Plots the landscape graph, with or without the species occupation (respectively lists returned by <code>species.graph</code> or <code>rland.graph</code>) and with or without the links between patches.
range_expansion	Produce a range expansion model	This function returns the expansion probability, from a landscape with a given set of parameters, into the four cardinal directions. This can subsequently be converted in a dispersal model by the function <code>range_raster</code> . The dispersal model can be combined with an ecological niche model.
range_raster	Probability of occupancy, dispersal model	This function creates a raster map, estimating probability of occupancy, at a given time step, based on species dispersal and landscape configuration. <code>range_raster</code> uses the output from <code>range_expansion</code> and a raster map with the species current occupancy.
rland.graph	Function to create a random landscape graph	One of the key functions of the package, which allows the creation of random landscapes (represented as graphs) with two categories: habitat patch and non-habitat matrix. The landscapes can be different depending on the parameters chosen.
simulate_graph	Simulate species occupancy in one dynamic landscape	Simulates the species' occupation on a landscape sequence, resorting to the <code>spom</code> function.

Table SM3B. Description of the object classes used in MetaLandSim.

Class	Description
Landscape	<p>Class representing a landscape graph, as produced by <code>land.graph</code>, <code>convert.graph</code> and <code>import.shape</code>.</p> <ul style="list-style-type: none"> • <code>mapsize</code> - Side of the landscape in meters. • <code>minimum.distance</code> - Minimum distance between patches centroids, in meters. • <code>mean.area</code> - Mean patch area in hectares. • <code>SD.area</code> - Standard deviation of patches area. • <code>number.patches</code> - Total number of patches. • <code>dispersal</code> - Species mean dispersal ability, in meters. • <code>nodes.characteristics</code> - Data frame with patch (node) information (coordinates, area, radius, cluster, distance to nearest neighbor and ID).
Metapopulation	<p>Class representing a landscape graph with species' patch occupancy data, as produced by <code>species.graph</code>, <code>convert.graph</code> and <code>import.shape</code>.</p> <ul style="list-style-type: none"> • <code>mapsize</code> - Landscape mosaic side length, in meters. • <code>minimum.distance</code> - Minimum distance between patches' centroids, in meters. • <code>mean.area</code> - Mean patch area in hectares. • <code>SD.area</code> - Standard deviation of patches area. • <code>number.patches</code> - Total number of patches. • <code>dispersal</code> - Species mean dispersal ability, in meters. • <code>distance.to.neighbours</code> - Data frame with pairwise distance between patches, in meters. • <code>nodes.characteristics</code> - Data frame with patch (node) information (coordinates, area, radius, cluster, distance to nearest neighbor, ID and species occupancy).
Expansion	<p>Class representing an expansion object, as produced by <code>range_expansion</code>. A list of four data frames with the proportion of occupation at several distances from the closest occupied landscape mosaic. These four data frames correspond to the proportion of occupation to the north, south, east and west. Each data frame has the following columns:</p> <ul style="list-style-type: none"> • <code>EXPANSION.DISTANCE</code> - Distance given as the product between the side of a landscape in meters (<code>mapsize</code>) and the number of landscapes. • <code>OCCUPATION</code> - How many times did the landscape at this distance got occupied by the species (from a total of 'iter' repetitions). • <code>PROPORTION</code> - Proportion of occupation for the landscape at this distance (<code>OCCUPATION/iter</code>).

Table SM4. Description of the 15 landscape connectivity metrics computed by MetaLandSim using function “metrics.graph”. See the user’s manual for computation details.

Metric	Description	Reference
NC	Number of groups of connected patches (components in graph-related literature).	Urban and Keitt, (2001)
LNK	Number of links amongst patches.	Pascual-Hortal and Saura, (2006)
SIC	Area of the largest component.	Pascual-Hortal and Saura, (2006)
MSC	Mean area of the components.	Pascual-Hortal and Saura, (2006)
HI	Harary Index - Originally developed to characterize molecular graphs by Plavsic et al. (1993) it was later transposed to the landscape context by Ricotta et al. (2000).	Ricotta et al. (2000)
NH	Normalization of the Harary Index, which facilitates analysis because it will set the values to the range between 0 and 1.	Ricotta et al. (2000)
ORD	Order- Originated in the graph theory and later brought into the landscape context by Urban and Keitt (2001). It provides a simple structural evaluation of the graph: it is the number of patches of the component (group of patches) with more patches.	Urban and Keitt (2001)
GD	Graph diameter- Another index directly derived from graph theory, providing a simple quantification of the graph structure. The graph diameter, or ‘longest shortest path’, between the two most distant patches in a network.	Bunn et al. (2000); Urban and Keitt, (2001)
CCP	Class coincidence probability - It is defined as the probability that two randomly chosen points within the habitat belong to the same component. Ranges between 0 and 1.	Pascual-Hortal and Saura (2006)
LCP	Landscape coincidence probability - It is defined as the probability that two randomly chosen points in the landscape (whether in a habitat patch or not) belong to the same habitat component. Ranges between 0 and 1.	Pascual-Hortal and Saura (2006)
CPL	Characteristic path length - Mean of all the shortest paths between all reachable nodes (habitat patches).	Minor and Urban (2008)
ECS	Expected cluster size - It corresponds to the area-weighted mean cluster size. For any given unit of habitat, it is the mean area of habitat in the cluster containing that unit.	O’ Brien et al. (2006); Fall et al. (2007)
AWF	Area-weighted Flux - Evaluates the flow, weighted by area, between all pairs of patches.	Bunn et al. (2000); Urban and Keitt (2001)
IIC	Integral index of connectivity - It is based on habitat availability and on a binary connection model (as opposed to a probabilistic). This index is considered to be the most adequate because it allows the evaluation of spatial changes and patch prioritization. It ranges from 0 to 1 (higher values indicating more connectivity).	Pascual-Hortal and Saura (2006)
PC	Probability of connectivity - Similar to IIC, although assuming probabilistic connections between patches.	Saura and Pascual-Hortal (2007)

Supplementary Material #2

Worked Examples

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- Metapopulation simulations in dynamic landscapes
- Simulations of metapopulation range expansion
- Computation time
- Supplementary references

1. Metapopulation simulations in dynamic landscapes

1.1. Simulation conditions

The commented examples presented here were run using the traditional command line of R, though MetaLandSim may also be used with a graphical user interface (function “MetaLandSim.GUI”). The simulation process started by specifying a virtual landscape of 100-hectares (1000 m x 1000 m; mapsize), comprising 200 patches (Npatch) with a mean size of 0.1 ha (areaM) and a standard deviation of 0.057 (areaSD). The size of patches was randomly selected considering the mean and standard deviation of patches, and they were located randomly in the virtual landscape subject to the constraint of maintaining a mean nearest distance of 30m between patch centroids (dist_m). To exemplify landscape dynamism, we specified an external disturbance (par1) producing a loss of 4% (par2) of the patches at each time step. However, MetaLandSim allows the specification of a wide range of landscape dynamic conditions, including destruction and creation of patches at different rates, variations in patch size, and spatial correlation of patch dynamics (see details in the user manual).

As for the initial condition of the metapopulation, we assumed a random occupancy of 50% (parm) of the patches in the initial landscape. We also assumed a virtual species, with parameters given by the data frame in the param_df argument: $\alpha = 0.001$; $x = 0.5$; $y = 2$; and $e = 0.047$. We specified one of the alternative functions available in MetaLandSim for the dispersal kernel (kern), connectivity (conn), and extinction (ext) and colonization (colnz) rates, selecting in each case the first option (“op1”). The simulation period was 100 time steps (span), and the number of iterations was 100 (iter). Finally, we asked for a graphical output (graph), which returned graphs showing the results averaged across iterations. The complete command was thus:

```
it1 <- iterate.graph(iter = 100, mapsize = 1000, dist_m = 30,
areaM = 0.1, areaSD= 0.057, Npatch = 200, disp = 800, span =
100, par1 = “hab”, par2 = 4, method = “percentage”, parm = 50,
nsew = “none”, param_df = param1, kern = “op1”, conn = “op1”,
colnz = “op1”, ext = “op1”, b = 1, graph = TRUE)
```

The evolution of the simulation was depicted graphically in HTML format, using the interface with Google Chart Tools API through googleVis package (Gesmann and Castillo 2011).

1.2. Results

The detailed output of the simulation was a list of data frames with values describing landscape structure at each time step. From the graphical output (Fig. S1) it was apparent that the number of patches decayed rapidly during the simulation, at the same time that there were smaller declines in mean patch size and increases in the mean nearest-neighbour distance between patches. The patch occupancy increased rapidly from 50% to almost 100% in the first three time steps, but it declined thereafter following approximately a sigmoid curve. The occupancy turnover peaked at the beginning of the simulation, corresponding to the rapid occupation of all patches. There was a second peak in turnover at about 50 times steps, albeit smaller than the first, when there was approximately an occupation of 50% of patches.

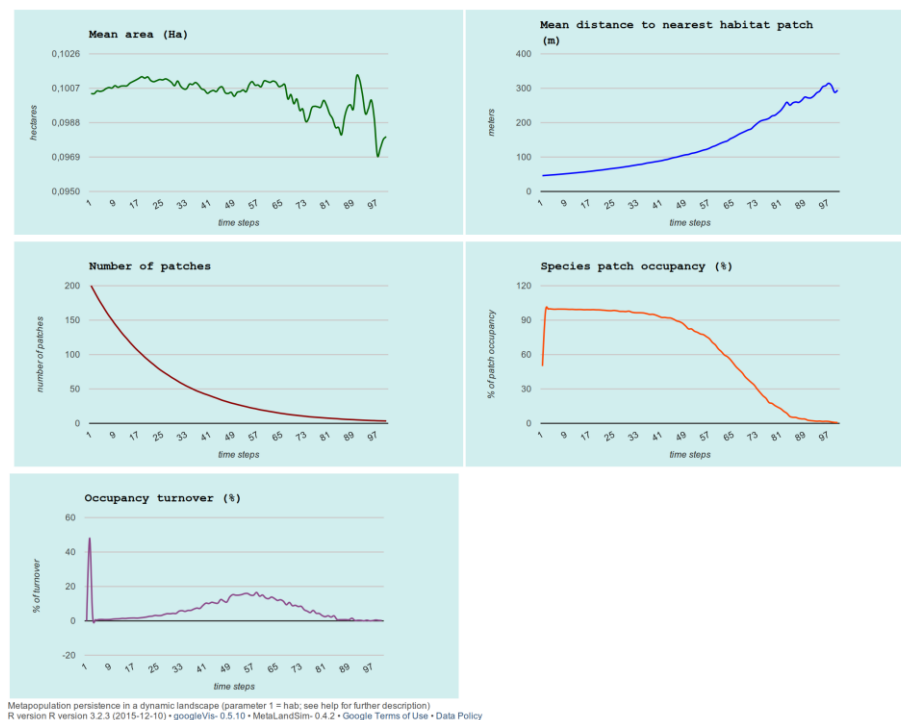


Figure SM1. Example of a HTML Graphic output produced by `iterate.graph`, showing mean values across iterations of landscape (mean patch area, mean distance to the nearest patch,

and number of patches) and metapopulation (patch occupancy and occupancy turnover) attributes over time.

2. Simulations of metapopulation range expansion

2.1. Simulation conditions

To simulate metapopulation expansion, we used function “`rland.graph`” to set an initial occupied landscape with 10,000 m² (`mapsize`), 250 patches (`Npatch`), mean patch area of 0.1 hectares (`areaM`), and standard deviation of patch area of 0.05 (`areaSD`). We asked for a graphical output of the landscape (`plotG`), and we set the dispersal parameter at 800 (`disp`) to represent the edges corresponding to interpatch distances that are half the dispersal ability of the species modelled. The complete command to define the basic landscape topology was:

```
r11 <- rland.graph(mapsize = 10000, dist_m = 10, areaM = 0.1,
areaSD = 0.05, Npatch = 250, disp = 800, plotG = TRUE)
```

To simulate metapopulation expansion into adjacent empty landscape we resorted to the function “`range_expansion`”, using the landscape with `r11` parameters (`rl`) and specifying an initial occupancy of 50% of patches (`percI`). The parameters of the metapopulation simulated were specified as the data frame “`param1`” (`param`), corresponding to those used in section 1 of this Supplementary Material. The simulation period was 100 time steps (`span`), and the number of iterations was 100 (`iter`). The complete command to compute the expansion simulation was:

```
rg_exp1 <- range_expansion(rl = r11, percI = 50, param = param1,
b = 1, tsteps = 100, iter = 100)
```

This function returns a list, of class “`expansion`”, of four data frames with the proportion of occupations at several distances from the closest occupied landscape mosaic (see details in the user manual). These four data frames correspond to the proportion of occupation to the north, south, east and west. This computation is time-intensive, taking from a few hours to several days to run, depending on computer power and number of iterations. Therefore, we provide the results of the simulations

for users wanting to test subsequent related functions. The command to call the existing dataset is:

```
data(rg_exp)
```

2.2. Simulating large scale range expansion

The output (rg_exp1) of the range_expansion function provided the basis for upscaling the metapopulation processes occurring at the landscape scale, to estimate potential range expansion dynamics at regional or even biogeographical scales. The use of this function required the function “initGRASS” from the package rgrass7 (Bivand 2015) for specifying the GRASS folder and the mapset location. The commands required were:

```
#Loading rgrass7 - a package which makes the connection between  
R and GRASS 7
```

```
library(rgrass7)
```

```
#Starting GRASS7 from R
```

```
initGRASS(gisBase = “grass folder”, home = tempdir(), gisDbase =  
“mapset”, override = TRUE)
```

After this, the procedure involved importing a raster file with the current range of the species and a mask defining the area available for expansion (i.e., a map with the focal region where potential expansion is evaluated). In this example we used the distribution of a virtual species and a mask corresponding roughly to the Iberian Peninsula. The commands to load the species occurrences and the mask were:

```
presences<-system.file("examples/presences.asc",  
package="MetaLandSim")
```

```
mask<-system.file("examples/landmask.asc",  
package="MetaLandSim")
```

After this step, we called the function “range_raster”, which produces a raster map with the probability of landscape occupancy within the entire study area (i.e., the mask). This function uses the metapopulation expansion patterns estimated in each cardinal direction with the range_expansion function, fitting in each case a sigmoid curve describing the probability of landscape occupancy in relation to the distance to the nearest landscape occupied at the beginning of the simulation (i.e., the dispersal models). These sigmoid curves are then applied to each pixel in the ‘mask’ map, estimating its probability of occupancy in relation to the range border of the species specified by the ‘presences’ map. In our example, we asked for the production of graphics for the expansion model functions and raster maps with expansion probabilities in all four cardinal directions (plot.directions). The command used to produce the map of probability of occupancy was:

```
range.expansion <- range_raster (presences.map=presences,  
re.out=rg_exp1, mask.map=mask, plot.directions =TRUE)
```

If using the MetaLandSim sample dataset (“rg_exp”) instead of computing the example provided in this supplementary material (“rg_exp1”), users may view the results graphically with the command:

```
plot(range.expansion)
```

A graphical summary of the results of the procedure is presented in Fig. SM2. These results suggest that under the conditions simulated, our virtually species expand rapidly in the Iberian Peninsula, occupying nearly the entire area available during the 100 time steps. However, the probability of occupancy would be lower in the eastern side of the Peninsula, where the probability of reaching the Pyrenees would be relatively low <50%.

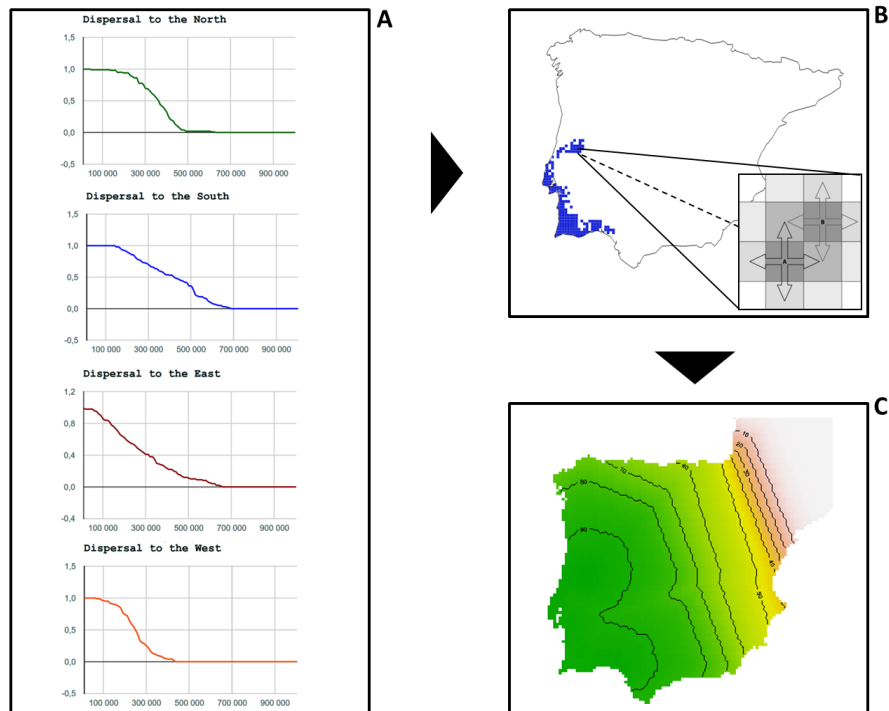


Figure SM2. Example of range expansion simulation. a) Graphical output of the dispersal model for each cardinal direction estimated using “range_raster”; b) Raster map with current range of the virtual species; c) Map of the probabilities of landscape occupancy resulting from metapopulation expansion into empty landscapes.

The raster map of probabilities of landscape occupancy generated by MetaLandSim can be used to refine range shift forecasts under future climatic conditions, obtained for instance by Ecological Niche Models (Peterson et al. 2011). This can be done by exporting the raster map to GIS software, where it can be combined through simple operations with maps of future climatic suitability. For instance, a future range may be predicted by cutting the areas of high climatic suitability (say, >50% of probability of occurrence) with the areas of high probability of range expansion (say, > 50% of landscape occupancy), thereby highlighting areas that are both climatically suitable and can effectively be reached by the species during a given time frame. Other alternative may simply be to multiply the probabilities generated by the MetaLandSim dispersal model and the Ecological Niche Model, thereby generating a continuous map of probabilities considering both climate and dispersal. A detailed discussion of integrating dispersal models with ecological niche models is provided by Bateman et al. (2013).

2.3. Simulating expansion under different landscape scenarios

MetaLandSim allows the user to evaluate how the dispersal models are affected by variation in landscape characteristics, in terms of the number, sizes, spatial distribution and dynamism of patches. In this example we use the function “manage_expansion_sim” to evaluate how range expansion is affected by varying patch sizes from 0.01 ha (var_min) and 0.6 ha (var_max) by 0.1 ha increments (by), using the same metapopulation parameters as in section 2.1 (“param1”). We specified an initial landscape unit with 100 hectares (1000x1000 m; mapsize), with 300 habitat patches (Npatch), which are distributed randomly with no constraints regarding the minimum distance between centroids (dist=0), and with a metapopulation occupancy of 50% of patches. The simulation was run for 100 time steps (tsteps) with 100 repetitions each (iter). The command for running the simulations was:

```
sim_range <- manage_expansion_sim(mapsize = 1000, dist_m = 0,
areaM, areaSD = 0.001, Npatch = 300, percI = 50, param = param1,
b = 1, tsteps = 100, iter=100, variable = "area", var_min =
0.01, var_max = 0.6, by = 0.1)
```

As an output of this function, the user obtains a list with eight data frames with the following information:

- NORTH, SOUTH, EAST and WEST - landscape characteristics that were evaluated (mean patch area in the preceding example), maximum dispersal distance (km) and dispersal speed (km/time step).
- simN, simS, simE and simW – detailed information on the simulation. Each data frame has a column for distance (in km) and one for each simulation with the time step at which each distance was colonized.

Additionally a graphical output is produced depicting the evolution of the simulation in HTML format, using the interface with Google Chart Tools API through googleVis package (Gesmann and Castillo 2011).

In this example, we found that the maximum distance of dispersal increases rapidly when patch size increase from 0.01ha to 0.1ha, levelling off at 100km. This is the

maximum expansion possible in this simulation, because the initial landscape had 1km^2 , and simulations were run during 100 time steps. The pattern is equal in all cardinal directions, because the random landscapes generated have the same characteristics irrespective of geographic direction.

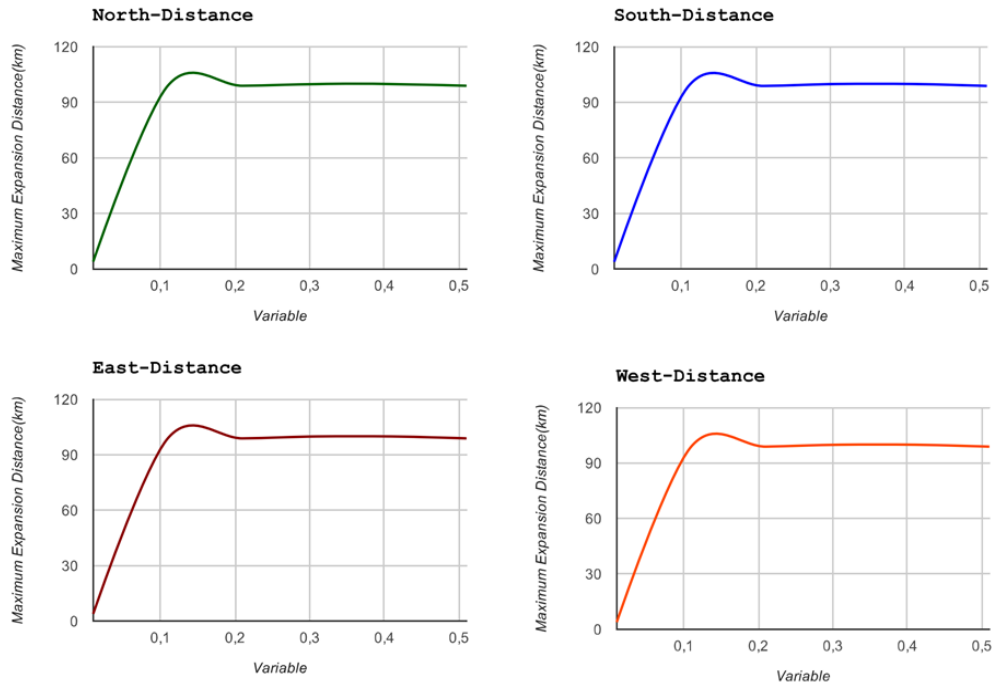


Figure SM3. Graphic output of “manage_expansion_sim”, showing variation in the estimated maximum distance (km) reached by an expanding metapopulation (Y axis), in relation to the mean patch area of the simulated landscapes (X axis).

2.4. Limitations

The users should note that the approach provided in MetaLandSim to simulate range expansion has some limitations, which will be addressed in future versions of MetaLandSim:

- i. Expansion is simulated explicitly only along the four cardinal directions, while diagonal dispersal is accounted for indirectly through rook-like movements in a chessboard pattern. This implies that dispersal is necessarily slower along the

diagonals, though the effect should decline rapidly with increasing number of time steps.

- ii. The landscape characteristics simulated are the same along the four cardinal directions, and thus the expansion process tends to be homogeneous irrespective of direction. This reduces the flexibility of the simulation conditions, though this may probably be taken as a reasonable assumption when there is no prior information on spatial heterogeneities in landscape characteristics.
- iii. The procedure assumes that landscape characteristics throughout the dispersion surface remain constant, and similar to those of the initial landscape. Although these landscapes are not exactly equal to each other, they are always randomly generated using the same parameters, and so the average dispersal through space should be constant. This reduces the realism of simulations, because it is likely that a metapopulation expanding at the regional scale will cross landscapes with different characteristics due for instance to variation in land uses and fragmentation patterns. To partly solved this problem, we have implemented the function “manage_expansion_sim” (see Section 2.3 of this Supplementary Material), which allows the user to explore the consequences of changes in landscape parameters to the speed and pattern of metapopulation expansion. This tool can be used to evaluate the sensitivity of the results to changes in landscape characteristics, providing a basis, for instance, to evaluate how large scale range expansion will be affected by different levels of landscape fragmentation.
- iv. Related with the previous limitation, we assumed that the key metapopulation parameters remain constant throughout the area of expansion, though it is conceivable that changes may occur due for instance to variation in environmental conditions or even local adaptations. As indicated before, this can be partly addressed by assessing the sensitivity of results to changes in metapopulation parameters.

- v. The application of MetaLandSim to model the expansion of real species is conditional on the quantity and quality of information available for the species, including data on its typical metapopulation parameters and the features of the landscape that it inhabits. As these features are likely to vary in time and space, users of MetaLandSim should be aware that predictions represent approximations of the potential expansion patterns of the species. This important limitation is generally applicable to any modelling approach designed to forecast future species distributions, irrespective of being based on ecological niche models, dispersal models, or both.
- vi. Related to the previous point, the user should be aware that errors and uncertainties in SPOM simulations accumulate with increasing number of steps (e.g., Moilanen 2002). Therefore, particular care should be taken when carrying out and interpreting simulations involving long term projections into the future and/or spatial predictions that are far beyond the initial occupied landscape.

3. Computation time

To evaluate the computation efficiency of MetaLandSim, we provide below the time needed to implement the key simulation steps described in sections 1 and 2 of this Supplementary Material, using an Intel(R) Core(TM)2 Duo CPU, with 2.53 GHz and 4.00 GB of RAM, 64 bits laptop (all simulations involve 100 time steps and 100 iterations):

- Simulation of metapopulation dynamics using `iterate.graph`: ≈ 0.25 hours.
- Simulation of metapopulation expansion under a single landscape scenario using `range_expansion`: ≈ 1.6 hours.
- Simulations of metapopulation expansion under different landscape scenarios using `manage_expansion_sim`: ≈ 11.5 hours.

Supplementary Material #3

MetaLandSim

Package Manual and Vignettes

Package ‘MetaLandSim’

October 3, 2016

Type Package

Title Landscape and Range Expansion Simulation

Version 0.5.4

Date 2016-09-29

Depends R (>= 2.10), tcltk

Imports Biobase, e1071, fgui, grDevices, graphics, googleVis,
maptools, rgeos, rgrass7, raster, spatstat, stats, sp,
minpack.lm

Suggests rasterVis

Author Frederico Mestre, Fernando Canovas, Ricardo Pita, Antonio Mira, Pedro Beja.

Maintainer Frederico Mestre <mestre.frederico@gmail.com>

Description Tools to generate random landscape graphs, evaluate species occurrence in dynamic landscapes, simulate future landscape occupation and evaluate range expansion when new empty patches are available (e.g. as a result of climate change).

License GPL (>= 2)

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Description

The package MetaLandSim is a simulation environment, allowing the generation of random landscapes, represented as graphs, the simulation of landscape dynamics, metapopulation dynamics and range expansion.

The package was developed as part of the Ph.D. thesis of Frederico Mestre (SFRH/BD/73768/2010), funded by European Social Funds and the Portuguese Foundation for Science and Technology, and included in the project NETPERSIST (PTDC/AAG-MAA/3227/2012), funded by European Regional Development Fund (ERDF) through COMPETE programme and Portuguese national funds through the Portuguese Foundation for Science and Technology.

MetaLandSim is intended to provide a virtual environment, enabling the experimentation and simulation of processes at two scales: landscape and range. The simulation approach, taken by MetaLandSim, presents several advantages, like allowing the test of several alternatives and the knowledge of the full system (Peck, 2004; Zurell et al. 2009). The role of simulation in landscape ecology is fundamental due to the spatial and temporal scale of the studied phenomena, which frequently hinders experimentation (Ims, 2005).

MetaLandSim-package

Here, graph and metapopulation theories are combined, which is a broadly accepted strategy to provide a modelling framework for metapopulation dynamics (Cantwell & Forman, 1993; Bunn et al. 2000; Ricotta et al. 2000; Minor & Urban, 2008; Galpern et al. 2011). Also, several graph-based connectivity metrics can be computed from the landscape graphs. This set of metrics have been proven useful elsewhere (Urban & Keitt, 2001; Calabrese & Fagan, 2004). The graph representation of landscape has one major advantage: it effectively summarizes spatial relationships between elements and facilitates a multi-scale analysis integrating patch and landscape level analysis (Calabrese & Fagan, 2004).

MLS operates at two scales, providing researchers with the possibility of:

- Landscape scale - Simulation of metapopulation occupation on a dynamic landscape, computation of connectivity metrics.
- Range scale - Computes dispersal model and range expansion scenario simulation.

The landscape unit, an object of class `landscape`, is the basic simulation unit at both these scales. At the landscape scale, the persistence of the metapopulation in a dynamic landscape is evaluated through the simulation of landscape dynamics using the function `iterate_graph` or `manage_landscape_sim`. At the range scale the metapopulation is allowed to expand to other, empty, landscape units using `range_expansion`, producing an object of class `expansion`. The function `range_raster` allows the conversion of the dispersal model obtained with the previous function into a raster. Finally, also at the range scale, the user can analyse the outcome of several alternative landscapes in range expansion speed and maximum dispersal distance, using the function `manage_expansion_sim`.

Reference paper: Mestre, F.; Canovas, F.; Pita, R.; Mira, A.; Beja. P. (2016). An R package for simulating metapopulation dynamics and range expansion under environmental change. *Environmental Modelling and Software*, 81: 40-44.

Details

Package:	MetaLandSim
Type:	Package
Version:	0.5.4
Date:	2016-09-29
License:	GPL (>=2)

Author(s)

Frederico Mestre, Fernando Canovas, Ricardo Pita, Antonio Mira and Pedro Beja.

Maintainer: Frederico Mestre <mestre.frederico@gmail.com>

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Ims, R.A. (2005). The role of experiments in landscape ecology. In: Wiens, J.A., and Moss, M.R. (eds.). *Issues and Perspectives in Landscape Ecology*. Cambridge University Press. pp. 70-78.

Minor, E. S. and Urban, D. L. (2008). A Graph Theory Framework for Evaluating Landscape Connectivity and Conservation Planning. *Conservation Biology*, 22(2), 297-307.

Peck, S. L. (2004). Simulation as experiment: a philosophical reassessment for biological modelling. *Trends in Ecology & Evolution*, 19(10), 530-534.

Ricotta, C., Stanisci, A., Avena, G. C., and Blasi, C. (2000). Quantifying the network connectivity of landscape mosaics: a graph-theoretical approach. *Community Ecology*, 1(1), 89-94.

Urban, D. and Keitt, T. (2001). Landscape connectivity: a graph-theoretic perspective. *Ecology*, 82(5), 1205-1218.

Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Munkemuller, T., Nehrbass, N., Pagel, J., Reineking, B., Schroder, B. and Grimm, V. (2009). The virtual ecologist approach: simulating data and observers. *Oikos*, 119(4), 622-635.

addpoints

Add a given number of patches to a landscape

Description

Adds a given number of patches to the landscape.

Usage

```
addpoints(r1, nr)
```

Arguments

r1	Object of class 'landscape'.
nr	Number of patches to be added (see 'note').

Value

Returns an object of class 'landscape'.

Note

The number of patches to be added might be impaired by the minimum distance between points.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [removepoints](#)

cabrera

Examples

```
data(rland)

#Checking the number of patches in the starting landscape:

rland$number.patches

#60

#Adding 10 patches to a landscape:

r11 <- addpoints(r1=rland, nr=10)

#Checking the number of patches in the output landscape:

r11$number.patches

#70
```

cabrera

Modified patch occupancy data of Cabrera vole

Description

One season patch occupancy dataset for *Microtus cabreræ* in SW Portugal. This dataset is in the format produced by [species.graph](#), [convert.graph](#) or [import.shape](#) (class 'metapopulation'), and it was created by converting a data frame using the function `convert.graph`. The data frame had the information of one snapshot of patch occupancy data of Cabrera vole (*Microtus cabreræ*) in southwestern Portugal.

Usage

```
data(cabrera)
```

Format

A list with the following elements:

- `mapsize` - 8200 (landscape mosaic side length, in meters).
- `minimum.distance` - 10.04 (minimum distance between patches centroids).
- `mean.area` - 0.46 (mean area, in hectares).
- `SD.area` - 1.05 (SD of the area).
- `number.patches` - 793 (number of patches).
- `dispersal` - 800 (mean dispersal ability of the species).
- `distance.to.neighbours` - data frame with pairwise distance between patches.
- `nodes.characteristics` - data frame with the characteristics of each patch.

Details

To create this sample dataset the occupancy status of patches was scrambled, however the proportion of occupied patches was kept.

Source

Original field data was obtained during project PERSIST (PTDC/BIA-BEC/105110/2008).

Examples

```
data(cabrera)
```

cluster.graph	<i>Delivers the number of patches per cluster</i>
---------------	---

Description

Returns a data frame with the number of nodes (habitat patches) in each component of the landscape graph (in this case a component is a group of patches connected by the species dispersal distance).

Usage

```
cluster.graph(r1)
```

Arguments

r1 Object of class 'landscape'.

Details

The components are defined based on the species mean dispersal ability. This implies that the connectivity model between patches is binary (connected/not connected) as opposed to probabilistic.

Value

This function returns a data frame with the number of patches of each component (group of patches). The returned data frame has two fields: cluster (Id of the component) and number of nodes (the number of nodes of the respective component).

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#)

cluster.id

Examples

```
data(rland)

cluster.graph(r1=rland)

#Output:

# cluster number of nodes
#1      1          11
#2      2           1
#3      3          13
#4      4           1
#5      5           1
#6      6          15
#7      7           2
#8      8           1
#9      9           3
#10     10           1
#11     11           1
#12     12           2
#13     13           4
#14     14           1
#15     15           1
#16     16           1
#17     17           1
```

<code>cluster.id</code>	<i>Classify patches in clusters</i>
-------------------------	-------------------------------------

Description

reclassify clusters of a landscape according to a given mean dispersal distance.

Usage

```
cluster.id(r1)
```

Arguments

`r1` Object of class 'landscape'.

Details

After changing the landscape some components (groups of connected patches) might suffer changes (e.g. the removal of patches might split components). This function re-attributes a code to each patch, identifying the groups of connected patches (components), after this type of disturbance to the habitat network. Mainly to be used internally.

Value

Returns the same landscape object, with the clusters reclassified.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#)

Examples

```
data(rland)

#After removing 30 (50%) of the patches of a landscape:

rland2 <- removepoints(r1=rland, nr=35)

#A reclassification might be needed to identify components:

rland2 <- cluster.id(r1=rland2)

#After removing 35 patches, there's a different number of components:

components.graph(r1=rland)

#21

components.graph(r1=rland2)

#16
```

components.graph

Number of components of a landscape

Description

Returns the number of components in the landscape graph (in this case a component is a group of patches connected by the species dispersal distance).

Usage

```
components.graph(r1)
```

Arguments

r1 Object of class 'landscape'.

Value

Returns the number of components (groups of connected patches) of a landscape.

Author(s)

Frederico Mestre and Fernando Canovas

`convert.graph`

See Also

[rland.graph](#)

Examples

```
data(rland)

components.graph(r1=rland)

#21
```

<code>convert.graph</code>	<i>Convert data frame to landscape</i>
----------------------------	--

Description

Converts a given data frame in a list which can be used in the following functions, an object of class 'metapopulation'.

Usage

```
convert.graph(dframe, mapsize, dispersal)
```

Arguments

dframe	data frame with the original data and the following columns, in this order: <ul style="list-style-type: none">• ID - patch Id.• X - Coordinate.• Y - Coordinate.• Area - Patch area, in hectares.• Occupation - Species presence status (0/1).
mapsize	Landscape mosaic side length, in meters.
dispersal	Species mean dispersal ability, in meters.

Value

Delivers an object of class 'metapopulation'.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[species.graph](#)

Examples

```
data(mc_df)

#Checking the columns of the data frame:

head(mc_df)

# ID      x      y area mc
#1  1 1248.254  0.000 0.079  0
#2  2 1420.857  46.725 0.781  1
#3  3 1278.912  52.629 1.053  1
#4  4 6370.625  62.637 0.788  0
#5  5 1151.337  97.140 0.079  0
#6  6 1295.796 104.839 0.137  1

#In order to import the data frame mc_df:

sp1 <- convert.graph(dframe=mc_df, mapsize=8300, dispersal=800)

#verify class

class(sp1)

# [1] "metapopulation"
```

create.parameter.df	Create parameter data frame
---------------------	-----------------------------

Description

This function creates a parameter data frame, using parameter values computed with the application available in the papers of Moilanen (1999) and ter Braak and Etienne (2003).

Usage

```
create.parameter.df(alpha, x, y, e)
```

Arguments

alpha	Alpha parameter
x	x parameter
y	y parameter
e	e parameter

Details

It is highly recommended that the user reads both papers, as well as the help files.

edge.graph

Value

Returns a data frame, with the same format as the one returned by [parameter.estimate](#) for the methods 'Rsnap_1' and 'Rsnap_x'.

Author(s)

Frederico Mestre and Fernando Canovas

References

Moilanen, A. (1999). Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. *Ecology*, 80(3): 1031-1043.

ter Braak, C. J., & Etienne, R. S. (2003). Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation. *Ecology*, 84(1): 231-241.

See Also

[parameter.estimate](#)

Examples

```
param2 <- create.parameter.df(alpha=0.5, x=0.1, y=5, e=0.1)
```

```
param2
```

```
#      par_output
#alpha      0.5
#x          0.1
#y          5.0
#e          0.1
```

<code>edge.graph</code>	<i>Produce an edge (links) data frame</i>
-------------------------	---

Description

Returns a data frame with the information on the connections between patches (assuming binary connections).

Usage

```
edge.graph(r1)
```

Arguments

`r1` Object of class 'landscape'.

Value

Produces a data frame with the information on the edges (links): the IDs of both patches, the area, the coordinates and the Euclidean distance.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#)

Examples

```
data(rland)

edge_df <- edge.graph(r1=rland)
```

expansion

Class 'expansion'

Description

Class representing an expansion object, as produced by [range_expansion](#).

Slots

A list of four data frames with the proportion of occupation at several distances from the closest occupied landscape mosaic. These four data frames correspond to the proportion of occupation to the north, south, east and west. Each data frame has the following columns:

- DISTANCE - Distance (mapsize x number of landscapes).
- OCCUPATION - How many times did the landscape at this distance got occupied by the species (from a total of 'iter' repetitions).
- PROPORTION - Proportion of occupation for the landscape at this distance (OCCUPATION/iter).

Author(s)

Frederico Mestre and Fernando Canovas

extract.graph

<code>extract.graph</code>	<i>Extract landscape from <code>span.graph</code> generated list</i>
----------------------------	--

Description

Extracts a landscape from an object delivered by [span.graph](#). The output is an object of class 'landscape'.

Usage

```
extract.graph(r1, rlist, nr)
```

Arguments

<code>r1</code>	Object of class 'landscape' used to generate the list, with span.graph .
<code>rlist</code>	Object delivered by span.graph .
<code>nr</code>	Position of the landscape in the list (rlist).

Value

Delivers an object of class 'landscape'.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[span.graph](#), [rland.graph](#)

Examples

```
data(rland)
data(landscape_change)

#Extracting the landscape of the 50th time step:

r11 <- extract.graph(r1=rland, rlist=landscape_change, nr=50)
```

import.shape	<i>Import a shapefile</i>
--------------	---------------------------

Description

Imports a shapefile, converting it to an object of class 'metapopulation'.

Usage

```
import.shape(filename, path, species.col, ID.col, area.col, dispersal)
```

Arguments

filename	Character vector with the shapefile name.
path	Character vector with the path to the file.
species.col	Character vector with the name of the column (in the shapefile) with the species occupancy data.
ID.col	Character vector with the name of the column (in the shapefile) with the patch Id.
area.col	Character vector with the name of the column (in the shapefile) with the patch area, in hectares.
dispersal	Species mean dispersal ability, in meters.

Value

Delivers an object of class 'metapopulation'.

Note

The shapefile must be in project coordinates (units=meters and hectares).

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [convert.graph](#)

Examples

```
## Not run:

r11 <- import.shape(filename = "yourshapefile.shp"
, path = "C:/yourpath..."
, species.col= "column with species"
, ID.col="column with patch Id"
, area.col="Column with area"
, dispersal=800#Mean dispersal ability of the species
#(used to generate patch clusters, or components)
```

```
iterate.graph
```

```
)
```

```
## End(Not run)
```

```
iterate.graph
```

```
Simulate landscape series occupation
```

Description

Repeats the process of simulation by [simulate_graph](#) as many times as required (argument 'iter').

Usage

```
iterate.graph(iter, mapsize, dist_m, areaM, areaSD, Npatch, disp,
span, par1 = "none", par2 = NULL, par3 = NULL, par4 = NULL,
par5 = NULL, method = "percentage", parm, nsew = "none",
succ="none", param_df, kern, conn, colnz, ext, beta1,
b = 1, c1 = NULL, c2 = NULL, z = NULL, R = NULL, graph)
```

Arguments

iter	Number of repetitions of the simulation.
mapsize	Landscape mosaic side length, in meters. To be internally passed to rland.graph .
dist_m	Minimum distance between patches (centroid). To be internally passed to rland.graph .
areaM	Mean area (in hectares). To be internally passed to rland.graph .
areaSD	SD of the area of patches, in order to give variability to the patches area. To be internally passed to rland.graph .
Npatch	Number of patches (might be impaired by the dist_m, see the "Note" section). To be internally passed to rland.graph .
disp	Species mean dispersal ability, in meters. To be internally passed to rland.graph .
span	Number of time steps (e.g. years) to simulate. To be internally passed to span.graph .
par1	One of the following (default 'none'): <ul style="list-style-type: none"> • 'hab' percentage of the number of patches to eliminate. • 'dincr' minimal distance (between centroids of patches) increase over the simulation (in meters). • 'darea' percentage of increase/decrease of the mean area of patches, without changing SD. • 'stoc' simultaneous creation and destruction of patches. • 'ncsd' simultaneous creation and destruction of patches to the north and south of the landscape. • 'aggr' correlated habitat destruction. • 'none' no change. To be internally passed to span.graph .

par2	Parameter specifying details for the options in par1: percentage of patches to delete (if par1 = 'hab'); distance, in meters (if par1 = 'dincr'); percentage of increase/decrease of the mean area of patches (if par1 = 'area'); percentage of new patches (if par1 = 'stoc'); 'northerndness' of created patches (if par1 = 'ncsd'); percentage of destroyed patches (if par1 = 'aggr'). To be internally passed to span.graph . Default NULL.
par3	Additional parameter specifying details for the options in par1: percentage of destroyed patches (if par1 = 'stoc'); 'southerndness' of destroyed patches (if par1 = 'ncsd'); aggregation of destruction (if par1 = 'aggr'). Minimum area for patch deletion, in hectares (if par1='darea'). To be internally passed to span.graph . Default NULL.
par4	Percentage of created patches (if par1 = 'ncsd'). To be internally passed to span.graph . Default NULL.
par5	Percentage of destroyed patches (if par1 = 'ncsd'). To be internally passed to span.graph . Default NULL.
method	One of the following (default 'percentage'): click - individually select the patches with occurrence of the species by clicking on the map. Use only for individual landscape simulations. However, this option should not be used with <i>iterate.graph</i> . percentage - percentage of the patches to be occupied by the species. number - number of patches to be occupied by the species. To be internally passed to species.graph .
parm	parameter to specify the species occurrence - either percentage of occupied patches or number of occupied patches, depending on the method chosen. To be internally passed to species.graph .
nsew	'N', 'S', 'E', 'W' or none - point of entry of the species in the landscape. By default set to "none". To be internally passed to species.graph .
succ	Set the preference of the species for patch successional stage: 'none', 'early', 'mid' and 'late'.
param_df	Parameter data frame delivered by parameter.estimate , including: <ul style="list-style-type: none"> • alpha - Parameter relating extinction with distance. • y - Parameter y in the colonization probability. • e - Parameter defining the extinction probability in a patch of unit area. • x - Parameter scaling extinction risk with patch area. To be internally passed to simulate_graph .
kern	'op1' or 'op2'. Dispersal kernel. See details in the spom function. To be internally passed to spom .
conn	'op1' or 'op2'. Connectivity function. See details in the spom function. To be internally passed to spom .
colnz	'op1', 'op2' or 'op3'. Colonization function. See details in the spom function. To be internally passed to spom .
ext	'op1', 'op2' or 'op3'. Extinction function. See details in the spom function. To be internally passed to spom .
beta1	Parameter affecting long distance dispersal probability (if the Kern='op2'). To be internally passed to spom .
b	Parameter scaling emigration with patch area (if conn='op1' or 'op2'). To be internally passed to spom . By default set to 1.

iterate.graph

c1	Parameter scaling immigration with the focal patch area (if conn='op2'). To be internally passed to spom .
c2	Parameter c in the option 3 of the colonization probability (if colnz='op3'). To be internally passed to spom .
z	Parameter giving the strength of the Allee effect (if colnz='op3'). To be internally passed to spom .
R	Parameter giving the strength of the Rescue effect (if ext='op3'). To be internally passed to spom .
graph	TRUE/FALSE, to show graphic output.

Value

Returns a list of five data frames with information regarding the values of mean area, mean inter-patch distance, number of patches occupancy and patch occupancy turnover in each of the iterations, as well as the mean values and SD.

Author(s)

Frederico Mestre and Fernando Canovas

References

References in the [spom](#) function.

See Also

[rland.graph](#), [span.graph](#), [species.graph](#), [simulate_graph](#), [spom](#)

Examples

```
## Not run:
data(param1)

#Example with 2 iterations (ideally >100):

it1 <- iterate.graph(iter = 2, mapsize = 10000, dist_m = 10, areaM = 0.05,
  areaSD = 0.02, Npatch = 250, disp = 800, span = 100,
  par1 = "hab", par2 = 2, par3 = NULL, par4 = NULL,
  par5 = NULL, method = "percentage", parm = 50,
  nsew = "none", succ="none", param_df = param1, kern = "op1",
  conn = "op1", colnz = "op1", ext = "op1",
  beta1 = NULL, b = 1, c1 = NULL, c2 = NULL, z = NULL,
  R = NULL, graph = TRUE)

## End(Not run)
```

landscape	<i>Class 'landscape'</i>
-----------	--------------------------

Description

Class representing a landscape graph, as produced by `rland.graph`, `convert.graph` and `import.shape`.

Slots

- `mapsize` - Side of the landscape in meters.
- `minimum.distance` - Minimum distance between patches centroids, in meters.
- `mean.area` - Mean patch area in hectares.
- `SD.area` - Standard deviation of patches area.
- `number.patches` - Total number of patches.
- `dispersal` - Species mean dispersal ability, in meters.
- `nodes.characteristics` - Data frame with patch (node) information (coordinates, area, radius, cluster, distance to nearest neighbor and ID).

Author(s)

Frederico Mestre and Fernando Canovas

landscape_change	<i>Landscape loosing 5% of patches per time step</i>
------------------	--

Description

This dataset is a list of 100 landscapes with a loss of 5% of each patch's area at each time step. The first landscape is the sample empty landscape.

Format

List of 100 data frames, that represent the evolution of the landscape during 100 time steps.

Examples

```
data(landscape_change)
```


list.stats

`list.stats`

Returning information on a dynamic landscape list

Description

This function allows the computation of some statistics of the sequence of landscapes obtained from `simulate.graph`. Namely: mean area of the patches, standard deviation of the area, mean pairwise Euclidean distance, total number of patches, species occupation and turnover and mean distance to nearest habitat patch. It allows the graphical representation of the evolution of these statistics.

Usage

```
list.stats(sim_list, stat, plotG)
```

Arguments

<code>sim_list</code>	list from function simulate_graph .
<code>stat</code>	'mean_area', 'sd_area', 'mean_distance', 'n_patches', 'occupation', 'turnover' and 'mean_nneigh'.
<code>plotG</code>	TRUE/FALSE, plot output.

Value

Returns a vector with the evolution of the specified statistics throughout the list of landscapes representing the changes in a dynamic landscape and its occupation. A graphical output is also possible. It is possible to visualize the evolution of mean patch area, standard deviation of the patch area, mean distance between all pairs of patches, number of patches, species percentage of occupation, patch turnover (change in occupational state) and mean distance to nearest habitat patch.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[span.graph](#)

Examples

```
data(rland)
data(landscape_change)
data(param1)

#First, using simulate graph, simulate the occupation on a dynamic landscape
#(output of span.graph):

sim1 <- simulate_graph( rl=rland, rlist=landscape_change, simulate.start=TRUE,
  method="percentage", parm=50, nsew="none", succ = "none",
  param_df=param1, kern="op1", conn="op1", colnz="op1",
  ext="op1", beta1=NULL, b=1, c1=NULL, c2=NULL, z=NULL, R=NULL)
```

```
#Then evaluate species occupancy through the changes suffered by the landscape:
```

```
occ <- list.stats(sim_list=sim1, stat="occupation", plotG=TRUE)
```

```
#Checking the percentage of occupation in the 40 first landscapes:
```

```
head(occ,40)
```

```
#Output:
```

```
#[1] 50.000000 65.000000 90.000000 96.666667 93.333333 91.666667
#[7] 91.666667 90.000000 93.333333 90.000000 85.000000 83.333333
#[13] 85.000000 88.333333 83.333333 86.666667 81.666667 68.333333
#[19] 70.000000 75.000000 80.000000 73.333333 63.333333 56.666667
#[25] 55.000000 51.666667 46.666667 41.666667 38.333333 21.666667
#[31] 13.333333 13.333333 10.000000 6.666667 5.000000 3.389831
#[37] 1.694915 1.694915 0.000000 0.000000
```

manage_expansion_sim *Simulate range expansion simulation*

Description

This function produces dispersal scenarios, considering different habitat networks properties, evaluating the variation in dispersal speed and dispersal maximum distance (of range expansion).

Usage

```
manage_expansion_sim(mapsize, dist_m, areaM, areaSD, Npatch,percI,
                      param, b=1, tsteps, iter, variable,var_min,var_max,by)
```

Arguments

mapsize	Landscape mosaic side length, in meters. To be internally passed to rland.graph
dist_m	Minimum distance between patches (centroid).To be internally passed to rland.graph
areaM	Mean area (in hectares). To be internally passed to rland.graph
areaSD	SD of the area of patches, in order to give variability to the patches area. To be internally passed to rland.graph
Npatch	Number of patches. To be internally passed to rland.graph
percI	Percentage of patch occupancy in the starting landscape. To be internally passed to range_expansion
param	Parameter data frame delivered by parameter.estimate . To be internally passed to range_expansion It includes: <ul style="list-style-type: none"> • alpha - Parameter relating extinction with distance. • y - Parameter y in the colonization probability. • e - Parameter defining the extinction probability in a patch of unit area. • x - Parameter scaling extinction risk with patch area.

manage_expansion_sim

b	Parameter scaling emigration with patch area (if conn='op1' or 'op2') in spom . By default, equal to 1. To be internally passed to range_expansion
tsteps	Number of time steps to simulate (e.g. years).
iter	Number of iterations of the simulation procedure.
variable	Landscape graph characteristic to be varied. One of the following: <ul style="list-style-type: none">• area - Mean patch area (in hectares).• dist - Minimum distance between patches (centroid).• npatch - Number of patches.• sizevar - SD of the area of patches.
var_min	Minimum value the changing variable can assume (beware of units used in each case).
var_max	Maximum value the changing variable can assume (beware of units used in each case).
by	Rate of variation of the changing variable.

Details

For details regarding the arguments that are to be internally passed to other functions, see the respective functions. Any of the arguments `dist_m`, `areaM`, `areaSD`, `Npatch` would be unnecessary if the respective variable is the one to be evaluated (it depends on the parameter variable).

Value

Returns a list of eight data frames. For the first four data frames (NORTH, SOUTH, EAST and WEST) each data frame's first column is the name of the variable to be changed. The other two columns are:

MEAN EXPANSION SPEED

Expansion speed in each simulated scenario. Speed given in km/time step

MAXIMUM EXPANSION DISTANCE

Maximum distance of the expanded range, from an occupied site. Given in km.

The other four data frames have detailed information on the simulations for each of the values of parameter "variable". The first column has the distance (in km), and each of the following columns has the time step at which each distance was colonized for each of the simulations.

Warning

This function might be time consuming, and the code is experimental and should be improved in future versions of MetaLandSim.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [range_expansion](#), [expansion](#)

Examples

```
## Not run:

data(param1)

sim_range <- manage_expansion_sim(mapsize=1000, dist_m=0, areaM, areaSD=0.001,
                                  patch=300,percI=50, param=param1, b=1,
                                  tsteps=100, iter=100,variable="area",var_min=0.01,
                                  var_max=0.6,by=0.1)

## End(Not run)
```

manage_landscape_sim	<i>Batch landscape simulation</i>
----------------------	-----------------------------------

Description

Runs a series of simulations, using [iterate.graph](#), allows changing the simulations parameters in several sequential simulations.

Usage

```
manage_landscape_sim(par_df, parameters_spom)
```

Arguments

par_df	<p>Arguments data frame to be used by iterate.graph (each row of this data frame is a set of Arguments). The data frame has to have the following columns in this order (the name of the column is not relevant):</p> <ul style="list-style-type: none"> • MDST - Minimum inter-patch distance (in meters). • NPATCH - Number of patches in the landscape. • AREA_M - Mean area of the patches (in hectares). • AREA_SD - SD of the patches' area. • MAPSIZE - Landscape mosaic side length (in meters). • SPAN - Number of time steps in the simulation. • ITER - Number of iterations of the simulation. • PAR1_SPAN - parm1 for the span.graph function. • PAR2_SPAN - parm2 for the span.graph function. • PAR3_SPAN - parm3 for the span.graph function. • PAR4_SPAN - parm4 for the span.graph function. • PAR5_SPAN - parm5 for the span.graph function. • NSEW_SPECIES - Argument nsew for the species.graph function. • PARM_SPECIES - Argument parm for the species.graph function. • METHOD_SPECIES - Argument method for the species.graph function. • KERN - Argument kern for the spom function. • CONN - Argument conn for the spom function. • COLNZ - Argument colnz for the spom function.
--------	--

manage_landscape_sim

- EXT - Argument ext for the spom function.
- BETA1 - Argument beta1 for the spom function.
- B - Argument b for the spom function.
- C1 - Argument c1 for the spom function.
- C2 - Argument c2 for the spom function.
- Z - Argument z for the spom function.
- R2 - Argument R for the spom function.
- DISPERSAL - Species mean dispersal ability (in meters).

parameters_spom

Parameters data frame, as given by [parameter.estimate](#).

Details

For details regarding the arguments see the respective functions.

Value

Returns a data frame with the parameters used for the simulations and the results (mean occupation, mean number of patches, mean turnover, mean distance and mean area).

Note

Depending on computing capacity, this function can take from several hours to several days to run.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [span.graph](#), [species.graph](#), [spom](#)

Examples

```
#Setup the parameters for each simulation:
PAR1_SPAN2 <- rep("ncsd",820)#parameter 1 for the span function
PAR2_SPAN2 <- rep(seq(from=0,to=80,by=2), each=20)#parameter 2 for the span function
PAR3_SPAN2 <- rep(seq(from=0,to=80,by=2),20)#parameter 3 for the span function
PAR4_SPAN2 <- rep(2,820)#parameter 4 for the span function
PAR5_SPAN2 <- rep(2,820)#parameter 5 for the span function
NSEW_SPECIES2 <- rep("none",820)#where to start populating the landscape
PARM_SPECIES2 <- rep(5,820)#parameter for the species function
METHOD_SPECIES2 <- rep("percentage",820)#method for populating the landscape
MAPSIZE2 <- rep(10000,820)#dimension of the landscape
SPAN2 <- rep(100,820)#number of time steps of each simulation
ITER2 <- rep(5,820)#number of iterations of each simulation
NPATCH2 <- rep(800,820)#number of patches
AREA_M2 <- rep(0.45,820)#mean area
AREA_SD2 <- rep(0.2,820)#area sd
MDST2 <- rep(0,820)#minimum distance between
KERN <- rep("op1",820)#kernel
CONN <- rep("op1",820)#connectivity function
COLNZ <- rep("op1",820)#colonization function
```

```

EXT <- rep("op1",820)#extinction function
BETA1 <- rep("NULL",820)
B <- rep(1,820)
C1 <- rep("NULL",820)
C2 <- rep("NULL",820)
Z <- rep("NULL",820)
R2 <- rep("NULL",820)
DISPERSAL2 <- rep(800,820)#mean dispersal ability of the species

#Build parameter data frame (keep the order of the parameters):
simulation <- data.frame(MDST2,NPATCH2,AREA_M2,AREA_SD2,
MAPSIZE2,SPAN2,ITER2,PAR1_SPAN2,PAR2_SPAN2,PAR3_SPAN2,PAR4_SPAN2,PAR5_SPAN2,
NSEW_SPECIES2,PARM_SPECIES2,METHOD_SPECIES2,KERN,CONN,COLNZ,EXT,BETA1,B,C1,C2,Z,R2,
DISPERSAL2)

#Delete vectors used for data frame creation:
rm('PAR1_SPAN2','PAR2_SPAN2','PAR3_SPAN2','PAR4_SPAN2','PAR5_SPAN2',
'NSEW_SPECIES2','PARM_SPECIES2','METHOD_SPECIES2','MAPSIZE2','SPAN2','ITER2',
'NPATCH2','AREA_M2','AREA_SD2','MDST2','KERN','CONN','COLNZ','EXT',
'BETA1','B','C1','C2','Z','R2','DISPERSAL2')

## Not run:
data(param1)

ms2 <- manage_landscape_sim(par_df=simulation,parameters_spom=param1)

## End(Not run)

```

matrix.graph

Returning a matrix with information on connections between patches

Description

Based on a landscape graph, this function allows the creation of a matrix of Euclidean distances (straight-line pairwise distance between the margins of all the patches), matrix of topological distances (minimum number of connections between any two patches) and adjacency matrix (this a matrix of 0 and 1, showing the adjacency between any two patches, where 0 means that the patches are not connected and 1 means that the patches are connected).

Usage

```
matrix.graph(r1, mat)
```

Arguments

- | | |
|-----|--|
| r1 | Object of class 'landscape'. |
| mat | mat - one of the following: <ul style="list-style-type: none"> • 'euc_distance' - euclidian distance between patches (edge-to-edge). • 'centr_distance' - euclidian distance between patches (centroid-to-centroid). |

mc_df

- 'adjacency' - adjacency matrix, with values d_{ij} , taking value 0 if patches i and j are not connected and value 1 if those patches are connected.
- 'top_matrix' - topological distance, with values d_{ij} , where the value d is the minimum number of connections between the patches i and j . Topological distance is defined as the minimum number of links between patches i and j .

Value

This function returns a matrix (each one of the specified matrices: Euclidean distance, topological distance and adjacency matrix).

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#)

Examples

```
data(rland)

#Computing matrix of topological distances:

matrix.graph(rl=rland, mat="top_matrix")
```

mc_df

Modified patch occupancy data of Cabrera vole as a data frame

Description

One season patch occupancy dataset for *Microtus cabreræ* in SW Portugal (modified). This dataset is in a format directly used by [convert.graph](#) and converted to an object class 'metapopulation'.

Usage

```
data(mc_df)
```

Format

A data frame with 685 observations on the following 5 variables.

ID Patch Id.

x X coordinate.

y Y coordinate.

area Patch area, in hectares.

mc Occupancy state (0/1).

Details

To create this sample dataset the occupancy status of patches was scrambled, however the proportion of occupied patches was kept.

Source

Original field data was obtained during project PERSIST (PTDC/BIA-BEC/105110/2008).

Examples

```
##To be converted in a object of class "metapopulation":
#mc1 <- convert.graph(dframe=mc_df, mapsize=8200, dispersal=800)

data(mc_df)

#Check the columns:

head(mc_df)
```

#	ID	x	y	area	mc
#1	1	1248.254	0.000	0.079	0
#2	2	1420.857	46.725	0.781	1
#3	3	1278.912	52.629	1.053	1
#4	4	6370.625	62.637	0.788	0
#5	5	1151.337	97.140	0.079	0
#6	6	1295.796	104.839	0.137	1

MetaLandSim-internal *Internal functions for the MetaLandSim package.*

Description

Internal functions for the MetaLandSim package

Details

These are not to be called by the user.

Source

Coded by Tal Galili. URL: <http://www.r-statistics.com/2012/01/merging-two-data-frame-objects-while-preserving-the-rows-order/>

Description

User-friendly graphic user interface that allows running the main functions of the package.

Usage

```
MetaLandSim.GUI()
```

Value

Displays the graphic user interface.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [species.graph](#), [simulate_graph](#), [iterate.graph](#), [range_expansion](#),
[range_raster](#)

Examples

```
## Not run:  
#In order to display the GUI:  
  
MetaLandSim.GUI()  
  
## End(Not run)
```

Description

Class representing a landscape graph with species' patch occupancy data, as produced by [species.graph](#), [convert.graph](#) and [import.shape](#).

Slots

- `mapsize` - Landscape mosaic side length, in meters.
- `minimum.distance` - Minimum distance between patches centroids, in meters.
- `mean.area` - Mean patch area in hectares.
- `SD.area` - Standard deviation of patches area.
- `number.patches` - Total number of patches.

- dispersal - Species mean dispersal ability, in meters.
- distance.to.neighbours - Data frame with pairwise distance between patches, in meters.
- nodes.characteristics - Data frame with patch (node) information (coordinates, area, radius, cluster, distance to nearest neighbor, ID and species).

Author(s)

Frederico Mestre and Fernando Canovas

metrics.graph	<i>Computes landscape connectivity metrics</i>
---------------	--

Description

Computes several landscape metrics, mostly derived from graph theory or assuming a graph representation of the landscape.

Usage

```
metrics.graph(rl, metric)
```

Arguments

- | | |
|--------|--|
| rl | Object of class 'landscape'. |
| metric | one of the following connectivity metrics: <ul style="list-style-type: none"> • 'NC' - Number of components. • 'LNK' - Number of links connecting the patches. • 'SLC' - Area (in hectares) of the largest group of patches. • 'MSC' - Mean area (in hectares) of a group of patches. • 'HI' - Harary Index. • 'NH' - Normalization of the Harary Index. • 'ORD' - Landscape (graph) order. • 'GD' - Landscape (graph) diameter. • 'CCP' - Class coincidence probability. • 'LCP' - Landscape coincidence probability. • 'ECS' - Expected cluster size. • 'AWF' - Area-weighted Flux. • 'PC' - Probability of connectivity. |

Details

These metrics assume different types of links between nodes (patches). Some assume probabilistic connections between nodes (e.g. PC) while others assume binary connections (e.g. NC, SLC, LNK, IIC). Also, these metrics have several degrees of complexity, from the simpler ones (such as NC and LNK) to the more complex (such as IIC and PC). Some are purely structural; the same landscape has the same index whatever the species, while others are measures of functional, where the connectivity of a given landscape is dependent on the species (dispersal ability). Precaution must be taken when looking at the outputs produced by some of these metrics (particularly the

simpler, structural ones). Regardless of being simpler to compute, the outputs might be misleading. This metrics can however be used as exploratory tools.

Detail about each of the metrics:

- 'NC' - Number of components, groups of connected patches, in the landscape graph (Urban and Keitt, 2001). Patches in the same component are accessible, while patches in different components are not connected. More connected landscapes have less components. Threshold dependent (dispersal distance).
- 'LNK' - Number of links connecting the patches (considering that the maximum distance is the species dispersal distance and that these graphs are binary, which means that nodes are either connected or unconnected) (Pascual-Hortal and Saura, 2006). Higher LNK implies higher connectivity. Threshold dependent (dispersal distance).
- 'SLC' - Area (in hectares) of the largest group of patches, or component (Pascual-Hortal and Saura, 2006). Threshold dependent (dispersal distance).
- 'MSC' - Mean area (in hectares) of a group of patches, or component (Pascual-Hortal and Saura, 2006). Threshold dependent (dispersal distance).
- 'HI' - Harary Index. Originally developed to characterize molecular graphs by Plavsic et al. (1993) it was later transposed to the landscape context by Ricotta et al. (2000). This index was considered by Ricotta et al. (2000) to be more effective from a statistical and ecological perspective. Higher HI implies higher connectivity. Threshold dependent (dispersal distance).
- 'NH' - Normalization of the Harary Index, facilitates analysis because this normalization will set the values between 0 and 1 and allow direct comparison of different habitat networks (Ricotta et al. 2000). Threshold dependent (dispersal distance).
- 'ORD' - Order. Index originated in the graph theory and later translated into the landscape context by Urban and Keitt (2001) provides a simple structural evaluation of the graph: it is the number of patches of the component (group of patches) with more patches. Threshold dependent (dispersal distance).
- 'GD' - Graph diameter. Another index directly derived from graph theory, providing a simple quantification of the graph structure. The graph diameter is the maximum of all the shortest paths between the patches of an habitat network. It is computed in meters (euclidean distance), instead of number of links (such as HI, NH and IIC) (Bunn et al. 2000, Urban and Keith, 2001). Shorter diameter implies faster movement in the habitat network (Minor and Urban, 2008). Threshold dependent (dispersal distance).
- 'CCP' - Class coincidence probability. It is defined as the probability that two randomly chosen points within the habitat belong to the same component. Ranges between 0 and 1 (Pascual-Hortal and Saura 2006). Higher CCP implies higher connectivity. Threshold dependent (dispersal distance).
- 'LCP' - Landscape coincidence probability. It is defined as the probability that two randomly chosen points in the landscape (whether in an habitat patch or not) belong to the same habitat component. Ranges between 0 and 1 (Pascual-Hortal and Saura 2006). Threshold dependent (dispersal distance).
- 'CPL' - Characteristic path length. Mean of all the shortest paths between the network nodes (patches) (Minor and Urban, 2008). The shorter the CPL value the more connected the patches are. Threshold dependent (dispersal distance).
- 'ECS' - Expected cluster size. Mean cluster size of the clusters weighed by area. (O' Brien et al., 2006 and Fall et al, 2007). This represents the size of the component in which a randomly located point in an habitat patch would reside. Although it is informative regarding the area of the component, it does not provide any ecologically meaningful information regarding the total area of habitat, as an example: ECS increases with less isolated small components or

patches, although the total habitat decreases (Laita et al. 2011). Threshold dependent (dispersal distance).

- 'AWF' - Area-weighted Flux. Evaluates the flow, weighted by area, between all pairs of patches (Bunn et al. 2000 and Urban and Keitt 2001). The probability of dispersal between two patches (p_{ij}), required by the AWF formula, was computed using $p_{ij} = \exp(-1/\text{dispersal} * d_{ij})$, where dispersal value is given by the 'dispersal' field in the 'landscape' object. The user might change the code in order to set up different ways of deriving p_{ij} (as the one suggested by Minor and Urban, 2007). Does not depend on any distance threshold (probabilistic).
- 'IIC' - Integral index of connectivity. Index developed specifically for landscapes by Pascual-Hortal and Saura (2006). It is based on habitat availability and on a binary connection model (as opposed to a probabilistic). It ranges from 0 to 1 (higher values indicating more connectivity). Threshold dependent (dispersal distance).
- 'PC' - Probability of connectivity. Probability that two points randomly placed in the landscape are in habitat patches that are connected, given the number of habitat patches and the connection probabilities (p_{ij}). Similar to IIC, although assuming probabilistic connections between patches (Saura and Pascual-Hortal 2007). Probability of inter-patch dispersal is computed in the same way as for AWF. Does not depend on any distance threshold (probabilistic).

Value

Returns the numeric value(s), corresponding to the chosen connectivity metric(s) for a given landscape.

Author(s)

Frederico Mestre and Fernando Canovas

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min_distance

Ricotta, C., Stanisci, A., Avena, G. C., and Blasi, C. (2000). Quantifying the network connectivity of landscape mosaics: a graph-theoretical approach. *Community Ecology*, 1(1): 89-94.

Saura, S., and Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landscape and Urban Planning*, 83(2): 91-103.

Urban, D., and Keitt, T. (2001). Landscape connectivity: a graph-theoretic perspective. *Ecology*, 82(5): 1205-1218.

See Also

[rland.graph](#)

Examples

```
data(rland)

#Compute the Integral index of connectivity of a landscape:

metrics.graph (rl=rland, metric="AWF")
```

<code>min_distance</code>	<i>Computes topological distance</i>
---------------------------	--------------------------------------

Description

Function to compute topological distance between patches. Topological distance is defined as the minimum number of links between any two patches.

Usage

```
min_distance(rl)
```

Arguments

`rl` Object of class 'landscape'.

Value

Returns a matrix with the topological distance between the nodes.

Author(s)

Frederico Mestre and Fernando Canovas.

See Also

[rland.graph](#)

Examples

```
data(rland)

min_distance(r1=rland)
```

occ.landscape	<i>Sample landscape with one simulated occupancy snapshot</i>
---------------	---

Description

Sample random landscape graph, with species occupancy data (occupancy rate - 50%). Simulated data.

Usage

```
data(occ.landscape)
```

Format

A list with the following elements:

- mapsize - landscape mosaic side length, in meters.
- minimum.distance - minimum distance between patches centroids.
- mean.area - mean area, in hectares.
- SD.area - standard deviation of the area.
- number.patches - number of patches.
- dispersal - mean dispersal ability of the species.
- distance.to.neighbours - data frame with pairwise distance between patches.
- nodes.characteristics - data frame with the characteristics of each patch.

Examples

```
data(occ.landscape)
```

occ.landscape2

`occ.landscape2`

Sample landscape with 10 simulated occupancy snapshots

Description

Sample species occupancy in a network during 10 time steps. Simulated data.

Usage

```
data(occ.landscape2)
```

Format

A list with the following elements:

- `mapsize` - landscape mosaic side length, in meters.
- `minimum.distance` - minimum distance between patches centroids.
- `mean.area` - mean area, in hectares.
- `SD.area` - standard deviation of the area.
- `number.patches` - number of patches.
- `dispersal` - mean dispersal ability of the species.
- `distance.to.neighbours` - data frame with pairwise distance between patches.
- `nodes.characteristics` - data frame with the characteristics of each patch, (species 1 to 10 - occupancy snapshots).

Examples

```
data(occ.landscape2)
```

`param1`

Sample parameter data frame number 1

Description

Sample data frame, as produced by [parameter.estimate](#). These parameters are to be passed to [spom](#). These are made up parameters, not related to any species.

Usage

```
data(param1)
```

Format

A data frame with 4 rows displaying the four parameters (`alpha`, `x`, `y`, `e`) to be passed to [spom](#):

- `alpha` - Parameter relating extinction with distance.
- `y` - Parameter `y` in the colonization probability.
- `e` - Parameter defining the extinction probability in a patch of unit area.
- `x` - Parameter scaling extinction risk with patch area.

Details

The four parameters are to be passed to [spom](#).

Examples

```
data(param1)

param1

#      par_output
#alpha 0.00100000
#x      0.50000000
#y      2.00000000
#e      0.04662827
```

param2

Sample parameter data frame number 2

Description

Sample data frame, as produced by [parameter.estimate](#). These parameters are to be passed to [spom](#). These are made up parameters, not related to any species.

Usage

```
data(param1)
```

Format

A data frame with 4 rows displaying the four parameters (alpha, x, y, e) to be passed to [spom](#):

- alpha - Parameter relating extinction with distance.
- y - Parameter y in the colonization probability.
- e - Parameter defining the extinction probability in a patch of unit area.
- x - Parameter scaling extinction risk with patch area.

Details

The four parameters are to be passed to [spom](#).

Examples

```
data(param1)

param1

#      par_output
#alpha 0.00250000
#x      0.50000000
```


parameter.estimate

```
#y      2.00000000  
#e      0.04662827
```

parameter.estimate	<i>Estimate parameters</i>
--------------------	----------------------------

Description

Estimates the parameters of the Stochastic Patch Occupancy Model with the following approaches: regression of snapshot data (Hanski, 1994); Monte Carlo simulation (Moilanen, 1999) and Bayesian MCMC on the full dataset (ter Braak and Etienne, 2003).

Usage

```
parameter.estimate(sp, method, alpha = NULL, nsnap)
```

Arguments

sp	Object of class 'metapopulation' with real patch occupancy data of the focal species.
method	Method to be used in parameter estimation. Available methods: <ul style="list-style-type: none">• Rsnap_1 - Regression of snapshot data, using one snapshot (code based on Oksanen, 2004).• Rsnap_x - Regression of snapshot data, using more than one snapshot (code based on Oksanen, 2004).• MCsim - Monte Carlo simulation.• norescue - Bayesian MCMC, not considering Rescue effect.• rescue - Bayesian MCMC, considering Rescue effect.
alpha	Boolean (TRUE/FALSE). Estimate the alpha parameter.
nsnap	Number of snapshots considered.

Details

Parameter alpha describes the effect of distance to dispersal (inverse of the average dispersal distance). Parameter x describes the dependence of the extinction risk on patch size, and consequently on population dimension. Parameter y scales colonization with connectivity. Parameter e is the intrinsic extinction rate of local populations, which is the extinction rate not considering immigration. In the current version the methods 'MCsim', 'rescue' and 'norescue' only create the files to be used in the applications already available. Future versions should allow the direct estimation of parameters without the need for the applications of Moilanen (1999) and Ter Braak and Etienne (2003).

Future versions should include the estimation of other parameters, using the virtual migration model (Hanski et al. 2000).

Regarding the method 'MCsim' the settings file produced (.set) by default has the method Nlr (non-linear regression) chosen. The user should read the file readme.txt, available with the application, where a three step estimation process is described. The objective is to produce the priors for the Monte Carlo simulation to run.

It is highly recommended that the user reads both papers that provide the applications to compute the methods 'MCsim', 'rescue' and 'norescue'. Several editions to the settings and parameters files

of both applications might be needed in order to customize the estimation process. This function only generates the input files with the basic needed structure.

Parameter estimation is not the main purpose of this package. As such, the user can estimate the parameters using other available software tools and then apply the estimated parameters in the simulations. The function `create.parameter.df` can be used to create the data frame of the basic spom parameters. Other required parameters can be directly given as arguments to the `iterate.graph`, `spom` or `range_expansion` functions.

The application of the Moilanen paper considers the kernel 'op1', connectivity 'op1', colonization 'op1' and extinction 'op1'. This SPOM (Stochastic Patch Occupancy Model) is known as Incidence Function Model (Hanski, 1994 and 1999). In the original version of the model $b=1$. However this might be a useful parameter as it scales emigration with patch area. This parameter can be estimated with field data. Moilanen (1998) obtained the value for this parameter by regressing the patch area with known population size.

Value

With the methods 'Rsnap_1' and 'Rsnap_x' returns a data frame with 4 rows displaying the four parameters (alpha, x, y, e) to be passed to `spom`:

- alpha - Parameter relating extinction with distance.
- y - Parameter y in the colonization probability.
- e - Parameter defining the extinction probability in a patch of unit area.
- x - Parameter scaling extinction risk with patch area.

Regarding the methods 'MCsim', 'rescue' and 'norescue' it returns the files to be used as input in the applications. The files will be saved in the working directory. After running the applications, a data frame can be created in R using the function `create.parameter.df`. This will return a data frame with the same structure as the first two methods.

Note

A vignette is available with detailed information about the computation of the parameters using each method. The method 'MCsim' creates the files (data and settings files) to be used with the application available with the paper by Moilanen (1999). The methods 'rescue' and 'norescue' create the files (data, parameters and distance files) to be used with the application available with the paper by ter Braak and Etienne (2003).

The application by Moilanen is available in <http://www.esapubs.org/archive/ecol/E080/003/>. The application by ter Braak and Etienne is available in <http://www.esapubs.org/archive/ecol/E084/005/suppl-1.htm>.

Author(s)

Frederico Mestre and Fernando Canovas

References

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Moilanen, A. (1998). Long-term dynamics in a metapopulation of the American Pika. *The American Naturalist*, 152(4), 530-542.

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Oksanen, J. (2004). Incidence Function Model in R. url.: <http://cc.oulu.fi/~jarioksa/opetus/openmeta/metafit.pdf>.

ter Braak, C. J., & Etienne, R. S. (2003). Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation. *Ecology*, 84(1): 231-241.

See Also

[create.parameter.df](#), [iterate.graph](#), [range_expansion](#) and [spom](#)

Examples

```
data(occ.landscape)

#Using the Regression of snapshot data:

param1 <- parameter.estimate (sp=occ.landscape, method="Rsnap_1")
```

`plotL.graph`

Plot one landscape of the list created by [span.graph](#)

Description

Plots a given landscape of a landscape sequence from [span.graph](#).

Usage

```
plotL.graph(rl, rlist, nr, species, links, ...)
```

Arguments

<code>rl</code>	Object of class 'landscape'.
<code>rlist</code>	List returned by span.graph .
<code>nr</code>	index of the landscape to display graphically.
<code>species</code>	TRUE/FALSE, TRUE if 'rl' is of class 'metapopulation' or 'FALSE' if rl is of class 'landscape'.
<code>links</code>	TRUE/FALSE, show links between connected patches.
<code>...</code>	Other arguments.

Value

Graphical display of the landscape.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[plot_graph](#), [span.graph](#), [rland.graph](#)

Examples

```
data(rland)
data(landscape_change)

plotL.graph(r1=rland, rlist=landscape_change, nr=50, species=FALSE, links=FALSE)
```

plot_expansion

Graphical display of the expansion

Description

Plots the expansion object.

Usage

```
plot_expansion(exp)
```

Arguments

exp Object of class 'expansion'.

Value

Graphical display of the 'expansion' class.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[expansion](#)

Examples

```
data(rg_exp)

plot_expansion(exp=rg_exp)
```

plot_graph

plot_graph	<i>Graphical display of the landscape</i>
------------	---

Description

Plots the landscape graph, with or without the species occupation (respectively lists returned by [species.graph](#) or [rland.graph](#)) and with or without the links between patches.

Usage

```
plot_graph(rl, species, links)
```

Arguments

rl	Object of class 'landscape' (species=FALSE) or 'metapopulation' (species=TRUE).
species	TRUE/FALSE, TRUE if 'x' is of class 'metapopulation' or 'FALSE' if x is of class 'landscape'.
links	TRUE/FALSE, show links between connected patches.

Value

Graphical display of the landscape.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [species.graph](#)

Examples

```
data(rland)
data(occ.landscape)

#Without the species occupancy:
plot_graph(rl=rland, species=FALSE, links=FALSE)

#With the species occupancy:
plot_graph(rl=occ.landscape, species=TRUE, links=FALSE)
```

range_expansion	<i>Produce a range expansion model</i>
-----------------	--

Description

This function returns the expansion probability, from a landscape with a given set of parameters, into the four cardinal directions. This can subsequently be converted in a dispersal model by the function [range_raster](#). The dispersal model can be combined with an ecological niche model.

Usage

```
range_expansion(rl, percI, param, b, tsteps, iter)
```

Arguments

rl	Object of class 'landscape'. Starting landscape for the expansion procedure.
percI	Percentage of patch occupancy in the starting landscape.
param	Parameter data frame delivered by parameter.estimate , including: <ul style="list-style-type: none"> • alpha - Parameter relating extinction with distance. • y - Parameter y in the colonization probability. • e - Parameter defining the extinction probability in a patch of unit area. • x - Parameter scaling extinction risk with patch area.
b	Parameter scaling emigration with patch area (if conn='op1' or 'op2') in spom . By default, equal to 1.
tsteps	Number of time steps to simulate (e.g. years).
iter	Number of iterations of the simulation procedure.

Details

The expansion algorithm has been improved, since the paper Mestre et al. (2016) describing the package was published. Now, instead of the transition between adjacent landscape units being dictated by the occupation of a spurious node (representing the margin through which the expansion takes place) a somewhat more realistic approach is followed. If, during the metapopulational dynamics simulation, any patch located between the landscape unit (LU) margin and a parallel line placed at a distance equivalent to half of the mean dispersal ability of the species is occupied, then the algorithm assumes that the species will have the ability to go across to the next LU. In this new empty LU initial occupation is defined as follows: a new line is placed, with a spacing equivalent to half the dispersal ability of the species. In the area defined by the margins of the LU and this line the species will occupy in the same proportion as in the preceding LU.

An example, with the expansion eastward (the process is repeated 4 times, one in each cardinal direction): One LU with 200 patches, occupation of 50%, mapsize (length of the LU side) 1000 species mean dispersal ability of 200. Metapopulational dynamics are simulated until one patch is occupied in a area defined by the north, south, east margins of the LU and a vertical line placed at x=800 (1000-200). Then, if any of this patches is occupied, a new LU (a random realization of the same parameter set) is created and initial occupation is defined at an area defined between the west, north and south margins and a line placed at x=200. This occupation level has the same percentage as the previous landscape.

range_raster

Value

This function returns a list, of class 'expansion', of four data frames with the proportion of occupations at several distances from the closest occupied landscape mosaic. These four data frames correspond to the proportion of occupation to the north, south, east and west. Each data frame has the following columns:

- DISTANCE - Distance (mapsize x number of landscapes).
- OCCUPATION - How many times did the landscape at this distance got occupied by the species (from a total of 'iter' repetitions).
- PROPORTION - Proportion of occupation for the landscape at this distance (OCCUPATION/iter).
- TIME STEP - The average time steps at which a given distance is occupied.

Note

Depending on computing power and number of iterations (parameter 'iter') this function can take from a few hours to several days to run.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[range_raster](#)

Examples

```
## Not run:
#Produce a model of range expansion:
#Note: this function should be run with >100 iterations (parameter "iter").

data(rland)
data(param2)

rg_exp1 <- range_expansion(rl=rland, percI=50, param=param2, b=1, tsteps=100, iter=100)

## End(Not run)
```

range_raster

Probability of occupancy, dispersal model

Description

This function intends to create a raster map, estimating probability of occupancy, at a given time step, based on species dispersal and landscape configuration. *range_raster* uses the output from [range_expansion](#) and a raster map with the species current occupancy.

Usage

```
range_raster(presences.map, re.out, mask.map=NULL, plot.directions=TRUE)
```

Arguments

<code>presences.map</code>	string of the raster file name with species occurrence.
<code>re.out</code>	object of class list expansion. Output from range_expansion .
<code>mask.map</code>	default NULL. String of the raster file name with the mask. Usually, 1 over the area where the analyses should be done.
<code>plot.directions</code>	default TRUE. Whether It will (TRUE) or will not (FALSE) return a graphics for the expansion model functions and raster maps with expansion probabilities in all four cardinal points.

Details

The function automatically reads the raster input files (`presences.map` and `mask.map`, if present). Usually, 0 for absence and 1 for presence in every square cell over a given resolution. Supported file types are those that can be read via `rgdal` (see [gdal](#)). Note that the projection for the raster layer should be one of those supporting metric units (i.e., linear scale is equal in all directions around any point such as Transverse Mercator; see <http://spatialreference.org/>).

Then, it computes and fits single sigmoidal functions for every direction on the expansion movements (building four sub-models, one to each main cardinal direction), as previously computed by [range_expansion](#). Four different raster maps are generated (the sub-models), each estimating the probability of expansion for north, south, east and west directions. The four maps are finally summarized into a single range expansion map, which is returned to the user as an object of class `RasterLayer` and saved in the working directory. These four maps do not directly express the probabilities in the output of [range_expansion](#). Rather, the outputs are weighted by directionality, so that e.g. the north model favours the dispersal towards the north while penalizing dispersal in every other direction. As such, the resulting dispersal model is not a direct spatial transcription of the four data frames provided by [range_expansion](#) but an interpretation weighted by the spatial context given by directionality.

Additionally, a raster file is computed, showing the time steps at which each distance is reached. This output depicts the adjustment of a linear model to the output of the four sub-models together, considering the four equally. This output should not be used as guideline to mask the model if running to several time periods. For example if projections to 2050 and 2080 are to be made than the dispersal model should be run twice, adjusting the time steps to the desired date.

This function internally uses a connection to **GRASS GIS software** through the package `rgrass7`-package, in order to increase the performance for geographical calculations.

Finally, the user might have to manually adjust the starting values of the function `fit.sigmoid`, (defined internally in this function) if it has difficulty adjusting to the output of [range_expansion](#).

Value

Produces the spatial realization of the dispersal model, composed by a stack of two objects of the class `RasterLayer` (see [Raster-class](#) package for further description), with the probability of occupancy and the time step a given distance is occupied. This version of `MetaLandSim` uses GRASS, version 7 through the package `rgrass7`. Additionally these rasters are saved in the working directory (files 'PROB' and 'TSTEP') defined by the user and can be directly imported to any GIS software.

remove.species

Note

This function depends on [rgrass7](#).

Author(s)

Frederico Mestre and Fernando Canovas

References

The same as `range_expansion`.

See Also

[range_expansion](#), [Raster-class](#), [rgrass7](#), [initGRASS](#)

Examples

```
## Not run:

data(rg_exp)

presences <- system.file("examples/presences.asc", package="MetaLandSim")
mask <- system.file("examples/landmask.asc", package="MetaLandSim")

require(rgrass7)

#Initializing a GRASS session in a temporal directory:
#### Under Linux systems:
initGRASS("/usr/bin/grass", home=tempdir())
#### Under Windows systems:
initGRASS("C:/GRASS", home=tempdir())

range_raster(presences.map=presences, re.out=rg_exp, mask.map=mask) -> range.map

plot(range.map)

require(rasterVis)

levelplot(range.map, contour=TRUE)

## End(Not run)
```

`remove.species`

Remove the species occupancy from the landscape

Description

This function converts an object of class 'metapopulation' (with the species occupancy) in a object of class 'landscape' (without the species occupancy).

Usage

```
remove.species(sp)
```

Arguments

sp Object of class 'metapopulation'.

Value

Delivers an object of class 'landscape'.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [species.graph](#)

Examples

```
data(occ.landscape)

r11 <- remove.species(sp=occ.landscape)
```

removepoints

Remove a given number of patches from the landscape

Description

Randomly removes a given number of patches from the landscape.

Usage

```
removepoints(r1, nr)
```

Arguments

r1 Object of class 'landscape'.
nr Number of patches to remove.

Value

Returns an object of class 'landscape'.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [addpoints](#)

rg_exp

Examples

```
data(rland)

#Checking the number of patches in the starting landscape:

rland$number.patches

#60

#Removing 10 patches from the landscape:

r11 <- removepoints(r1=rland, nr=10)

#Checking the number of patches in the output landscape:

r11$number.patches

#50
```

rg_exp

List with range.expansion output

Description

Output of [range_expansion](#). Object of class 'expansion'.

Usage

```
data(rg_exp)
```

Format

List of four data frames ('NORTH', 'SOUTH', 'EAST' and 'WEST') with the probability of occupations at several distances from the closest occupied landscape mosaic. These four data frames correspond to the probability of occupation to the north, south, east and west. Each data frame has the following columns:

- DISTANCE - Distance (mapsize x number of landscapes).
- OCCUPATION - How many times did the landscape at this distance got occupied by the species (from a total of 'iter' repetitions).
- PROPORTION - Proportion of occupation for the landscape at this distance (OCCUPATION/iter).
- TIME STEP - The average time step during which a given distance is reached.

Examples

```
data(rg_exp)
```

rland	<i>Random landscape</i>
-------	-------------------------

Description

Sample random landscape graph, object of class 'landscape'. It has 60 patches and the landscape mosaic has 1000 meters of side.

Usage

```
data(rland)
```

Format

A list with the following elements:

- mapsize - landscape mosaic side length, in meters.
- minimum.distance - minimum distance between patches centroids).
- mean.area - mean area, in hectares.
- SD.area - standard deviation of the area.
- number.patches - number of patches.
- dispersal - mean dispersal ability of the species.
- nodes.characteristics - data frame with the characteristics of each patch.

Examples

```
data(rland)
```

rland.graph	<i>Creates random landscape graph</i>
-------------	---------------------------------------

Description

One of the key functions of the package, which allows the creation of random landscapes (represented as graphs) with two categories: habitat patch and non-habitat matrix. The landscapes can be different depending on the parameters chosen.

Usage

```
rland.graph(mapsize, dist_m, areaM, areaSD, Npatch, disp, plotG)
```

rland.graph

Arguments

<code>mapsize</code>	Landscape mosaic side length, in meters.
<code>dist_m</code>	Minimum distance between patches (centroid).
<code>areaM</code>	Mean area (in hectares).
<code>areaSD</code>	SD of the area of patches, in order to give variability to the patches area.
<code>Npatch</code>	Number of patches (might be impaired by the <code>dist_m</code> , see the "Note" section).
<code>disp</code>	Species mean dispersal ability, in meters.
<code>plotG</code>	TRUE/FALSE, to show graphic output.

Details

The dispersal distance, as given by the parameter 'disp', is used for the computation of some of the connectivity metrics (function [metrics.graph](#)) and for the graphic representation of the landscapes (in both cases defining the groups of patches, or components). For the simulation of the metapopulational dynamics, the dispersal distance is given through the 'alpha' parameter (the inverse of the mean dispersal ability) in the parameter data frame created by [create.parameter.df](#). This has an important consequence: no thresholding (considering the dispersal ability) is assumed when simulating the metapopulational dynamics.

Value

Returns a list, with the following elements:

- `mapsizeSide` of the landscape in meters.
- `minimum.distance` Minimum distance between patches centroids, in meters.
- `mean.area` Mean patch area in hectares.
- `SD.area` Standard deviation of patches area.
- `number.patches` Total number of patches.
- `dispersal` Species mean dispersal ability, in meters.
- `nodes.characteristics` Data frame with patch (node) information (coordinates, area, radius, cluster, distance to nearest neighbour and ID).

An additional field, `colour`, has only graphical purposes.

Note

If the mean distance between patches centroid and the number of patches are both too high then the number of patches is lower than the defined by the user.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[span.graph](#), [species.graph](#)

Examples

```
#Example to create a random landscape graph with 60 patches with a mean area
#of 0.05 hectares.
#The landscape mosaic is a square with 1000 meters side.
#The species mean dispersal ability is 120 meters (in order to connect the patches).
#A plot with the landscape graph is displayed graphically.

r1l <- rland.graph(mapsize=1000, dist_m=80, areaM=0.05, areaSD=0.02, Npatch=60,
disp=120, plotG=TRUE)
```

simulate_graph	<i>Simulate species occupancy in one dynamic landscape</i>
----------------	--

Description

Simulates the species' occupation on a landscape sequence, resorting to the [spom](#) function.

Usage

```
simulate_graph(r1, rlist, simulate.start, method, parm, nsew="none", succ="none",
param_df, kern, conn, colnz, ext, beta1, b, c1, c2, z, R)
```

Arguments

r1	Object of class 'landscape' or 'metapopulation'.
rlist	List delivered by span.graph .
simulate.start	TRUE (r1 is of class 'landscape') or FALSE (r1 is of class 'metapopulation')
method	One of the following: click - individually select the patches with occurrence of the species by clicking on the map. Use only for individual landscape simulations. However, this option should not be used with iterate.graph . percentage - percentage of the patches to be occupied by the species. number - number of patches to be occupied by the species. To be internally passed to species.graph .
parm	Parameter to specify the species occurrence - either percentage of occupied patches or number of occupied patches, depending on the method chosen. To be internally passed to species.graph .
nsew	'N', 'S', 'E', 'W' or none - point of entry of the species in the landscape. By default set to "none". To be internally passed to species.graph .
succ	Set the preference of the species for patch successional stage: 'none', 'early', 'mid' and 'late'.
param_df	Parameter data frame delivered by parameter.estimate , including: <ul style="list-style-type: none"> • alpha - Parameter relating extinction with distance. • y - Parameter y in the colonization probability. • e - Parameter defining the extinction probability in a patch of unit area. • x - Parameter scaling extinction risk with patch area. To be internally passed to simulate_graph .

simulate_graph

kern	'op1' or 'op2'. Dispersal kernel. See details in the spom function. To be internally passed to spom .
conn	'op1' or 'op2'. Connectivity function. See details in the spom function. To be internally passed to spom .
colnz	'op1', 'op2' or 'op3'. Colonization function. See details in the spom function. To be internally passed to spom .
ext	'op1', 'op2' or 'op3'. Extinction function. See details in the spom function. To be internally passed to spom .
beta1	Parameter affecting long distance dispersal probability (if the Kern='op2'). To be internally passed to spom .
b	Parameter scaling emigration with patch area (if conn='op1' or 'op2'). To be internally passed to spom .
c1	Parameter scaling immigration with the focal patch area (if conn='op2'). To be internally passed to spom .
c2	Parameter c in the option 3 of the colonization probability (if colnz='op3'). To be internally passed to spom .
z	Parameter giving the strength of the Allee effect (if colnz='op3'). To be internally passed to spom .
R	Parameter giving the strength of the Rescue effect (if ext='op3'). To be internally passed to spom .

Value

Returns a list of occupied landscapes, representing the same occupied landscape at different time steps.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[spom](#), [span.graph](#), [rland.graph](#), [iterate.graph](#)

Examples

```
data(rland)
data(landscape_change)
data(param1)

sim1 <- simulate_graph(rl=rland,
  rlist=landscape_change,
  simulate.start=TRUE,
  method="percentage",
  parm=50,
  nsew="none",
  succ = "none",
  param_df=param1,
  kern="op1",
  conn="op1",
  colnz="op1",
```

```

ext="op1",
beta1=NULL,
b=1,
c1=NULL,
c2=NULL,
z=NULL,
R=NULL
)

```

span.graph

Simulate landscape dynamics over a number of time steps

Description

This function gets an initial landscape graph and gradually applies changes. For a good review and classification of such changes see Bogaert et al. (2004) (not all described changes have been applied here). Future versions of the package should include other methods to change the landscape.

Usage

```

span.graph(r1, span = 100, par1 = 'none', par2 = NULL,
           par3 = NULL, par4 = NULL, par5 = NULL)

```

Arguments

- | | |
|------|---|
| r1 | Object of class 'landscape'. |
| span | Number of time steps (e.g. years) to simulate. |
| par1 | One of the following (default 'none'): <ul style="list-style-type: none"> • 'hab' percentage of the number of patches to eliminate. • 'dincr' minimal distance (between centroids of patches) increase over the simulation (in meters). • 'darea' percentage of increase/decrease of the mean area of patches, without changing SD. Patches with area <1 square meter are deleted. • 'stoc' simultaneous creation and destruction of patches (with variation in the number of created and destroyed patches). • 'stoc2' simultaneous creation and destruction of patches (same percentage of created and destroyed patches derived from the number of patches of the landscape in the preceeding time step). • 'ncsd' simultaneous creation and destruction of patches to the north and south of the landscape. • 'aggr' correlated habitat destruction. • 'none' no change. The percentage of patches to be generated or destroyed at each time step is not fixed (except for 'stoc2' in which case the percentage of created and destroyed patches is the same and directly computed from the number of patches in the preceeding time step, allowing to have landscape dynamism without change in the number of patches). For example if the landscape at the time step t-1 has 200 patches and the user wishes to set up a destruction rate of 5%, than the number of destroyed patches is given by a random number obtained from a Poisson distribution with mean 10 (5% of 200). |

species.graph

par2	Parameter specifying details for the options in par1: percentage of patches to delete (if par1='hab'); distance, in meters (if par1='dincr'); percentage of increase/decrease (increase with negative sign) of the mean area of patches (if par1='darea'); percentage of created/destroyed patches (if par1='stoc'); percentage of created patches (if par1='stoc2'); 'northernness' of created patches (if par1='ncsd'); percentage of destroyed patches (if par1='aggr').
par3	Additional parameter specifying details for the options in par1: percentage of destroyed patches (if par1='stoc2'); 'southernness' of destroyed patches (if par1='ncsd'); aggregation of destruction (if par1='aggr'). Minimum area for patch deletion, in hectares (if par1='darea').
par4	Percentage of created patches (if par1='ncsd').
par5	Percentage of destroyed patches (if par1='ncsd').

Value

Returns a list of data frames with the nodes characteristics of a given number of landscapes that suffer a specified change. The fields of these data frames are the same as those from the nodes characteristics resulting from [rland.graph](#).

Author(s)

Frederico Mestre and Fernando Canovas

References

Bogaert, J., Ceulemans, R., & Salvador-Van Eysenrode, D. (2004). Decision tree algorithm for detection of spatial processes in landscape transformation. *Environmental Management*, 33(1): 62-73.

See Also

[rland.graph](#), [simulate_graph](#), [iterate.graph](#)

Examples

```
data(rland)

#Simulating a decrease of 5% in the number of patches through 100 time steps:

span1 <- span.graph(r1=rland, span=100, par1="hab", par2=5, par3=NULL, par4=NULL, par5=NULL)
```

`species.graph`

Simulate landscape occupation

Description

Given a set of parameters, this function allows to simulate the occupation of an empty landscape, class "metapopulation".

Usage

```
species.graph(r1, method = 'percentage', parm, nsew = 'none', plotG = TRUE)
```

Arguments

r1	Object of class "landscape".
method	One of the following (default 'percentage'): click - individually select the patches with occurrence of the species by clicking on the map. Use only for individual landscape simulations. percentage - percentage of the patches to be occupied by the species. number - number of patches to be occupied by the species.
parm	Parameter to specify the species occurrence - either percentage of occupied patches or number of occupied patches, depending on the method chosen.
nsew	'N', 'S', 'E', 'W' or none - point of entry of the species in the landscape. By default set to "none".
plotG	TRUE/FALSE, to show graphic output.

Value

Returns a list, with the following elements:

- mapsize - Landscape mosaic side length, in meters.
- minimum.distance - Minimum distance between patches centroids, in meters.
- mean.area - Mean patch area in hectares.
- SD.area - Standard deviation of patches area.
- number.patches - Total number of patches.
- dispersal - Species mean dispersal ability, in meters.
- distance.to.neighbours - Data frame with pairwise distance between patches, in meters.
- nodes.characteristics - Data frame with patch (node) information (coordinates, area, radius, cluster, distance to nearest neighbour, ID and species).

An additional field, colour, has only graphical purposes.

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[rland.graph](#), [simulate_graph](#), [remove.species](#)

Examples

```
data(rland)

##Creating a 50% occupation in an empty landscape (using the "landscape" dataset):

sp1 <- species.graph(r1=rland, method="percentage", parm=50, nsew="none", plotG=TRUE)
```

spom	<i>Stochastic Patch Occupancy Model</i>
------	---

Description

This function predicts the occupancy status of each patch in a landscape in the time step $t+1$, based on the occupancy information on time step t .

Usage

```
spom(sp, kern, conn, colnz, ext, param_df,
      beta1 = NULL, b = 1, c1 = NULL, c2 = NULL,
      z = NULL, R = NULL, succ="none", max_age=1)
```

Arguments

sp	Landscape with species occupancy, object of class 'metapopulation'.
kern	'op1' or 'op2'. Dispersal kernel. See details.
conn	'op1' or 'op2'. Connectivity function. See details.
colnz	'op1', 'op2' or 'op3'. Colonization function. See details.
ext	'op1', 'op2' or 'op3'. Extinction function. See details.
param_df	Parameter data frame delivered by parameter.estimate , including: <ul style="list-style-type: none"> • alpha - Parameter relating extinction with distance. • y - Parameter y in the colonization probability. • e - Parameter defining the extinction probability in a patch of unit area. • x - Parameter scaling extinction risk with patch area.
beta1	Parameter affecting long distance dispersal probability (if the Kern='op2').
b	Parameter scaling emigration with patch area (if conn='op1' or 'op2'). By default set to 1.
c1	Parameter scaling immigration with the focal patch area (if conn='op2').
c2	Parameter c in the option 3 of the colonization probability (if colnz='op3').
z	Parameter giving the strength of the Allee effect (if colnz='op3').
R	Parameter giving the strength of the Rescue effect (if ext='op3').
succ	Set the preference of the species for patch successional stage: 'none', 'early', 'mid' and 'late'.
max_age	Default value set to 1. This argument should not be changed by the user. It is used only when the function runs inside others.

Details

In order to visualize which parameter combination is valid for each option, please refer to the following table (alpha, x, y and e are delivered by [parameter.estimate](#), as a data frame):

parameter	kern_1	kern_2	conn_1	conn_2	colnz_1	colnz_2	colnz_3	ext_1	ext_2	ext_3
alpha	x	x								
x								x	x	x

[illegible]

Dispersal Kernel

$$D(D_{ij}, \alpha) = \exp(-\alpha \cdot d_{ij})$$
$$D(D_{ij}, \alpha, \beta) = \frac{1}{1 + \alpha \cdot d_{ij}^\beta}$$

- Option 1 - Negative exponential. Earlier studies (until the end of the 1990) frequently used this type of thin-tailed kernels (Nathan et al. 2012).
- Option 2 - Fat-tailed kernel. The shape of the dispersal kernel is highly significant only when the metapopulation consists of several moderately small patch clusters, which are relatively far from each other. In this kind of a system, a patch cluster may go extinct, and long-distance dispersal will be important in determining the recolonization probability of the empty cluster (Shaw, 1995 and Moilanen, 2004). This type of fat-tailed kernels has become more frequent in recent works (Nathan et al. 2012). For

this is the Cauchy distribution.

$$S_i = \sum p_j.D(d_{ij}, \alpha).A_j^b$$
$$S_i = A_i^c \sum p_j . D(d_{ij}, \alpha) . A_j^b$$

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- Option 1 - In the version of Hanski (1994), the kernel is the negative exponential (option 1) and b is set to 1. In this more flexible version, the parameter b scales emigration with patch area (Moilanen, 2004).
- Option 2 - In Moilanen & Nieminen (2002) the kernel is the negative exponential (option 1). This metric considers the value of the focal patch's area, which was found to provide better results by Moilanen & Nieminen (2002), being less sensitive to errors in the estimation of a. Parameters b and c scale, respectively emigration and immigration, as a function of patch area (focal patch in the case of c). See 'note'.

Colonization function

Option 1 (Hanski, 1994, 1999)

$$C_i = \frac{S_i^2}{S_i^2 + y^2}$$

Option 2 (Moilanen, 2004)

$$C_i = 1 - \exp(-y \cdot S_i)$$

Option 3 (Ovaskainen, 2002)

$$C_i = \frac{S_i^z}{S_i^z + \frac{1}{c}}$$

where S_i is connectivity.

- Option 1 - It's the first version of the colonization probability, it includes Allee effect (however the strength of this effect cannot be modified) Hanski (1994). Colonization probability is defined as a sigmoid function of the connectivity of patch i.
- Option 2 - This option assumes that immigrating individuals originate colonization events independently, therefore, with no Allee effect. Adequate for species (plants) with passive dispersal (Moilanen, 2004).
- Option 3 - Here, as in option 1, the colonization probability is defined as a sigmoid function of the connectivity of patch i, and the user can change the strength of the Allee effect, by changing the parameter z, with values >1 reflecting the presence of this effect (Ovaskainen, 2002). In the original version of the IFM (option 1) Hanski (1994) assumed a relatively strong Allee effect (z=2). Parameter c describes the species ability to colonize (Ovaskainen & Hanski, 2001 and Ovaskainen, 2002).

Extinction function

Option 1 (Hanski, 1994, 1999)

$$E_i = \min(1, \frac{e}{A_i^x})$$

Option 2 (Hanski and Ovaskainen, 2000 and Ovaskainen and Hanski, 2002)

$$E_i = 1 - (\frac{-e}{A_i^x})$$

Option 3 (Ovaskainen, 2002)

$$E_i = \min[1, \frac{e}{A_i^x} \cdot (1 - C_i)^R]$$

where A_i is the area of the focal patch and C_i is the colonization probability of the focal patch.

- Option 1 - Original version developed by Hanski (1994).

- Option 2 - Used e.g. in the spatially realistic Levins model (Hanski & Ovaskainen, 2000 and Ovaskainen & Hanski, 2002). Parameter x scales extinction probability with patch area.
- Option 3 - Same as option 1, but considering the Rescue effect (with the strength of this effect being given by R). If $R=0$ there is no Rescue effect, however, if $R>0$, the Rescue effect grows exponentially with the probability of not being colonized. In the original version of this function Hanski (1994) assumed $R=1$.

Here, parameter x defines the degree to which the extinction rate is sensitive to the patch area. If $x>1$, with the increase of A_i the extinction rate rapidly approximates zero. The populations in the larger patches become almost impossible to extinguish. However, if x is small the extinction rate decreases slower with increasing A_i .

Value

Delivers a list similar to the class 'metapopulation' but with two additional columns in the data frame nodes.characteristics: 'species2' (which is the occupation in the next time step) and turn (turnover between occupancies).

Note

Future versions of the package should include the virtual migration model (Hanski et al. 2000), which allows the estimation of migration related parameters (relevant to the option 2 of connectivity).

Author(s)

Frederico Mestre and Fernando Canovas

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spom

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See Also

[species.graph](#), [simulate_graph](#), [iterate.graph](#)

Examples

```
data(occ.landscape)
data(param1)

#Simulating the occupation in the next time step:

landscape2 <- spom(sp=occ.landscape,
kern="op1",
conn="op1",
colnz="op1",
ext="op1",
param_df=param1,
beta1=NULL,
b=1,
c1=NULL,
c2=NULL,
z=NULL,
R=NULL,
succ="none"
)

#The output has two new columns in the data frame nodes.characteristics: species2
#(occupation in the next time step) and turn (turnover - change of occupation status,
#1 if changed and 0 if not)..

head(landscape2)

#      x      y  areas  radius cluster  colour nneighbour
#1 718.5011 228.47190 0.05741039 13.518245      1 #FF0000FF      91.80452
#2 494.3624  73.29165 0.08755563 16.694257      1 #FF0000FF      98.98432
#3 809.2326 245.90046 0.09384384 17.283351      1 #FF0000FF     166.68205
#4 638.8057 149.35122 0.08858989 16.792569      1 #FF0000FF      82.60306
#5 874.2010  19.78104 0.03621793 10.737097      1 #FF0000FF      92.26625
#6 605.3937  70.34944 0.03066018  9.878987      1 #FF0000FF     131.22261
#  ID species species2 turn
#1  1      1          1     0
#2  2      0          1     1
#3  3      1          1     0
#4  4      0          0     0
#5  5      0          1     1
#6  6      1          1     0
```

summary_landscape	<i>Summarize 'landscape' class objects</i>
-------------------	--

Description

This function summarizes a [landscape](#) class object.

Usage

```
summary_landscape(object)
```

Arguments

object Object of class [landscape](#)

Details

This function can be used to retrieve basic information on the objects of class 'landscape'.

Value

Returns a data frame with the following information on a [landscape](#) class object:

landscape area (hectares)	Landscape mosaic area, in hectares
number of patches	Number of patches in the landscape
mean patch area (hectares)	Mean patch area, in hectares
SD patch area	SD of the patch area
mean distance amongst patches (meters)	Mean inter-patch distance, in meters
minimum distance amongst patches (meters)	Minimum inter-patch distance, in meters

Note

The minimum distance between patches is different from that given in the object of class 'landscape', in the slot 'minimum.distance'. This is because this output is computed from the landscape structure and the one in the 'landscape' object was the parameter used to built the landscape. The minimum inter-patch distance given as a parameter in the function [rland.graph](#) will consider distance between patch centroids. The minimum inter-patch distance returned here considers the edge-to-edge distance, so this might be smaller that the parameter of [rland.graph](#). In order to see the difference between centroid-to-centroid and edge-to-edge inter-patch distance compute both using the [matrix.graph](#) function (methods are 'centr_distance' and 'euc_distance', respectively).

Author(s)

Frederico Mestre and Fernando Canovas

summary_metapopulation

See Also

[rland.graph](#), [landscape](#), [matrix.graph](#)

Examples

```
data(rland)

summary_landscape(object=rland)

#                               Value
#landscape area (hectares)      100.000
#number of patches              60.000
#mean patch area (hectares)     0.061
#SD patch area                  0.041
#mean distance amongst patches  528.345
#minimum distance amongst patches 51.780
```

`summary_metapopulation`

Summarize 'metapopulation' class objects

Description

This function summarizes a [metapopulation](#) class object.

Usage

```
summary_metapopulation(object)
```

Arguments

`object` Object of class [metapopulation](#)

Details

This function can be used to retrieve basic information on the objects of class 'metapopulation'.

Value

Returns a data frame with the following information on a [metapopulation](#) class object:

landscape area (hectares)	Landscape mosaic area, in hectares
number of patches	Number of patches in the landscape
mean patch area (hectares)	Mean patch area, in hectares
SD patch area	SD of the patch area
mean distance amongst patches (meters)	Mean inter-patch distance, in meters

minimum distance amongst patches (meters)
 Minimum inter-patch distance, in meters
 species occurrence - snapshot
 Occupation data of the focal species, numbered from 1 to the number of snapshots

Note

The minimum distance between patches is different from that given in the object of class 'landscape', in the slot 'minimum.distance'. This is because this output is computed from the landscape structure and the one in the 'landscape' object was the parameter used to built the landscape. The minimum inter-patch distance given as a parameter in the function [rland.graph](#) will consider distance between patch centroids. The minimum inter-patch distance returned here considers the edge-to-edge distance, so this might be smaller than the parameter of [rland.graph](#). In order to see the difference between centroid-to-centroid and edge-to-edge inter-patch distance compute both using the [matrix.graph](#) function (methods are 'centr_distance' and 'euc_distance', respectively).

Author(s)

Frederico Mestre and Fernando Canovas

See Also

[species.graph](#), [metapopulation](#), [matrix.graph](#)

Examples

```
data(occ.landscape)
data(occ.landscape2)

summary_metapopulation(object=occ.landscape)

#                               Value
#landscape area (hectares)      100.000
#number of patches              60.000
#mean patch area (hectares)     0.061
#SD patch area                  0.041
#mean distance amongst patches  528.345
#minimum distance amongst patches 51.780
#species occurrence - snapshot 1 50.000

summary_metapopulation(object=occ.landscape2)

#                               Value
#landscape area (hectares)      100.000
#number of patches              60.000
#mean patch area (hectares)     0.069
#SD patch area                  0.039
#mean distance amongst patches  521.717
#minimum distance amongst patches 45.905
#species occurrence - snapshot 1 50.000
#species occurrence - snapshot 2 58.333
#species occurrence - snapshot 3 61.667
#species occurrence - snapshot 4 61.667
```

summary_metapopulation

#species occurrence - snapshot 5	58.333
#species occurrence - snapshot 6	60.000
#species occurrence - snapshot 7	70.000
#species occurrence - snapshot 8	68.333
#species occurrence - snapshot 9	68.333
#species occurrence - snapshot 10	56.667

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Model Parameter Estimation

F. Mestre, F. Canovas, R. Pita, A. Mira, P. Beja

September 29, 2016

1 Introduction

The correct SPOM parametrization is one of the most crucial steps of every simulation procedure allowed by the package. The parameters are the numeric translation of the relation of the species with the landscape. Although this is not the main focus of this package, MetaLandSim offers some basic tools that will help to estimate the parameters to run the simulations. However, the user can have the parameters values available from other sources (whether published papers or estimated with other software tools) in each case the simulations can be run using those parameters. For a good overview of the several methods to parametrize the SPOM see Etienne et al. (2004). Most of the methods described can be implemented with MetaLandSim. Also, it is recommended that the user reads the book by Hanski (1999) in order to acquire the basic knowledge about metapopulation ecology and the first estimation procedures. The function `parameter.estimate` is the package tool to parametrize the spom function. This vignette clarifies the options available and gives a step-by-step guide of the function usage. The current version of the package does not executes all computations. Rather, some of the methods (`'MCsim'`, `'rescue'` and `'norescue'`) create the files needed as input to two applications provided by Moilanen (1999) (`MCsim`) and ter Braak and Etienne (2003) (`'rescue'` and `'norescue'`). Future versions of the package should incorporate these procedures in the R code. The objective of this vignette is to describe the parametrization procedures, allowing the user to produce robust estimates of the parameters in order to proceed with the landscape simulation process or with the range expansion simulation. Third vignette is run with made up data based upon real information.

2 Which method to choose

Currently, the following methods are available:

- *Rsnap_1* - Regression of snapshot data, using one snapshot (based on Oksanen, 2004).

- *Rsnap_x* - Regression of snapshot data, using more than one snapshot (based on Oksanen, 2004).
- *MCsim* - Monte Carlo simulation (Moilanen, 1999).
- *norescue* - Bayesian MCMC, not considering Rescue effect (ter Braak and Etienne, 2003).
- *rescue* - Bayesian MCMC, considering Rescue effect (ter Braak and Etienne, 2003).

Amongst the five methods allowed by MetaLandSim, the choice is facilitated by a careful consideration of the characteristics of each method and the dataset (such as number of snapshots). An examination of each method's advantages and drawbacks is available in Etienne et al. (2004). The methods 'rescue' and 'norescue' are computed using the application provided by ter Braak, and Etienne (2003) and the method 'MCsim' is computed using the application provided with Moilanen (1999). 'Rsnap_1' and 'Rsnap_x' are computed using the R code based on Oksanen (2004). Using the function `parameter.estimate`, the first three methods only create the needed files to run the applications. Next the user can use the function `create.parameter.df` to create a data frame with the estimated parameters. The application of Moilanen (1999) allows the estimation of the following parameters: x , y , e , A_0 , e' and α . The application by ter Braak and Etienne (2003) allow the estimation of the following parameters: e , x , y , z , α and b . Future versions of the package should include the virtual migration model (Hanski et al. 2000), allowing the estimation of b (which scales patch areas to population size and emigration rates) and c (here c_1 , which scales immigration with patch area).

3 Work-flow

3.1 Regression on Snapshot Data - method *Rsnap_1* or *Rsnap_x*

This is the simplest approach; it runs faster but provides the least reliable estimates of the parameters. It does not use turnover, only spatial structure and occupancy status.

```
> library(MetaLandSim)
> data(occ.landscape)
> data(occ.landscape2)
> #Using data with only one snapshot of the occupancy status
> param1 <- parameter.estimate(occ.landscape, method='Rsnap_1')
> param1

par_output
alpha 0.008333333
```

```

x      0.256707865
y      0.016724074
e      0.211572786

> #Using data with more than one snapshot of the occupancy status
> param2 <- parameter.estimate (occ.landscape2, method='Rsnap_x', nsnap=10)
> param2

      par_output
alpha 0.008333333
x     -0.172333542
y      0.021030749
e      0.742599240

```

3.2 Monte Carlo Simulation - method MCsim

This approach is more time-consuming (depending on computing power). This option calls for the functions on the paper by Moilanen (1999). Here, create.parameter.df only creates the files to be used as input to the application. The user should read the paper thoughtfully, as well as the available help files. A file with the settings (inputMCsim.set) and a file with the data (inputMCsim.dat) will be created into the working directory. Editions to the settings file will be needed in order to run the application using the three step procedure described in the readme.txt file. First run the application using Nlr, then using Bnlr and finally using mc (between each step the setting file should be edited to change the method). After running Nlr and Bnlr replace, in the settings file, 'edit x', 'edit y' and 'edit e' with those values (these are the priors to the simulation). The application and help files can be downloaded from the Ecological Archives, available (here).

```

> library(MetaLandSim)
> data(occ.landscape2)
> #First, generate the files to be the input of the application
> parameter.estimate (occ.landscape2, method='MCsim')
> #run the application mcm.exe from Moilanen (1999).
> #Previously read the readme.txt file #available with the
> #application.
> #Consider particularly the three step procedure for estimation,
> #using nonlinear regression (Hanski, 1994) to produce priors
> #for the Monte Carlo simulation). In the command line (first put
> #the application and the files in a folder with no spaces in the name.
> #e.g.: 'C:/moilanen/'):
>
> #mce.exe inputMCsim.dat inputMCsim
>
> #Or, from R:
>

```

```

> system('mce.exe inputMCsim.dat inputMCsim')
> #After, create a data frame, with create.parameter.df,
> #using the estimated parameters:
> param3 <- create.parameter.df(alpha, x, y, e)
>

```

3.3 Bayesian MCMC - methods 'rescue' and 'norescue'

This is the approach developed in the paper by ter Braak et al. (2003). The `parameter.estimate` function only produces the files needed to be used as input in this application. It produces a dataset file (`input_rescue.dat` or `input_norescue.dat`), a parameter file (`input_rescue.par` or `input_norescue.par`) and a distance file (`input_rescue.dis` or `input_norescue.dis`). Then, by using `create.parameter.df`, a data frame can be created with the parameters computed with the application. To understand what the created files contain, and to understand the method the user should read the paper by ter Braak et al. (2003) as well as the help files available with the application. Editions to the parameters file will be needed in order to run the application. It is recommended to run one of the simplest methods to provide priors to the Bayesian MCMC simulation. Then, in the parameter file, replace 'edit x', 'edit y' and 'edit e' with those values. Be attentive to the fact that the output is given log-transformed. Before using the parameters in the simulation procedure they need to be back-transformed, using an exponential. This application, the source code, help files and sample data can be downloaded from the Ecological Archives, available (here).

```

> library(MetaLandSim)
> data(occ.landscape2)
> #Method 'rescue'
> parameter.estimate (occ.landscape2, method='rescue')
> #run the application file fmetapop_rescue.exe from
> #the command line (first put the application and the
> #files in a folder with no spaces in the name.
> #e.g.: 'C:/terbraak/'):
>
> #fmetapop_rescue input_rescue
>
> #Or, from R:
>
> system('fmetapop_rescue input_rescue')
> #After, create a data frame, with create.parameter.df,
> #using the estimated parameters:
> #param4 <- create.parameter.df(alpha, x, y, e)
>
> #Method 'norescue'
> parameter.estimate (occ.landscape2, method='norescue')

```



```

> #run the application file fmetapop_norescue.exe from
> #the command line (first put the application and the
> #files in a folder with no spaces in the name.
> #e.g.: 'C:/terbraak/'):
>
> #fmetapop_norescue input_norescue
>
> #Or, from R:
>
> system('fmetapop_norescue input_norescue')
> #After, create a data frame, with create.parameter.df,
> #using the estimated parameters:
>
> param5 <- create.parameter.df(alpha, x, y, e)
>

```

4 References

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Occupation Simulation in DynamicLandscapes

F. Mestre, F. Canovas, R. Pita, A. Mira, P. Beja

September 29, 2016

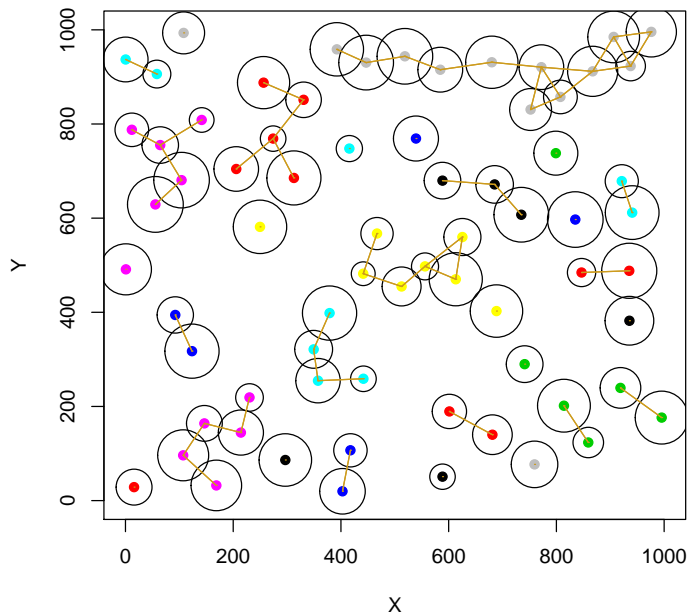
1 Introduction

This vignette explains the process of landscape and metapopulation simulation, using the package `MetaLandSim`. Previously, a crucial step has to be carried out, the parametrization of the SPOM model, using the function `parameter.estimate`. A vignette is available, detailing the process.

2 Landscape Simulation

Landscape simulation and dynamics are carried out respectively by the functions `rland.graph` and `span.graph`. Both these functions allow a different set of random landscapes (represented as graphs) to be created and to suffer dynamic changes, such as patch loss and habitat loss. In `MetaLandSim`, a landscape is represented as:

```
> library(MetaLandSim)
> rl <- rland.graph(mapsize = 1000, dist_m = 60,
+                  areaM = 0.5, areaSD = 0.2, Npatch = 70,
+                  disp = 100, plotG = TRUE)
```

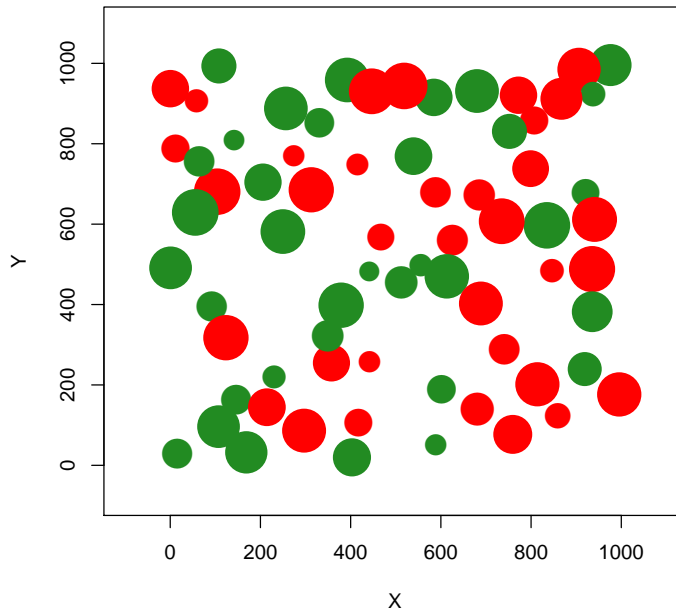


3 Occupation Simulation

The transition from an occupied landscape in time step t to time step $t+1$ can be achieved using the `spom` function, as described by Hanski (1999). This function runs within `simulate.graph` which sequentially simulates the occupation in a landscape throughout several time steps. The occupation and transition between time steps is carried out, respectively, by the functions `'species.graph'` and `'spom'`, as follows:

```
> library(MetaLandSim)
> #The occupation of a landscape is simulated by:
> sp_t0 <- species.graph(rl=rl, method="percentage", parm=50,
+                        nsew="none", plotG=TRUE)
> names(sp_t0)

[1] "mapsize"                "minimum.distance"      "mean.area"
[4] "SD.area"                "number.patches"       "dispersal"
[7] "distance.to.neighbours" "nodes.characteristics"
```



After loading the species parameters (param1), the transition is made by:

```
> data(param1)
> sp_t1 <- spom(
+ sp_t0,
+ kern="op1",
+ conn="op1",
+ colnz="op1",
+ ext="op1",
+ param_df=param1,
+ beta1=NULL,
+ b=1,
+ c1=NULL,
+ c2=NULL,
+ z=NULL,
+ R=NULL
+ )
> #Which has the following elements:
> names(sp_t1)
```

[1] "mapsize"	"minimum.distance"	"mean.area"
[4] "SD.area"	"number.patches"	"dispersal"
[7] "distance.to.neighbours"	"nodes.characteristics"	"turnover"

4 Sample Work-flow

Although this procedure can be carried out using the functions mentioned above, it is easier to complete the full simulation using only one function that runs all the others internally, while allowing for a repetition of the process, the function is `'iterate.graph'`.

Here the simulation process will run only with 2 iterations, for demonstration:

```
> #Loading species parameters
>
> data(param1)
> #Simulating occupation in dynamic landscape
>
> it1 <- iterate.graph(
+ iter = 2,
+ mapsize = 1000,
+ dist_m = 30,
+ areaM = 0.5,
+ areaSD= 0.1,
+ Npatch = 200,
+ disp = 800,
+ span = 100,
+ par1 = "stoc",
+ par2 = 2,
+ par3 = 2,
+ method = "percentage",
+ parm = 50,
+ nsew = "none",
+ succ = "none",
+ param_df = param1,
+ kern = "op1",
+ conn = "op1",
+ colnz = "op1",
+ ext = "op1",
+ b = 1,
+ graph = FALSE
+ )

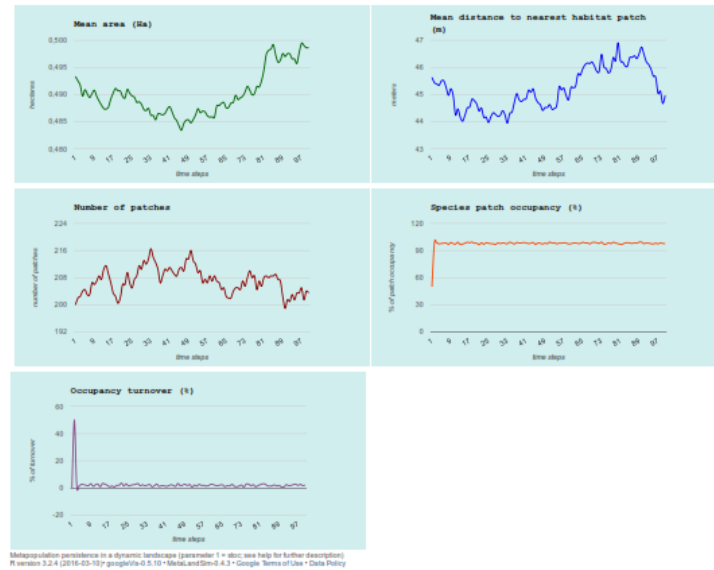
Completed iteration 1 of 2
Completed iteration 2 of 2

> #This file is composed by the following elements:
>
> names(it1)

[1] "mean_area"          "mean_distance"      "number_patches"     "occupancy"
[5] "turnover"
```

However, when running this function the argument 'graph' must be set to TRUE in order to produce graphs with the evolution of the simulations.

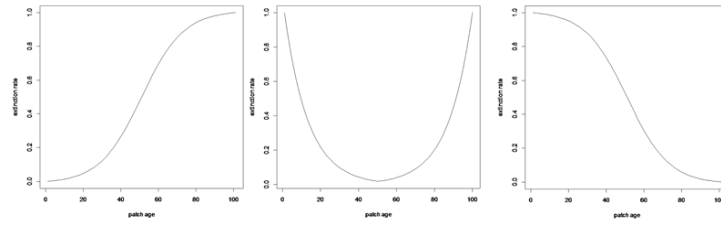
This simulation produces the following graphic output (which opens in an html page):



As a result the user will have a large number of simulations which represent the occupation of a species with a given set of characteristics (as defined by the parameters) in a dynamic landscape. The advantage of this approach is that it requires less parameters which can be estimated from real occupancy or turnover data. It does not require demographic data, the parameters can be derived using only patch occupancy data of one snapshot or sampling session (ideally more).

Here the simulation procedure is repeated only twice (parameter 'iter'), although more simulations have to be run in order to obtain robust results. However, depending on computing power, this simulation can be highly time-consuming (from hours to several days).

After version 0.5 of MetaLandSim an additional option was made available to the users: the argument 'succ'. This allows to chose different options regarding the species preference relating the successional stage of habitat patches, with the following options: 'none' - No discrimination regarding patch successional stage; 'early' - The species prefers patches in an earlier successional stage; 'mid' - The species prefers patches in the mid of the succession; 'late' - The species prefers patches in an later successional stage. This new option includes an additional factor to the extinction probability, changing it with patch age, as follows:



In the above figure it is visible that, when succ='early', the extinction concerning successional stage is lower for younger patches (left); when succ='mid', the extinction concerning successional stage is lower for habitat patches with intermediate ages; when succ='late', the extinction concerning successional stage is lower for older patches. This extinction factor is combined with the one derived from the application of the SPOM model considered (generally depending on patch area).

5 References

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Range Expansion Simulation

F. Mestre, F. Canovas, R. Pita, A. Mira, P. Beja

September 29, 2016

1 Introduction

Modelling approaches for estimating species ability to track environmental change over large scales may rely on different assumptions regarding the role of dispersal (Barbet-Massin et al. 2012; Engler et al. 2012; Bateman et al. 2013; Zhou and Kot, 2013): i) The species cannot disperse, thus considering null dispersal ability (which would, in most cases, underestimate the potential future area); ii) Infinite dispersal ability, which means that the species will be able to cope with the shifts of its ecological niche by fully occupying all newly available areas (in most cases, maybe with the exception of highly mobile species, this is an unrealistic assumption which will produce optimistic results); iii) A mean dispersal distance per decade (p.ex.) is defined, considering the ability of the species to disperse (this approach can be a bit arbitrary, if not carefully considered); iv) a dispersal kernel is developed based on a set of species traits (this is a more realistic approach which represents a good compromise between the full dispersal and no-dispersal approaches). It is known however that the species ability to disperse depends not only on its own traits but also on the landscape configuration and composition (Nathan et al. 2012). This package allows a simplified approach to derive a dispersal model from the simulation of range expansion in landscapes with different characteristics, using the function `'range.expansion'`. Similar approaches require parameters about the demographic rates of the species, or other data that, in most cases, are difficult to obtain. This approach might be considered simpler, once it requires data that can be obtained from capture-recapture, telemetry or bibliography (such as dispersal ability) and the information on basic landscape structure, which can be obtained using GIS. Furthermore, the function `'range_raster'` allows the projection of the produced dispersal model into the geographical space.

2 Work-flow

2.1 Parametrization

This is crucial, and can be achieved using the function `parameter.estimate`. A vignette is available, detailing the process, which must be carefully implemented,

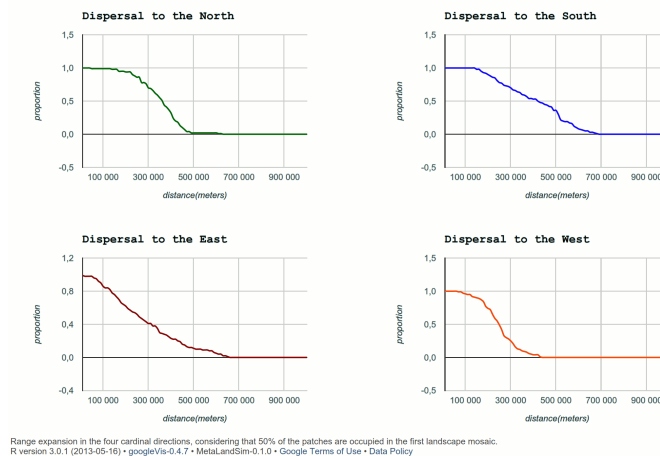
as this is the process that allows the characterization of the study species and its relation with the landscape.

2.2 Simulation of range expansion

This is done using the function `range.expansion`, which will simulate the range expansion into new, empty, landscape mosaics a given (user defined) number of times (defined by parameter `'iter'`). This simulation will be carried out for a given time period (defined by the parameter `'tsteps'`). The output of this function is a list of four data frames with the result of the occupation of sequences of landscapes in the four cardinal directions.

```
> library(MetaLandSim)
> #Load starting landscape (the simulation will assume that
> #all subsequent landscapes are built with the same parameter combination).
>
> data(rland)
> #Create range expansion model. Here run only with two repetitions (iter=2).
> #Ideally it should be run with more repetitions to provide more robust results.
>
> data(param1)
> rg_exp1 <- range_expansion(rl=rland, percI=50, param=param1,b=1, tsteps=100,
+ iter=2)
```

The previous range expansion simulation produces a graphic output similar to the following (which opens in a html page):



This represents the probability of occupation (in the four cardinal directions) of the landscape at a given distance from the closer current species occurrence.

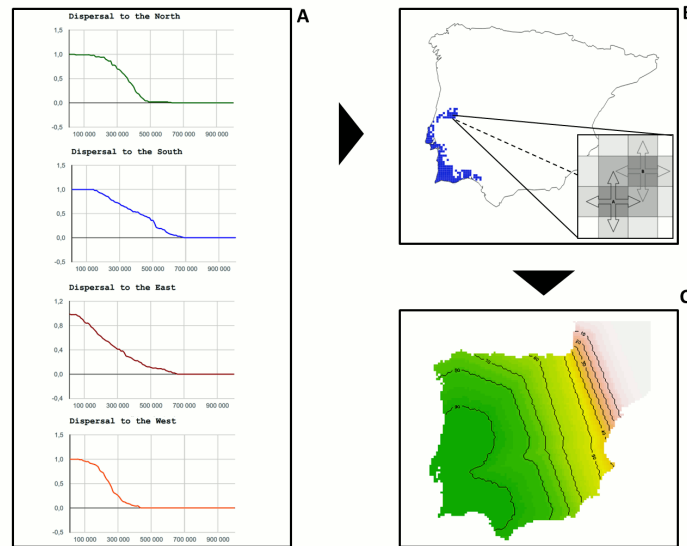
It is the dispersal model (DM) produced by MetaLandSim. Also, as an output of this simulation, the time steps at which each distance is reached is also estimated.

2.3 Conversion of the output to a spatial model

The dispersal simulation generated for each time step in the previous section should be converted into a model of species occurrence based only in the dispersal. This is done using the function `range.to.raster`. The output will be a raster file with the dispersal-only occupancy model after a given time period. This dispersal model can be, subsequently, combined with the output of an ecological niche model. This will allow the projection of potential occupancy considering three important factors: the species ecological niche, the species dispersal ability and the landscape characteristics. After MetaLandSim version 0.5.2, a new raster is produced representing the temporal factor. This raster depicts the average time step in which each distance is reached by the simulated range expansion. Furthermore, both these raster maps are saved in the working directory.

```
> data(rg_exp)
> presences <- paste(system.file(package="MetaLandSim"),
+   "/examples/presences.asc", sep="")
> landmask <- paste(system.file(package="MetaLandSim"),
+   "/examples/landmask.asc", sep="")
> library(rgrass7)
> #First, start GRASS from R:
> initGRASS(gisBase = "grass folder", home = tempdir(),
+   gisDbase = "mapset location", override = TRUE)
> #Create raster, using the sample dataset
> #rg_exp (generated with 100 repetitions)
>
> data("rg_exp")
> range_raster(presences.map = presences, re.out=rg_exp,
+   mask.map=landmask, plot.directions=FALSE)
```

By combining the expansion model with the current species occurrences (B) provides a future occurrence model based only on dispersal ability and landscape configuration, such as:



The four sub-models (A), considering each of the cardinal directions, are combined in a final dispersal model (C). The user should run several scenarios to evaluate the species expansion with a diversity of landscapes (or even species, depending on research question). This DM can then be combined with the output of an Ecological Niche Model projected into the future using any common GIS software or R GIS-related packages.

3 Note

The output of these functions is dependent upon species dispersal ability and current distribution. The mask should be chosen carefully, considering biological realism.

4 References

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distribution models. *Ecography*, 35(10), 872-878.

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Chapter 4

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

Submitted to Ecological Modelling as:

Mestre, F.; Risk, B.; Mira, A. & Beja, P.; Pita, R. (*submitted*). "A metapopulation approach to predict species range shifts under different climate change and landscape connectivity scenarios". Ecological Modelling.

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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 cabreræ*) 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. 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.

Keywords

dispersal, metapopulation, climate change, landscape change, ecological niche modelling.

1. Introduction

Ecological niche models (ENMs) based on climate envelopes are widely used in ecological studies 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; Sydes 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 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 in the literature (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, and it is predicted to restrict (at least to some extent) species ranges 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 (Sydes 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 are generally built with little or no attention to the spatial processes that drive real biogeographic 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, despite the fact that dispersal also depends 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), though these approaches 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 climate change (Franklin 2010b; Naujokaitis-Lewis et al. 2013).

Here we introduce a novel approach to achieve this goal, which is based on simulation 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 propagate on 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 also have great 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 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: i) build an ENM based on climate variables and ensemble forecasting; ii) develop an SEDM derived from IFM simulations of metapopulation dynamics under plausible scenarios of landscape connectivity; and iii) combine these two models to forecast species distribution ranges that account for the effects of both climate and landscape variation (see Mestre et al. 2016).

We highlight the innovative nature and outputs of our framework by modelling range shifts of the near-threatened Cabrera vole (*Microtus cabreræ*), a species confined at present to four geographical regions in the Iberian Peninsula (Garrido-Garcia et al. 2013). The Cabrera vole is a suitable model species to illustrate our approach because its populations are distributed in habitat patches consisting of tall wet herbaceous vegetation with evidence of metapopulation-like structure and dynamics (Pita et al., 2007). In addition, previous research on the phylogeography of the species has shown that it has suffered profound range changes in response to climatic variations (Barbosa et al. under review), while the results of preliminary niche modelling indicate that Cabrera voles will likely be highly vulnerable to future climate change (Mestre et al., 2015).

2. Methods

2.1. Ecological niche model

To assess the current and future suitable climate space of the Cabrera vole, we followed the methodology described in Mestre et al. (2015). Briefly, we used consensus methods or ensemble forecasting (Araújo and New, 2007) implemented in the BIOMOD package, version 1.1.7.4 (Thuiller et al. 2009b; Thuiller and Lafourcade, 2010), based on variables of current climatic conditions (1950-2000) obtained from the WorldClim website (<http://www.worldclim.org/>; Hijman et al., 2005). The model used presence data of the Cabrera vole across its entire distribution range, which was

obtained from all available literature documenting the occurrence of the species between 1970 and 2011 (see Supplementary Material SM1). This mismatch between species presence and climate data was assumed to be negligible given the large overlap between the two time periods (Mestre et al., 2015). The ensemble was built from eight alternative algorithms (generalized linear models, generalized boosting models, generalized additive models, classification trees, artificial neural networks, flexible discriminant analysis, multivariate adaptive regression splines, and random forests). For techniques requiring the use of presence-absence data, we generated pseudo absences at random locations over the entire Iberian Peninsula, where the number of locations equalled two times the sample size of the presence data. Model evaluation and selection criteria were based on the area under the receiver operator curve (AUC) and the true skill statistics (TSS), as recommended by Allouche al. (2006). Only the models with $TSS > 0.5$ were kept in the final ensemble (Mestre et al., 2015). The contribution of each variable to the final ensemble was evaluated through the variable importance metric (Thuiller et al. 2009b). The final model was projected to the current climate conditions and future (2050 and 2080) climate change scenarios (B2 and A1b), which describe two different alternative futures: A1b describes a world based upon fast economic growth with balanced use of fossil/non-fossil energy resources, and B2 describes a world focused on local environmental sustainability (IPCC, 2000).

2.2. Metapopulation model

The metapopulation dynamics of the Cabrera vole were specified using the Incidence Function Model (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 $J_i = C_i / (C_i + E_i)$, where C_i is the constant colonization probability per unit time 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 respectively given as (Hanski, 1994, 1999):

$$C_i = S_i^2 / (S_i^2 + y^2)$$

$$\begin{cases} E_i = e / A_i^x & \text{if } A_i > e^{1/x} \\ E_i = 1 & \text{if } A_i \leq e^{1/x} \end{cases}$$

where S_i is the connectivity, defined as $S_i = \sum p_j \exp(-\alpha d_{ij}) A_j^b$ (Hanski, 1994, 1999), with d_{ij} representing the distance between patches i and j . The constants e , x , y , α , and b represent the IFM parameters affecting the extinction risk and colonization probabilities in each patch (Hanski, 1999). Parameter y represents the colonization efficiency of empty patches; e corresponds to the extinction probability per year in a patch of unitary area; A_i is the area of the i th focal patch; x is the strength of the relation between extinction risk and patch area; α represents the survival rate of migrants over the distance d_{ij} ; and p_j and A_j are the occupancy and area, respectively, of the j th source patch. When A_i equals the critical patch area (the value of $e^{1/x}$), the local population goes extinct. Finally, the exponent b is a parameter defining the relationship between the expected population size and patch area (Molainen 2000).

Because IFM parameters for Cabrera voles were virtually unknown, we parameterized the SPOM using the empirical data reported in Pita et al (2007), which describe the seasonal (summer, autumn, winter, spring) occupancy dynamics of the species in a fragmented farmland landscape over three years (totalling twelve sampling occasions). Surveys consisted of searching for signs of presence for at least 30 min/patch. It is likely that the surveys largely minimized imperfect detection given the high detection probabilities (80-100%) estimated for a similar species (water voles) in a studies with less sampling effort (Fernández et al. 2016; Peralta et al. 2016 and Pita et al. 2016). Additionally, Cabrera voles breed continuously, and thus transitions in occupancy between sampling occasions were assumed to be due to either extinction or colonization events. Hence, we estimated the IFM parameters for the Cabrera voles using the “IFM naive” Bayesian formulation described in Risk et al. (2011), which

assumes no false absences and omits sites for particular seasons in which data were missing due to changes in habitat suitability not captured by the IFM; see Supplementary Material SM2 for additional details. The posterior distribution of IFM parameters (α , b , y , e , and x) was sampled using the Metropolis-Hastings algorithm (details in Supplementary Material SM2).

2.3. Spatially explicit dispersal models

Range expansion was predicted using the spatially explicit dispersal model (SEDM) from Mestre et al. (2016) with some improvements designed to make it more realistic, namely regarding the transition between landscape units. In short, the procedure is similar to an agent-based modelling approach, in which the IFM is simulated from currently occupied landscape units while allowing the transition into neighbouring empty landscapes. For example, consider dispersal northwards: a landscape strip is defined between the northern margin of the landscape unit and a parallel line is placed to the south at a distance equal to half of the dispersal ability of the focal species. If any patch in that area is occupied, then the species is assumed to be able to disperse into the next landscape (to the north). In that new landscape unit, a new habitat strip is defined between the southern margin and a line parallel to the north at a distance equivalent to half of the dispersal distance. In that area, patches are considered occupied in the same proportion as the landscape to the south. SPOMs are simulated for that landscape, and the process is repeated across landscapes that become progressively available to the metapopulations for the specified number of time units, thereby producing a map of the total number of landscapes occupied at the end of the simulation (Mestre et al. 2016).

In our example with Cabrera voles, this up-scaling of metapopulation dynamics into range expansion patterns across successive landscape units was repeated 1000 times for the same time steps considered in the ENM building (i.e. 2050 and 2080), and the outputs of these simulations were then used to build the SEDMs. We considered landscape units of 10x10 km² and three realistic scenarios of increasing landscape connectivity (low, medium, and high) based on empirical observations (Pita et al. 2007,

2014). Changes in connectivity were specified by varying the number of patches per landscape (Table 1), which in turn affected the mean distance and thus the probability of dispersal between patches. We have not explored alternative ways of specifying connectivity such as varying resistance to movement without changing the number of patches, but this could potentially be accommodated in our modelling framework by redefining distance with an effective distance. Also, for simplicity we assumed landscape parameters were constant through the current and future species ranges, but future work could adapt the model to account for spatially and/or temporally varying landscape conditions.

Table 1 - Landscape unit parameters for simulation of range expansion under three connectivity scenarios: low, medium and high. Parameters were set with reference to the study system in SW Portugal described in Pita et al (2007), where suitable habitats for voles covered about 0.44% of the study area (1600 ha), with a mean patch area of 0.12 ha and a mean inter-patch distance of about 330 m.

Connectivity Scenario	Habitat percentage (%)	Mapsize (length of side, m)	Minimum distance (m)	Mean patch area (ha)	Patch area SD	Number of patches
LOW	0.3	10.000	400	0.1	0.02	300
MEDIUM	0.4	10.000	300	0.1	0.02	400
HIGH	0.5	10.000	200	0.1	0.02	500

All simulations were made using the MetaLandSim R package, version 0.5.4 (Mestre et al. 2016), assuming an initial occupancy rate within currently occupied landscapes of 0.5 (a similar to occupation as in the metapopulations in Pita et al. 2007). Modelling procedures were run in R, version 3.3.1 (R Core Team, 2016). Parallel computing required the use of the packages “parallel” (R Core Team, 2016), “foreach” (Revolution Analytics and Weston, 2015a) and “doParallel” (Revolution Analytics and Weston, 2015b). The simulations were run in a processor cluster with the following technical characteristics: processor - 12x Intel(R) Core(TM) i7-3960X CPU, 3.30GHz; memory - 32 GB and operating System - Ubuntu 14.04.3 LTS. Parallel computing with 5 processors was used.

2.4. Combining niche and dispersal projections

The probabilities of occupancy given the environmental (ENM) and spatial (SEDM) factors were considered to be independent and had were combined as:

$$P(ENM, SEDM) = P(ENM) \times P(SEDM)$$

As such, probability maps of the predicted distribution of Cabrera voles in 2050 and 2080 estimated from the ENM under each scenario of climate change and by the SEDMs considering alternative scenarios of landscape connectivity were combined through raster multiplication on a cell-by-cell basis. This resulted in 12 final projections (2 climate change scenarios x 3 landscape connectivity scenarios x 2 time steps) depicting the grid cells with a higher probability of occurrence under alternative scenarios of environmental (climate, landscape) change. Because the ENM map produced in the BIOMOD was projected on a 0-1000 scale, and the SEDMs maps produced in MetaLandSim were projected in 0-100 scales, we re-scaled the ENM to 0 to 1 before multiplying it by the SEDMs. All map algebra operations were conducted within a GIS environment using QGIS, version 2.16.0 (QGIS Development Team, 2016).

3. Results

3.1. Ecological niche model projections

Variable importance (VI) scores resulting from the final ensemble model suggested that the Precipitation of the Warmest Quarter (PWQ in mm) had the strongest effect on Cabrera vole distribution (VI=0.496). The importance of the remaining variables was relatively low: Mean Diurnal Range (MDR) with VI= 0.200; Mean Temperature of Wettest Quarter (MTWQ, VI=0.184); Minimum Temperature of Coldest Month (MTCQ, VI=0.168); and Precipitation of Wettest Month (PWM, VI=0.100) (see Mestre et al. 2015). Overall, the model suggested that the ecological niche of the Cabrera vole was associated with intermediate levels of PWQ and PWM, moderate MTWQ, and relatively high MDR and MTCM. The predictive ability of the final ENM was high (AUC =

0.885 and AUCmax= 0.908). When projecting the ENM at 30 seconds resolution (approximately 1 Km) for the present (Figure 1) and for the future (2050 and 2080, Figure 2), a gradual loss of climatically suitable regions is apparent, with a tendency to become more fragmented and to shift northwards. As expected, this loss of suitability is more evident in the more intense climate change scenario (A1b) (Figure 2).

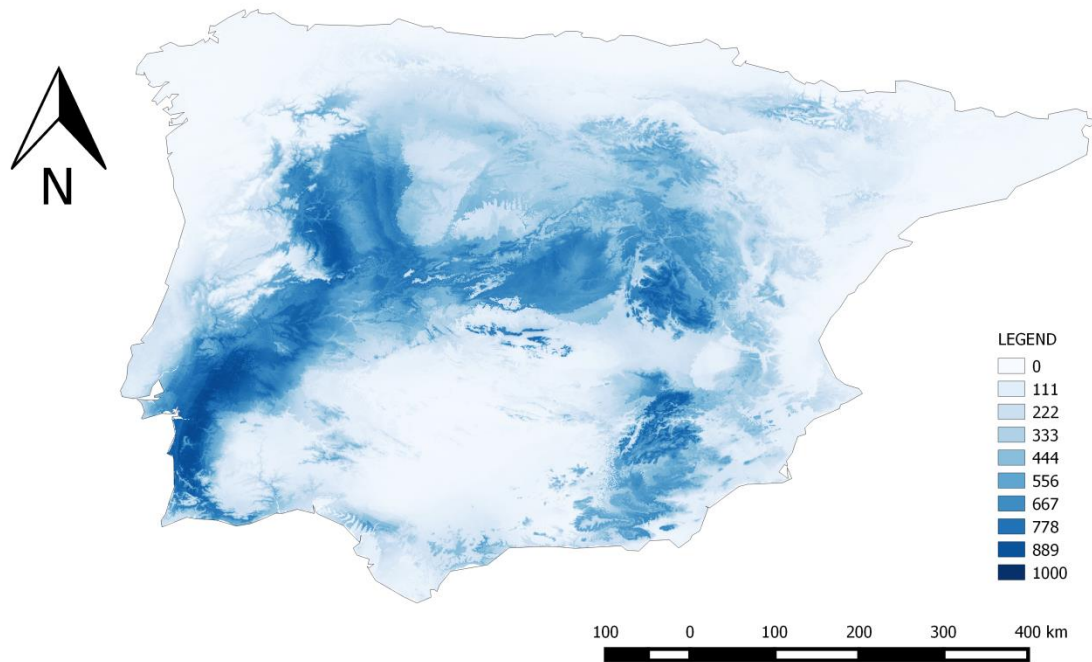


Figure 1 – Ecological Niche Model projection, depicting climatic suitability, generated by the R package BIOMOD for the current ecological niche distribution of *Microtus cabreræ*.

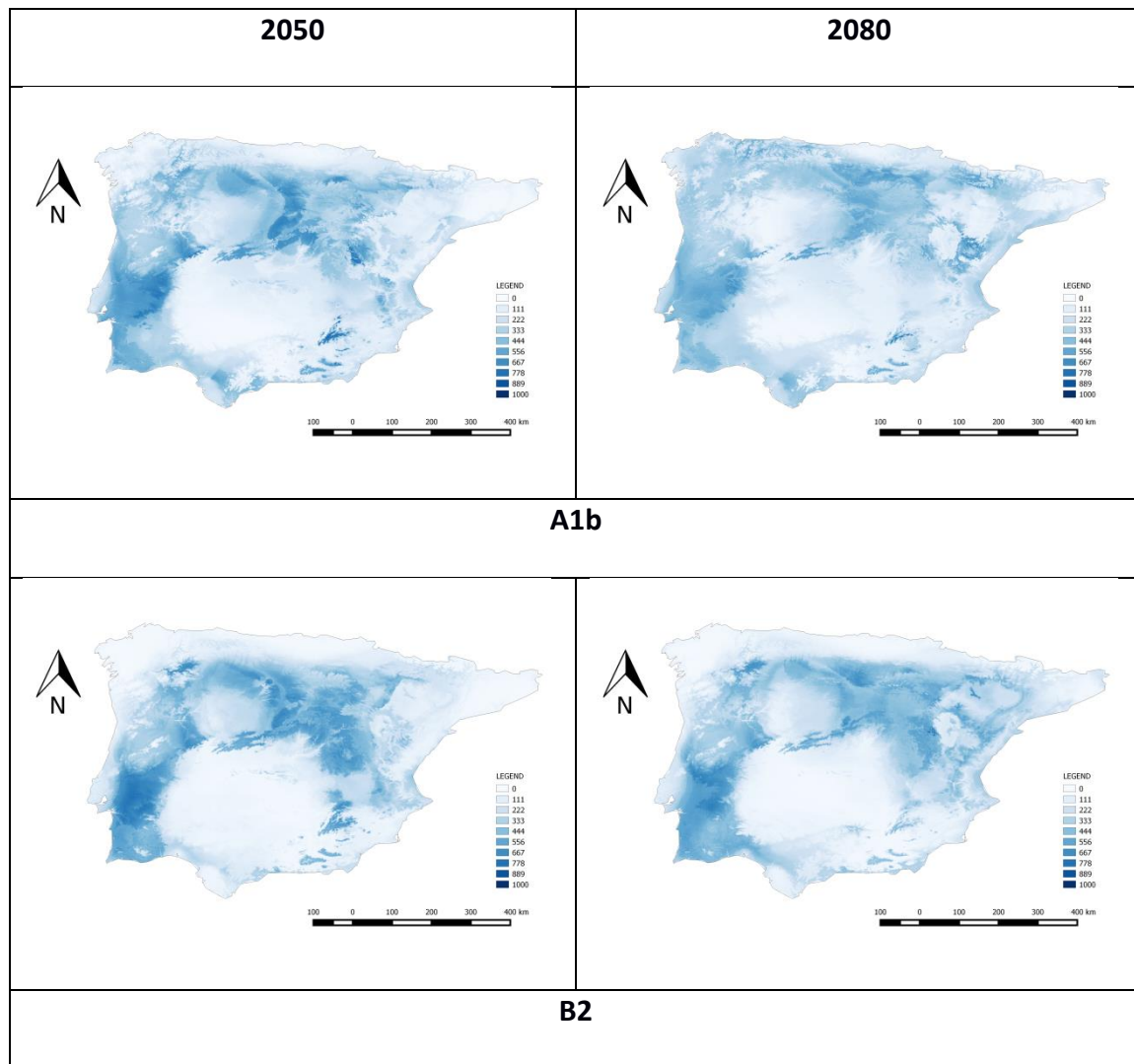


Figure 2 – Projections of Cabrera vole ranges in 2050 (left column) and 2080 (right column) in the Iberian peninsula estimated from Ecological Niche Models and considering two climate change scenarios: scenario A1b (top row) and B2 (bottom row).

3.2. Spatially explicit dispersal models

Cabrera vole's IFM parameterization using empirical data and the "IFM naive" Bayesian model resulted in the following maximum a posteriori parameter estimates (with the respective credible intervals): $x=0.44014$ (0.04012-1.22815); $y=18.15405$ (1.92319-19.59133); $e=0.00482$ (0.00174-0.04374); $\alpha=0.00047$, considering that $1/\alpha$ is dispersal, median is 2134.129 meters (1147.137- 4837.024); and $b=0.73724$ (0.23273-2.05192). Note that parameter estimates were sensitive to the choice of prior, and in particular, an informative prior was used for y (see Supplementary Material SM2).

When applying these IFM parameters to the algorithm used to predict range expansion of Cabrera voles based solely on SEDMs, the dispersal success increases under higher landscape connectivity, as shown by the increase in the occupancy probability as connectivity is higher (Figure 3). In particular, under low connectivity (3 patches per km²) the species seems to have limited ability to expand its distribution much beyond its current distribution, while under the scenario of higher connectivity (5 patches per km²), the species appears to have the ability to expand into the entire Iberian Peninsula by 2050 (Figure 3).

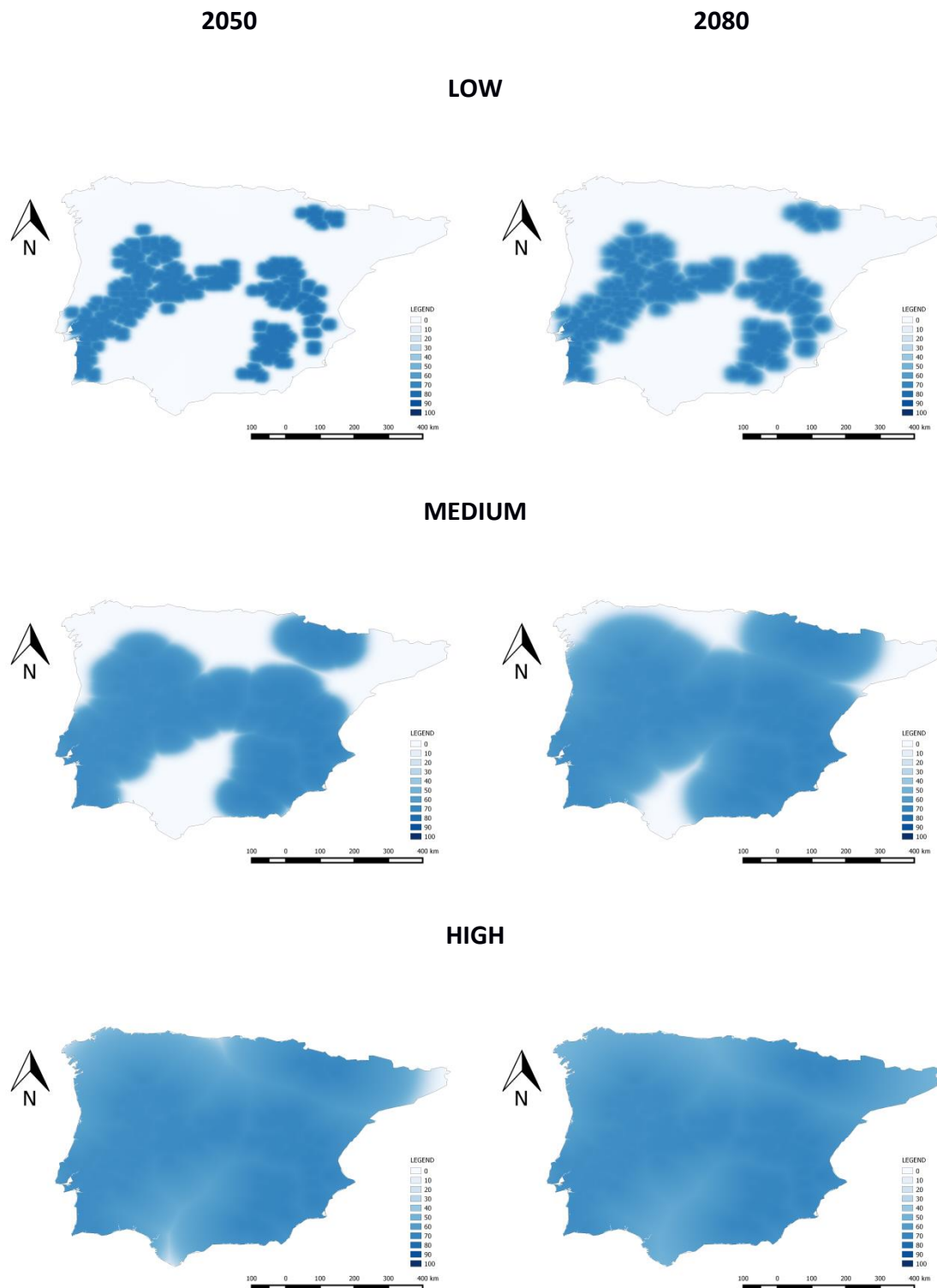


Figure 3 – Projections of Cabrera vole ranges in 2050 (left column) and 2080 (right column) in the Iberian peninsula estimated from Spatially Explicit Dispersal Models, and considering three landscape connectivity scenarios: low (upper row), medium (middle row) and high (lower row).

3.3. Combining niche and dispersal projections

The combination of the maps representing the potential future distribution of the Cabrera vole based on the ENM and on the SEDMs showed in general much reduced ranges than those predicted by the ENM alone (Figure 4). In general, larger ranges are predicted under the B2 scenario, particularly under higher landscape connectivity (Figure 4). Conversely, the combined projections representing the A1b scenario and lower connectivity resulted in more restricted predicted ranges (Figure 4).

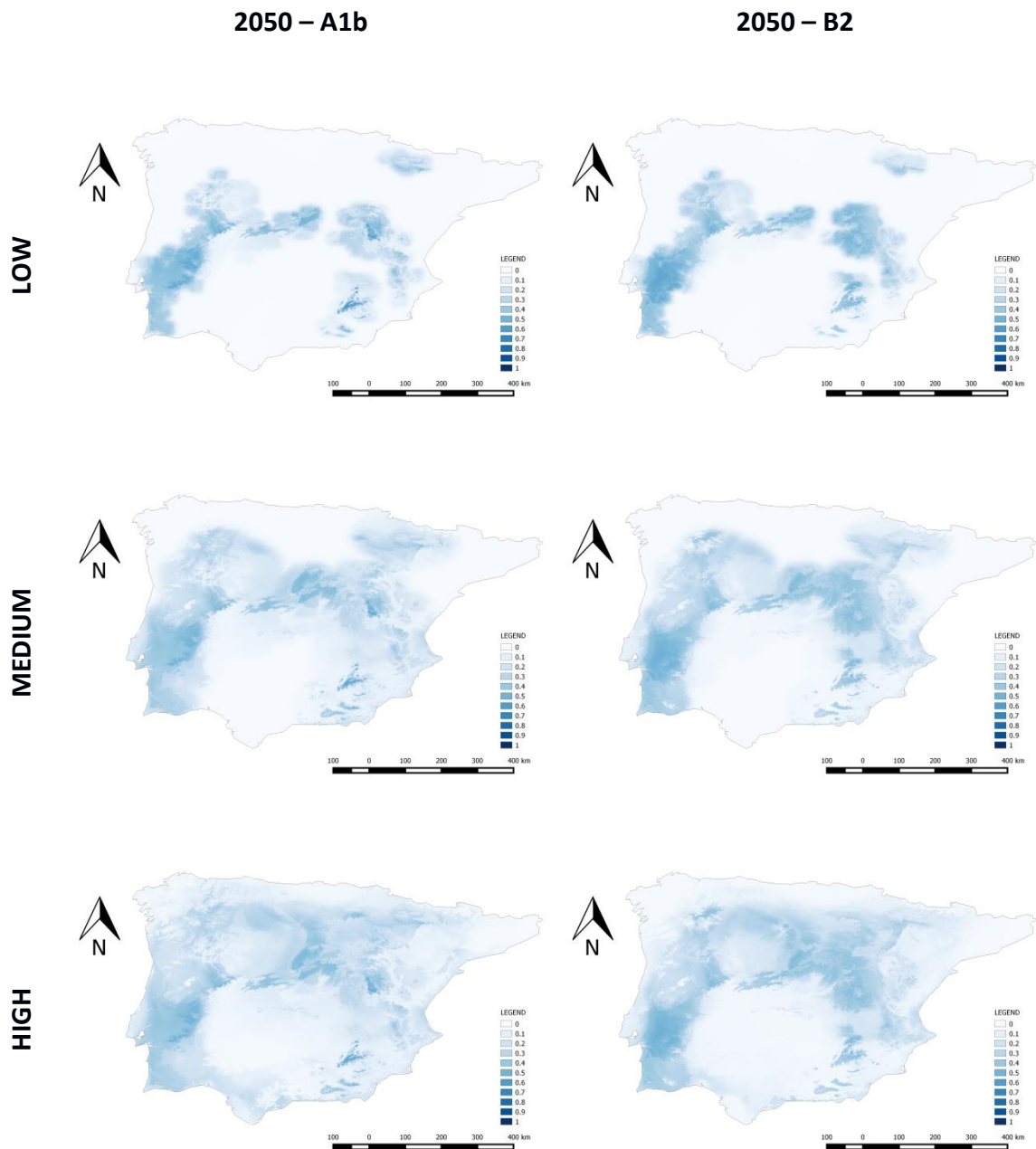


Figure 4 - Projections of Cabrera vole ranges in 2050 in the Iberian peninsula estimated from the combination of Ecological Niche Models and Spatially Explicit Dispersal Models, considering two climate change scenarios (A1b and B2) and three landscape connectivity scenarios (low, medium and high).

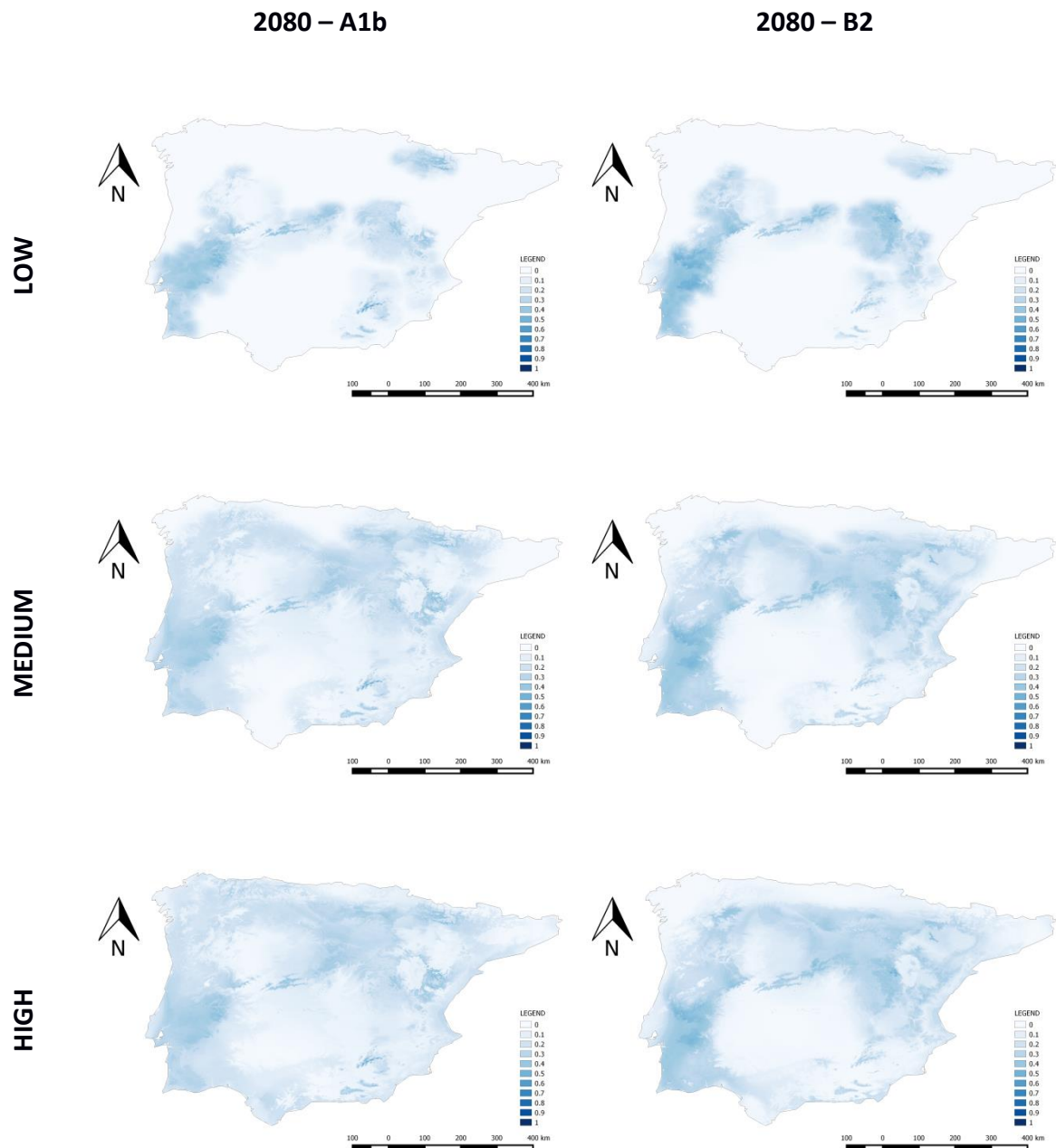


Figure 5 - Projections of Cabrera vole ranges in 2080 in the Iberian peninsula estimated from the combination of Ecological Niche Models and Spatially Explicit Dispersal Models, considering two climate change scenarios (A1b and B2) and three landscape connectivity scenarios (low, medium and high).

4. Discussion

Ecological niche models are a widespread method to assess species responses to future climate change (Peterson, 2011), and a broad range of predictions have already

been carried out to forecast the potential future distribution of many species. However, a limitation of the basic implementation of ENMs is that it does not account for population or metapopulation dynamics, dispersal limitation and landscape connectivity (Travis and Dytham, 2012). While some attempts have been made to couple these ecological attributes with ENMs (Anderson et al., 2009; Wilson et al. 2010; Barbet-Massin et al. 2011), there is still no general understanding on the best methodological practices for integrating them into the final projections (Travis and Dytham, 2012). In particular, despite the broad recognition of the increasing rates of habitat loss and fragmentation worldwide and their negative effects on the persistence and expansion abilities of species with metapopulation structure and dynamics (Opdam and Wascher, 2004; Hof et al. 2011), most studies still largely ignore the role of landscape connectivity for predicting potential future range shifts of such species (e.g. Mestre et al. 2015). In this context, the approach presented here represents an advance over earlier efforts, providing a straightforward mechanistic link between landscape-level processes and species distribution at regional and geographical scales, which likely result in more accurate predictions on how species respond to climate change and landscape scenarios. By generating dispersal models based on metapopulation dynamics under spatially explicit landscape settings, our approach allows the identification of the constraints arising from spatial, environmental, and species intrinsic factors limiting successful dispersal (Mestre et al., 2016). This, in turn, may aid reserve design, habitat restoration, reintroduction programs and conservation in the face of climate change (Guisan and Thuiller, 2005; Rodríguez et al. 2007).

Our application of this novel approach to the Iberian endemic Cabrera's vole highlights the pivotal role of landscape connectivity in the species' capacity to track its climatically suitable areas. Specifically, results indicated that the species should spread much farther into suitable climate space under higher landscape connectivity. While this result is intuitively obvious, we believe that the approach presented here provides more realistic predictions than those that would be obtained for instance from fixed dispersal rates that do not account for the dynamics of extinction-colonization events under particular landscape scenarios. The vulnerability of the Cabrera vole to both climate change and landscape connectivity is probably related to its high habitat

specialization (e.g. Pita et al., 2006, 2011; Santos et al., 2006; Luque-Larena and López, 2007) and dispersal limitation (e.g. Pita et al., 2007; Rosário and Mathias, 2007), which may preclude the species colonizing potential favourable environments. In particular, the species is mostly restricted to habitat patches of wet and tall herbaceous vegetation, which are typically scattered through a highly variable, inhospitable matrix (e.g. agricultural lands, forests, urban areas, or open dry lands). Consequently, Cabrera's voles may have to disperse through highly unsuitable habitats in order to expand into newly suitable climate spaces (e.g. Dale, 1997; Devictor et al. 2008; Foden et al. 2013).

It should be mentioned, however, that some important issues have been ignored in our approach, which may limit to some extent the accuracy of the predictions. In particular, IFM parameters were estimated using occupancy turnover data from a particular system, thus entailing the assumption that the spatial dynamics of the species is similar across its entire range. Although this assumption may be somewhat unrealistic, we believe that such a simplification still provides a practical solution for developing useful models linking metapopulation dynamics and dispersal with ENM. A further limitation is that within each simulation set, it is assumed that the species will encounter landscapes with identical connectivity levels. However, the effects of this limitation are lessened by considering different scenarios of landscape connectivity (as we did in our example), in the same way that different climate change scenarios are routinely considered and reported in traditional studies that project ENM into the future. Additionally, future research could collect data on the percentage of suitable habitat for landscapes across the range of the Cabrera vole and then parameterize landscape connectivity according to the nearest empirically observed connectivity. Also, our approach did not take into account other potential obstacles to successful migration, such as natural barriers to dispersal (e.g., large rivers, mountain chains) or the presence of natural enemies (e.g. competitors and predators) that may also hinder colonization success (Araújo and Luoto, 2007; Peterson et al. 2011), possibly leading to overoptimistic predictions, at least in some particular regions. Additionally, eventual adaptations at range margins were also disregarded in our approach, for example, individuals inhabiting such areas may be better dispersers than populations at the core

of the range (e.g., Simmons and Thomas, 2004). Finally, while the dispersal model alone does not account for range retraction at trailing range margins, this should be adequately captured by the loss of ecological suitability captured by the ENM.

While we acknowledge that these limitations need to be overcome in future research, we believe that our approach provides great advantages over those relying in overly simplistic dispersal models or requiring detailed demographic information. In particular, because the dynamics of local populations in metapopulation models are replaced by transitions between two states (presence-absence), our approach offers a good compromise between data requirements, computational time, and output accuracy. Since patch occupancy data are relatively easy to obtain (e.g. in existing monitoring schemes) and can be used to estimate dispersal ability (through the α dispersal-related parameter), we believe that our approach may be applied to a broad range of species and ecological systems. Future research should also evaluate the differences between the dispersal ability of populations in the core of the range and those at the expanding margin (e.g. Simmons and Thomas, 2004) and the eventual behavioural differences between populations in the core and expanding range margins (Duckworth, 2008).

5. Conclusions

Niche models based on climate envelope methods have been widely used to define the boundaries of a species niche, which are used to predict the potential limits of species distribution (Peterson et al. 2011). Similarly, it is possible to identify the limits to successful dispersal and define the boundaries of regions based on dispersal models, which can then be combined with ENM to produce more reliable forecasts of species' potential distributions. Here we provide a framework that couples the climate envelope method with a dispersal model that integrates metapopulation dynamics, dispersal limitation and landscape context. Although we acknowledge much is still to be done to improve such predictions (e.g. inclusion of natural barriers to dispersal, changes in connectivity within a simulation set, etc.), we believe that our approach illustrates how incorporating dispersal models based on metapopulation dynamics

under variable scenarios of landscape connectivity may impact the predictions of future distributions based on ENMs. Also, our approach provides an opportunity to identify regions that are not limited by dispersal, but are limited by environmental effects on mortality that can result in dispersal traps, such as the lower suitability regions in the southwestern tip of the Iberian Peninsula that are located to the east of the higher suitability area in the ENM, namely the southern interior of Portugal (Figure 1). We thus stress that coupling ENMs with metapopulation and dispersal models generated from spatially explicit landscape contexts should best reflect our understanding of ecological systems, thereby providing an important step forward for obtaining more realistic predictions of the response of biodiversity to environmental change.

Acknowledgements

This study was funded by the Portuguese Foundation for Science and Technology through the fellowships to FM (SFRH/BD/73768/2010) and RP (SFRH/BPD/73478/2010 and SFRH/BPD/109235/2015) and the project NETPERSIST (PTDC/AAG-MAA/3227/2012). The EDP Biodiversity Chair supported PB. We are grateful to Bruno Silva (CIBIO-UE – University of Évora) for assisting in the setting up of the parallel multicore computing.

Supplementary Material #1

SM1

Current distribution of the Cabrera vole

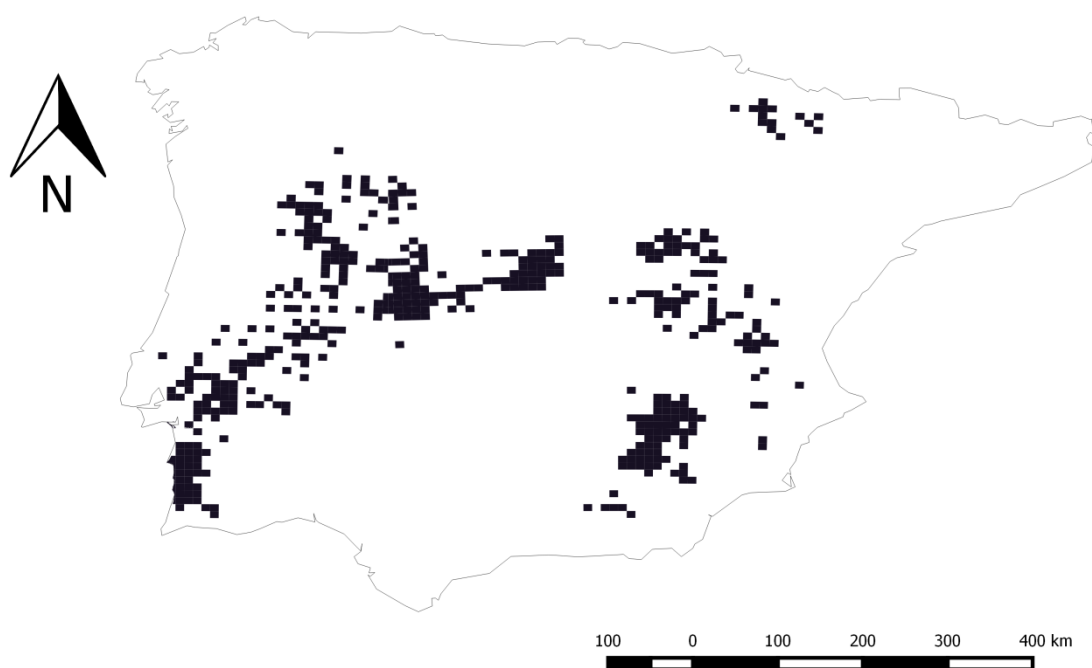


Figure SM1 – Current distribution (1970-2011) of the Cabrera vole (*Microtus cabreræ*) as updated in Mestre et al. (2015) and Garrido-García (2013).

SM2

Estimating the SPOM parameters for the Cabrera vole

The SPOM for the Cabrera vole was parameterized using empirical data on species patch-occupancy turnovers recorded over 12 seasonal surveys conducted at approximately 3-month intervals (summer, autumn, winter, spring) over three years in a fragmented landscape from SW Portugal (see Pita et al., 2007). In some instances, severe summer droughts, overgrazing, clear cutting, or ploughing for agricultural uses rendered habitat patches unsuitable. When estimating the IFM parameters, we were faced with the decision of including these instances as zeros or restricting the analysis to only consider dynamics between suitable patches. (More sophisticated modifications to the IFM model to include habitat quality were beyond the scope of this study.) Including the patches as zeros would result in violations of the assumption that extinction probability is completely determined by site area, since we would be omitting habitat quality. Thus, the transitions from unsuitable to suitable habitat were not included in the model likelihood. In other words, we only included successive seasons when the habitat was suitable in both seasons. Additionally, we assumed perfect detection as described in the main text. Thus, we used the “IFM naive” Bayesian formulation described in Risk et al. (2011), which excludes missing data, which here corresponds to the aforementioned transitions between habitat suitability, and assumes perfect detection. Posterior distributions of IFM parameters (α , b , y , e , and x) were sampled using the Metropolis-Hastings algorithm. To improve mixing of α near zero, distances were scaled to tens of kilometers (meters divided by ten thousand). The following uniform priors were used for IFM parameters: [1,30], [0,5], [0,20], [0,1], and [0,5] for α , b (beta in Risk et al 2011), y (gamma), e (mu), and x (chi). We initially tried using a more diffuse prior for y , but found that large values of b were negatively correlated with y , and the MH algorithm performed very poorly, as also observed in Risk et al (2011). It appears to be a challenge with using Hanski's formulation of the IFM, where the colonization probabilities vary little over negatively correlated pairs of b and y . We used symmetric proposal distributions from normal

distributions in which proposals that fell outside of the support of the prior were "reflected" to lie within the prior, as described in Risk et al (2011). The standard deviations of the proposal distributions were chosen to result in acceptance rates between 0.2 and 0.4 (Gelman et al. 2004), but for y , this was not possible and the acceptance rate was 0.7. We estimated two chains with 100,000 iterations each with initial values chosen randomly from parameter priors, and the first 1,000 iterations were discarded. Convergence was assessed using Gelman and Welch's potential scale reduction factors (all parameters less than 1.01), and visually (since some posteriors were not approximately normal) (see Figure SM1).

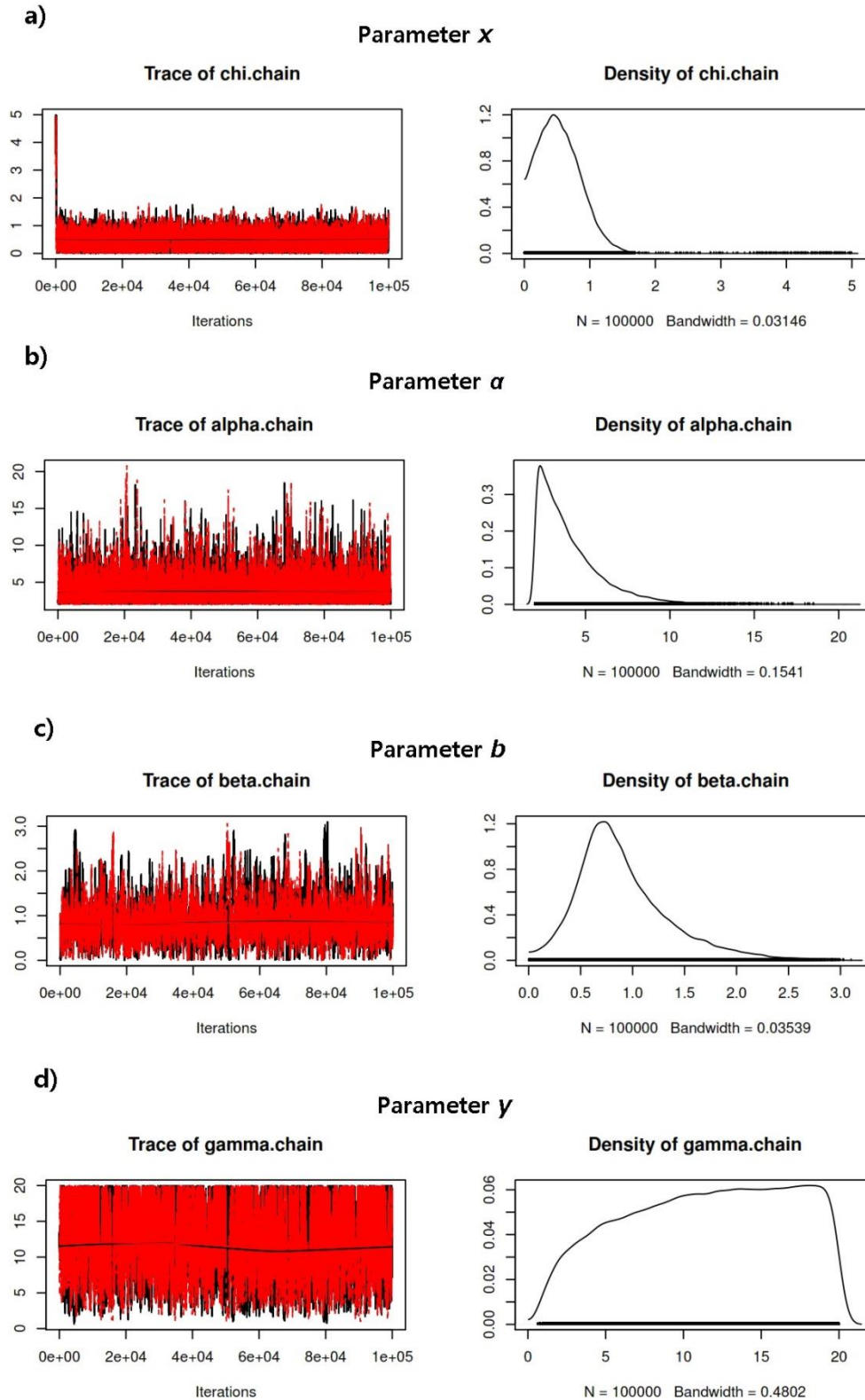


Figure SM2 – Trace and posterior density plots for each IFM parameter estimated with the Bayesian “IFM naïve” model: a) parameter x ; b) parameter α ; c) parameter b ; d) parameter y (note a burn-in period of 1,000 iterations is included in these figures but excluded from the final analysis).

Chapter 5

Metapopulations, patch turnover and successional dynamics: When does intermediate disturbance favours species persistence?

Submitted to *Oecologia* as:

Mestre, F.; Pita, R.; Mira, A. & Beja, P. (*submitted*). "Metapopulations, patch turnover and successional dynamics: When does intermediate disturbance favours species persistence?". *Oecologia*.

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Abstract

Creation and destruction of patches (i.e. patch turnover) in dynamic landscapes is generally expected to reduce metapopulation persistence. However, patch turnover may help maintaining a mosaic of patches in different successional stages, benefiting species with early- and mid-successional habitat affinities. Consequently, it is likely that metapopulation persistence for these species should be enhanced by intermediate levels of landscape disturbance. We used simulations to test the “intermediate disturbance hypothesis” for metapopulations, assessing whether some species are favoured by patch turnover and successional dynamics, and generally characterising such species. We used stochastic patch occupancy models to estimate equilibrium metapopulation densities for virtual species exhibiting different metapopulation parameters (dispersal ability, colonization efficiency, and extinction rate in colonized patches) and habitat preferences (early, mid and late successional), in landscapes with different habitat amounts and patch turnover rates. We found positive effects of intermediate disturbance only in early-successional species, particularly those with mid dispersal abilities in landscapes with relatively large amounts of suitable habitat, and those with high dispersal ability in landscapes with relatively low habitat amount. Increasing patch turnover always resulted in reduced metapopulation density for mid and late successional species. We confirmed that intermediate disturbances may be positive for some metapopulations, contributing to understand why some species thrive in highly-fragmented and dynamic landscapes. We suggest that early-successional species with mid to high dispersal ability may be the most likely to persist in such landscapes, but even these tend to decline when patch turnover rates are too high.

Keywords

Intermediate Disturbance Hypothesis, Incidence Function Model, ecological simulation, landscape fragmentation, virtual species.

1. Introduction

The metapopulation concept provides a unifying modelling framework for predicting species persistence ability under different landscape scenarios, and for identifying critical habitat thresholds for species occurrence (Ovaskainen and Hanski 2003), but metapopulation modelling often disregards how persistence is affected by landscape dynamics (e.g. Van Teeffelen et al. 2012). Landscape dynamics may involve, for instance, different rates of habitat destruction and creation, leading to temporal changes in habitat network structure (Stelter et al. 1997; Wahlberg et al. 2002). Furthermore, ecological succession after patch creation imply that habitats may become progressively more (or less) suitable over time, which further complicates temporal variation in patch networks. Although virtually every landscape should be subject to some level of dynamism (Turner 2010), metapopulation responses to landscape change over time have been addressed in only a relatively small number of studies (see Van Teeffelen et al. 2012).

Most studies addressing dynamic landscapes have found that patch turnover or disturbance intensity tend to reduce metapopulation persistence. However, it is also clear that the magnitude of responses depends on the biological features intrinsic to each species, such as habitat specialization and dispersal ability under variable matrix characteristics (Johst et al. 2002). Moreover, the range of responses to landscape dynamics may include positive relationships with habitat disturbance, such as may be the case of some early successional species (e.g. Stelter et al. 1997; Keymer et al. 2000; Wahlberg et al. 2002; DeWoody et al. 2005), for which occupancy may increase after disturbance, decreasing only in late successional habitats. This provides support for the idea that intermediate levels of landscape dynamics may benefit some species (Stelter et al. 1997; Kun et al. 2009; Govindan and Swihart 2012; Van Teeffelen et al. 2012; Zeigler and Fagan 2014; Govindan et al. 2015), thereby extending the “intermediate disturbance hypothesis” (IDH) originally proposed to explain species diversity in a community (Grime 1973), to single-species metapopulation dynamics in fragmented, dynamic habitat networks. To date, however, no study has yet evaluated thoroughly how biological traits and metapopulation parameters may affect the emergence of

IDH-like effects in dynamic landscapes affected by patch turnover and ecological succession.

In this study, we used SPOM simulations to test for IDH in metapopulations, evaluating what determines whether a species responds positively to intermediate levels of landscape dynamics. Specifically, we built on the recently developed simulation package *MetaLandSim* (Mestre et al. 2016), and assessed the equilibrium metapopulation density (i.e. fraction of occupied patches; e.g. Kun et al. 2009) of virtual species with different metapopulation parameters (dispersal ability, colonization efficiency, and extinction rate in colonized patches), in dynamic landscapes with different amounts of habitat and patch turnover rates. Also, we assumed that new patches undergo successional dynamics over time, and thus we have also considered species with affinities towards either early-, mid- or late-successional habitats. Globally, we predict that landscape dynamics should result in higher metapopulation densities for species with higher dispersal abilities and colonization efficiencies, and lower extinction probabilities (Johst et al. 2002; Kun et al. 2009). We also predict that, in general, early successional species should show higher metapopulation densities than late successional species in dynamic landscapes. Finally we predict that IDH effects should mostly occur for early successional species, particularly for those showing high dispersal abilities and occurring in landscape with relatively large amounts of suitable habitat (Stelter et al. 1997; Wahlberg et al. 2002; Govindan et al. 2015).

2. Methods

2.1. SPOM description

The study was based on SPOM simulations in dynamic habitat patch networks, as implemented in the package *MetaLandSim* (Mestre et al. 2016). The approach is based on the Incidence Function Model (IFM), defined by a linear, first-order Markov chain with two states, the presence-absence of the species in a patch (Hanski 1994). This is a spatially explicit minimalistic approach to the metapopulation dynamics, requiring a reduced number of parameters, while providing reliable results when compared with other more data hungry approaches (Sjögren-Gulve and Hanski 2000; Hokit et al.

2001). In the IFM, the stationary probability of occupying a given patch i at time t is given by $J_i = C_i / (C_i + E_i)$, where C_i is the constant colonization probability per unit time when patch i is empty, and E_i is the constant extinction probability per unit time when the patch i is occupied (Hanski 1994). In our study these probabilities were respectively given as (Hanski 1994, 1999):

$$\begin{cases} E_{is} = e / A_i^x & \text{if } A_i > e^{1/x} \\ E_{is} = 1 & \text{if } A_i < e^{1/x} \end{cases}$$

where S_i is the connectivity, defined as $S_i = A_i^c \sum p_j \exp(-\alpha d_{ij}) A_j^b$ (Moilanen and Nieminen 2002), with d_{ij} representing the distance between patches i and j . The constants e , x , y , and α represent the IFM parameters affecting the extinction risk and colonization probabilities in each patch (Hanski 1999). Parameter e gives the probability of extinction in a patch of unit area, which can be given by A_0^x , where A_0 is the critical area below which the species cannot persist (Etienne et al. 2004). Parameter x describes the strength of the relation between extinction risk and patch area (and consequently local population size, which is assumed to be directly proportional to the area). This parameter may be considered as a proxy of environmental stochasticity, with a lower x corresponding to higher stochasticity: $x > 1$ - there is a critical area beyond which extinction probability is very low; $x < 1$ - the extinction risk of even large populations (which are in larger patches) is high (Hanski 1994). Parameter y in the connectivity function defines how fast the colonization probability approaches one with increasing connectivity, giving the colonization efficiency of empty patches (Hanski 1994). Finally, parameter α is related with the dispersal ability ($\alpha = 1/\text{species dispersal ability}$) and it is a proxy for the survival rate of the individuals in the distance d_{ij} while moving between the patches i and crossing an inhospitable matrix (Hanski 1994). In our simulations, possible rescue or Allee effects were not considered, though the effect of the area of the focal patch (A_i) was accounted for, by setting the parameter $c=1$. This approach considers that larger patches attract more migrants, thus providing a better destination for emigrants (Moilanen and Nieminen 2002).

2.2. Generation of virtual species

Because estimating the impact of landscape dynamics under different scenarios of habitat availability is hard to approach experimentally, we generated a set of virtual species, each covering a particular IFM parameter space, and exhibiting one of three possible habitat successional preferences (early, mid, and late successional). The use of virtual species is widespread in ecological studies (e.g. Hirzel et al. 2001) and the value of simulation as an experimental environment has been widely acknowledged (Peck 2004; Zurell et al. 2009), particularly in complex ecological systems, and in studies involving large spatial and temporal scales (Ims 2005).

A total of 54 virtual species were defined, by considering 18 combinations of IFM parameters for each of three categories of successional habitat preferences. Parameter α was set at three levels defining high (0.001), mid (0.004), or low dispersal ability (0.02). ii) The species critical area, A_0 , (which is used in conjunction with x to compute e) was derived based on the mean patch area (MPA), with two levels: 0.05 (10% of MPA) and 0.1 (20% of MPA). Parameter y was varied in order to allow for three colonization probabilities considering patch connectivity: 5 (highest colonization efficiency), 10 and 20 (lowest colonization efficiency). Finally, the parameter x was kept at 1 in all virtual species, as our main focus is on the species ability to colonize the landscape and on landscape structure and dynamics (Table 1).

Table 1 – IFM parameter values used to generate the virtual species included in the study.

Parameter	Parameter value
α (inverse of mean dispersal ability - related with the minimum interpatch distance, MID)	0.02 (Lower dispersal ability)
	0.004
	0.001 (Higher dispersal ability)
γ (colonization efficiency)	5 (higher colonization efficiency)
	10
	20 (lower colonization efficiency)
x (Lower values correspond to higher environmental stochasticity)	1 (fixed value)
A_0 (Critical area – area below which the populations are extinguished)	0.05 (10% of MPA)
	0.1 (20% of MPA)
e (Local extinction – computed from all combinations of A_0 and x , using A_0^x)	0.05
	0.1

Habitat preferences (early-, mid- or late-successional patches) were specified by integrating patch age (i.e., time since patch creation) into the extinction probability formula (E_{is}), such that the ability of a patch to sustain a given species could be influenced by an additional temporal factor (E_{it}), described graphically in fig. 1.

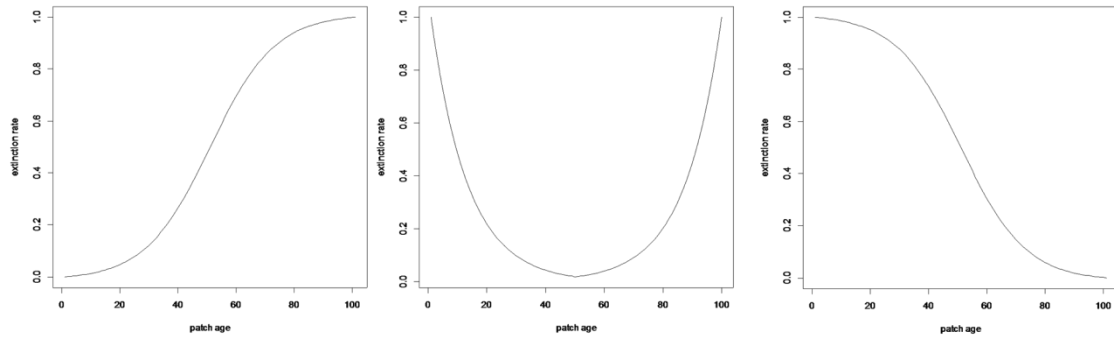


Figure 1 – Graphical representation of variation in extinction probability in relation to patch age (i.e., time since creation) for virtual species with different successional habitat affinities: a) early-successional (left): $E_{it} = \frac{1}{1+\exp(-0.09 \times \text{patch age})}$; b) mid-successional (center): for **patch age** < 50, $E_{it} = \exp(0.08 \times (-\text{patch age}))$ and for **patch age** ≥ 50, $E_{it} = \exp(0.08 \times (\text{patch age}))$; c) late-successional (right): $E_{it} = \frac{1}{1+\exp(0.09 \times \text{patch age})}$.

For species preferring early stages of habitat succession (i.e. “young” patches), the extinction probability was taken to change according to a negative sigmoid function (Fig. 1a), while for species preferring mid successional habitats a parabola was used (Fig. 1b). For species preferring late successional habitats (i.e. (“old” patches), the extinction probability was determined by a positive sigmoid function (Fig. 1c). These curves are representative, for instance, of different groups of plant, butterfly and bird species using Mediterranean forests during a long term successional vegetation recovery after undergrowth clearing (Porto et al. 2011; Santana et al. 2011, 2012; Verdasca et al. 2012).

2.3. Landscape simulation scenarios

Landscapes in our virtual ecological model consisted in 3163 x 3163 m² areas (ca. 1000 ha), which were represented as graphs considering two habitat classes: suitable habitat and matrix. We first set three scenarios of habitat availability by defining landscapes with 5%, 10%, and 20% habitat cover, and considering a mean (±sd) patch area of 0.5±0.2 ha, and a minimum inter-patch distance of 10 m. This resulted in

landscapes with 100, 200, and 400 initial habitat patches for the landscapes with 5%, 10% and 20% habitat cover, respectively. It should be noted that these areal measures are arbitrary, and so units expressed in meters could as well be expressed in kilometres, for instance, if we were interested in modelling species with larger range sizes and higher dispersal abilities.

Landscape dynamics was described as the number of patches being destroyed and created in each time step of the Markov process. This was defined by selecting the percentage of patches to be created and destroyed from a Poisson distribution. In each scenario of habitat availability, SPOM simulations considered landscape dynamics of 0%, 5%, 10% and 20%, totalling 12 scenarios of habitat availability and dynamics. Succession at each patch was accounted for by considering the time units since patch creation, which then interacted with the extinction probability as a function of patch age to determine species habitat preferences along the succession.

2.4. Computational implementation of SPOMs

Simulations were run using the “MetaLandSim” package, version 0.5.2 (Mestre et al. 2016), which provides a convenient virtual environment for studying metapopulation persistence in dynamic landscapes. The package was run in R, version 3.3.1 (R Core Team 2016), using a computer with a 12x Intel(R) Core(TM) i7-3960X CPU, 3.30GHz processor; 32 GB memory and an Ubuntu 14.04.3 LTS operating System. Parallel computing with 6 processors was used, requiring the packages “parallel” (R Core Team 2016), “foreach” (Revolution Analytics and Weston 2015a) and “doParallel” (Revolution Analytics and Weston 2015b).

SPOM simulations for each of the 54 species in each of the three scenarios of habitat availability and four landscape dynamisms considered (= 648 simulations) were run with 500 iterations, along 100 time steps, and considering an initial occupation of 50% of patches selected randomly. The metapopulation density was estimated as the fraction of occupied patches after 100 time steps, and averaged across iterations for each combination of parameters and habitat preferences. Preliminary analysis showed that the number of iterations was sufficient for obtaining stable results (Fig. A1 in the Supplementary Material #1). Simulations were grouped in three blocks defined

according to the species habitat successional preferences, totalling 216 simulations per simulation block. Each of the three simulation blocks took approximately five days to run.

3. Results

Simulations indicated that, in general, metapopulation density increases with increasing species dispersal abilities (i.e. higher α values) and, to a much lesser extent, colonization efficiencies (lower γ values) (fig. 2). In particular, the simulations regarding metapopulation dynamics along 100 time steps for species with the lowest dispersal abilities ($\alpha=0.02$), reached quasi-extinction (i.e., very low metapopulation densities) in all simulated scenarios of habitat amount and landscape dynamics, independently of habitat preferences. However, species showing preference for early-successional habitats tended to show higher metapopulation densities in dynamic landscapes than species associated with mid- and late-successional habitats (figures A2 to A4 in the Supplementary Material #1).

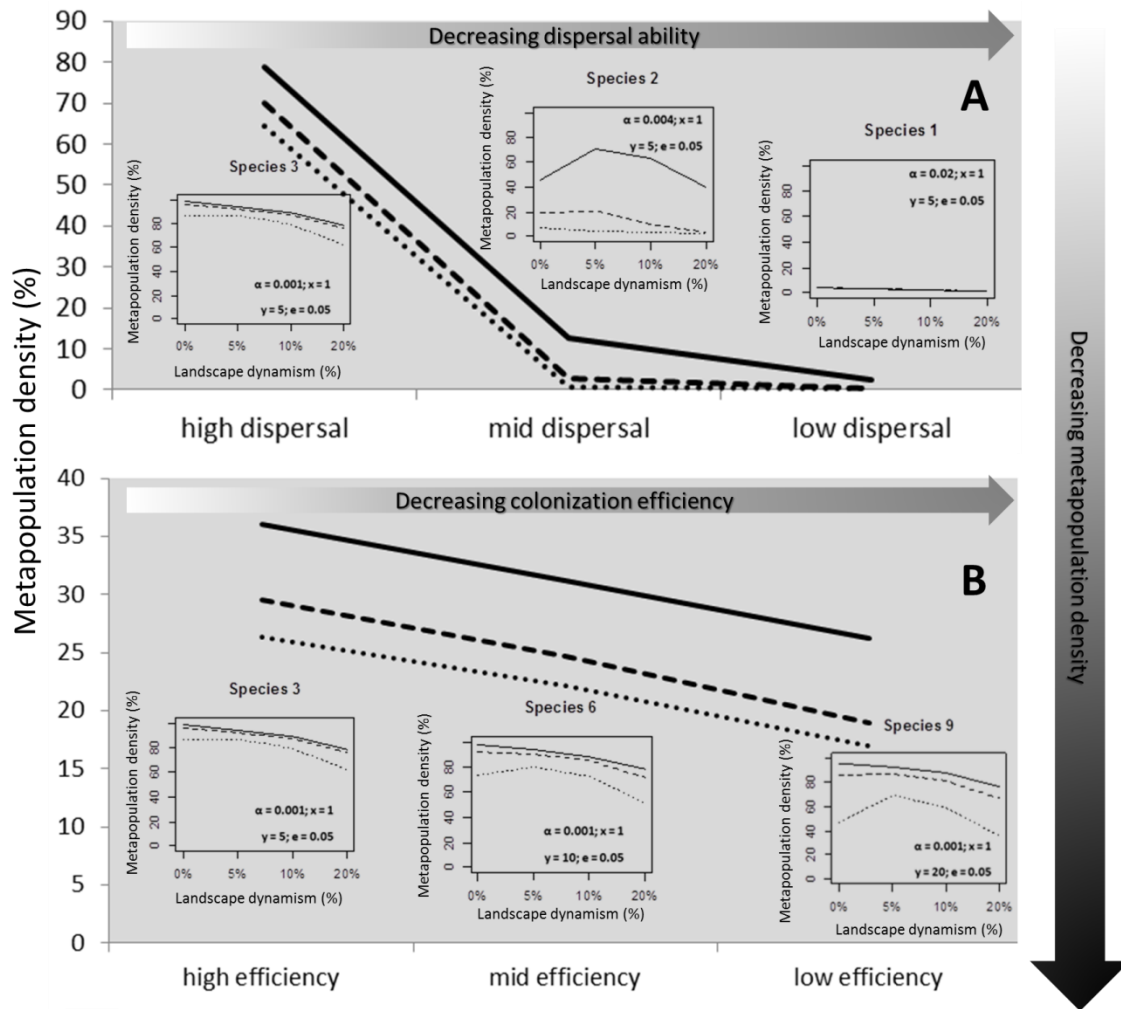


Figure 2 – General tendencies of variation in metapopulation density (i.e. fraction of occupied patches after 100 time steps) in relation to species dispersal ability (A) and colonization efficiency (B). Lines represent the averages observed for early- (full line), mid- (dashed line) and late-successional species (dotted line). The insets are examples of simulation results observed for virtual species.

Results further evidenced clear IDH effects in some of early-successional species, as indicated by the \cap -shaped responses to landscape dynamics in about 16.7% of species and habitat availability scenarios (Figure A2 in the Supplementary Material #1). In particular, metapopulation densities by species with mid to high dispersal abilities ($\alpha=0.004$ and $\alpha=0.001$) seemed to increase towards intermediate levels of patch turnover (5-10%) depending on the proportion of total habitat available (fig. 3). Colonization efficiency also appears to play a role in the IDH effect, though much less clear than dispersal distance. Species with mid dispersal abilities ($\alpha=0.004$) and mid to

high colonization efficiencies ($\gamma=5$ and $\gamma=10$) showed positive responses to intermediate landscape dynamics mostly at high habitat availability, with five cases with 20% habitat cover (species 2, 5, 8, 11 and 14; fig.3 and figure A2 in the Supplementary Material #1). The exception was species 8, which has low colonization efficiency but compensates by having low local extinction: $e=0.005$.

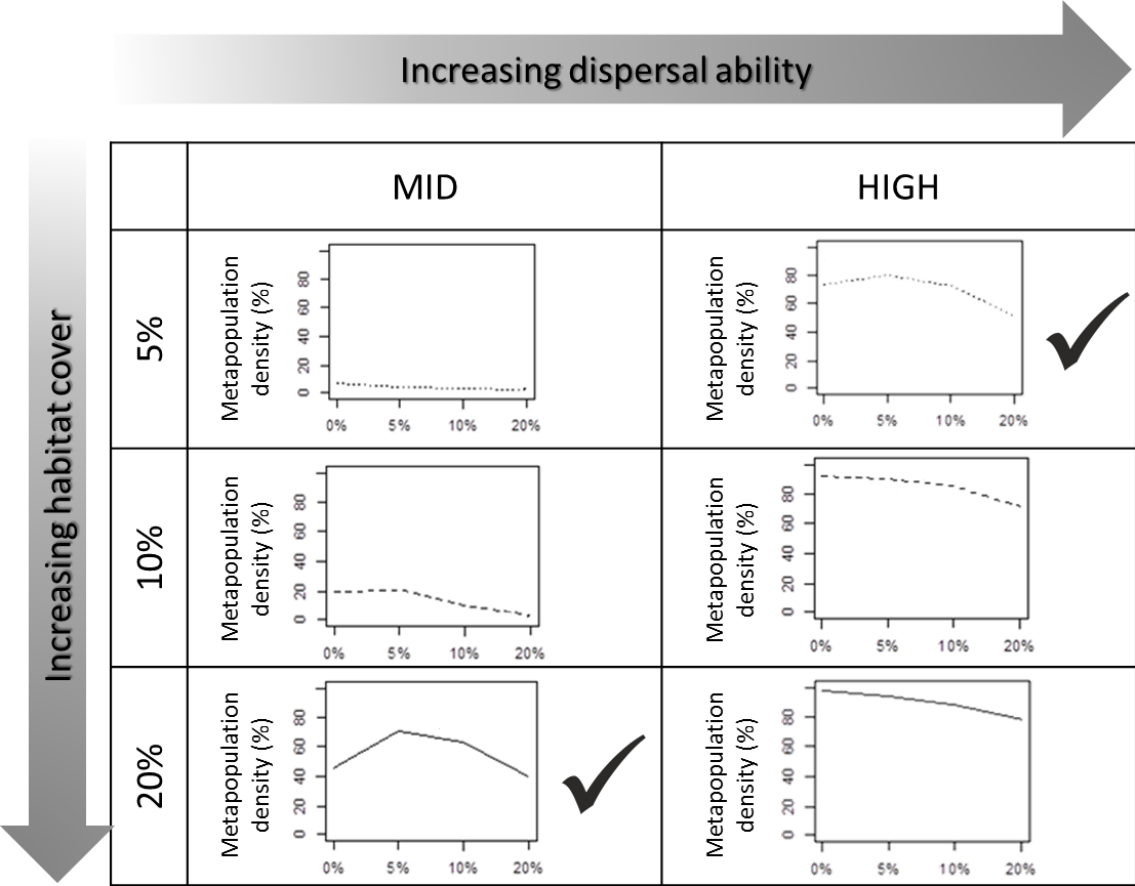


Figure 3 – Examples of variation in metapopulation density (i.e. fraction of occupied patches after 100 time steps) in relation to landscape dynamism, for early successional species with mid and high-dispersal ability, and landscapes with three levels of available cover. Positive responses to intermediate disturbances (i.e., IDH-like responses) are evident for species 2 (left column: $\alpha=0.004$; $x=1$; $\gamma=5$; $e=0.05$) and 6 (right column: $\alpha=0.001$; $x=1$; $\gamma=10$; $e=0.05$).

Species with high dispersal abilities ($\alpha=0.001$), and mid to low colonization efficiencies ($\gamma=10$ and $\gamma=20$ – with the exception of species 3), tended to exhibit positive responses to intermediate levels of landscape dynamics mostly at low amounts of available

habitat, with four cases with 5% habitat cover (figure A2 in the Supplementary Material #1, species 6, 9, 15 and 18), and 1 case with 10% habitat cover (figure A2 in the Supplementary Material #1, species 9).

No IDH effects were detected for species preferring mid- to late-successional habitats, for which increased levels of landscape dynamics consistently resulted in the decline of metapopulation densities rates, a tendency that was much amplified for species with reduced dispersal abilities (Figures A3 and A4 in the Supplementary Material #1). In particular, high metapopulation densities were only retained in dynamic landscapes for species showing high dispersal abilities ($\alpha=0.001$), and for mid-successional species with high colonization efficiencies ($\gamma=5$) in landscapes with larger amounts of suitable habitat (20% cover) and subjected to low (0-5%) dynamism (Figure A3 in the Supplementary Material #1, species 20 and 29). However, late-successional species with high dispersal abilities ($\alpha=0.001$) may also become extinct relatively fast in landscapes with reduced habitat availability, if they also show reduced colonization efficiencies ($\gamma=20$) (Figure A4 in the Supplementary Material #1, species 54).

4. Discussion

Our study based on simulated experimental trials on virtual species presenting different successional habitat preferences and metapopulation dynamics, largely confirmed the general idea that in most cases landscape dynamics should decrease metapopulation persistence, as local extinction probabilities will increase due to direct mortality resulting from patch destruction (e.g. Akçakaya et al. 2004; Snäll et al. 2005). However, it also confirmed the “intermediate disturbance hypothesis”, showing that, in some instances, metapopulations may respond positively to intermediate levels of landscape dynamics (e.g. Stelter et al. 1997; Wahlberg et al. 2002; Matlack and Monde 2005; Kun et al. 2009; Govindan et al. 2015). Additionally, it contributed to understand the combination of species traits and landscape characteristics that determine such responses (e.g. Van Teeffelen et al. 2012). Specifically, we found that intermediate landscape dynamics benefited some early successional species, which are well adapted to habitat disturbance and recovery (such as those in Stelter et al. 1997; Wahlberg et al. 2002; Govindan et al. 2015), but only under particular levels of patch turnover and

habitat amount, and depending on species dispersal and colonization efficiencies. Although these inferences were based on simulations rather than on empirical observations, we believe that they should apply over a wide range of real metapopulations, as our simulations encompassed a large variety of realistic metapopulation parameters and landscape scenarios. Overall, our simulation-based approach contributed to the identification of key population and ecological attributes that determine how species respond to landscape dynamics, which may help ecologists to predict general patterns of metapopulation responses to environmental disturbance over a range of taxa and ecological systems.

4.1. Limitations and potential shortcomings

The simulation conditions used in our study were necessarily limited, representing a compromise between computation time and the need to incorporate a range of variation as large as possible. Regarding the parameter space, we have tried to encompass the variability often observed in real metapopulations and landscapes, though we recognise that considering larger variation would allow exploring the dynamic behaviour of more metapopulation typologies. For instance, we restricted variation in habitat amount to between 5% and 20% of the landscape, though some metapopulations may occur in landscapes with more (or less) habitat. However, we placed a cap at 20% because species with high dispersal ability living in fragmented landscapes with larger habitat amounts may behave like a single population rather than as a true metapopulation (Hanski and Gilpin 1991; Harrison and Taylor 1997). Likewise, metapopulations inhabiting landscapes with very low habitat amounts (<5%) may go inevitably extinct or become completely isolated irrespective of landscape dynamics (Harrison and Taylor 1997). We suggest, however, that it may be worth exploring the dynamic behaviour of metapopulations using parameters beyond the range used in our study, particularly where these parameters are based on empirical observations from real populations.

In our study we have also restricted simulations to the case where the creation/destruction of patch follows a Poisson process with a given mean probability. This was considered reasonable as a first approximation to explore the consequences

of patch turnover and successional dynamics, though more complex situations may occur in real landscapes. For instance, patch creation/destruction may be spatially correlated due for instance to the effects of fire, flooding or human activities, which may have consequences to metapopulation dynamics (Johst and Drechsler 2003). Likewise, disturbance probability may not be evenly distributed across patch ages, as some ages may be far more vulnerable than others (Van Teeffelen et al. 2012). For instance, forest fuels accumulate with time since disturbance, and so the occurrence of high-intensity fires are most likely in late- and mid-successional habitat patches (Porto et al. 2013). Exploring such complexities should be the subject of further research, aiming to understand how they affect metapopulation persistence of species with different habitat affinities.

4.2. Metapopulation persistence in dynamic landscapes

Our results supported the prediction that metapopulation persistence is generally negatively affected by landscape dynamics (Keymer et al. 2000). However, such effects were much weaker for early successional species, supporting the prediction that patch turnover should be much less detrimental for species that are well adapted to disturbances, such as fire, flooding, clear-cutting, or forest clearing (e.g. Stelter et al. 1997). This is probably because static landscapes will cause the patches to evolve to late successional stages, thus rendering these patches inadequate. In contrast, dynamic landscapes will continuously produce new habitats, which if successfully colonized will slow down the metapopulation extinction rates over time (e.g. Stelter et al. 1997; Wimberly 2006). Moreover, among the early successional species, some metapopulations showed positive responses to intermediate levels of landscape dynamics, suggesting that habitat turnover may increase metapopulation persistence over time until some critical rate, above which it will quickly decline (e.g. Stelter et al. 1997; Keymer et al. 2000; Wahlberg et al. 2002). This suggests that, for such species, an intermediate level of landscape dynamics will promote the creation of a sufficient number of new patches without the effect of extinction being overwhelming, thus improving species occupancy and persistence.

According to our results the most important factor affecting the emergence of IDH effects on metapopulation persistence should be the species' habitat successional preference, since all the species that exhibited such an effect were early successional. However, the interaction between species dispersal abilities and habitat proportion seems to be also critical for the emergence of IDH effects on metapopulations of early successional species. In particular, those exhibiting relatively high dispersal abilities and colonization efficiencies (though the effect of dispersal is much more clear) in landscapes with lower amounts of suitable habitat. Also species with mid dispersal abilities and lower colonization efficiencies in landscapes with larger amounts of suitable habitat, frequently responded positively to intermediate levels of habitat dynamics. This seems contrary to the results of Kun et al. (2009), which suggest IDH effects on species with limited dispersal abilities. However, these authors considered overall habitat percentage covering between 40 and 60% of the landscape, which corroborates the idea that IDH effects should in part result from the interplay between habitat availability and species dispersal, appearing in species with long dispersal distances when habitat amount is small, and for species with small dispersal distances when habitat amount is large. It is worth mentioning that, in the context of true metapopulations, the availability of suitable habitat in the landscape should be generally much lower than 40-60%, since true metapopulations imply that species should have some interpatch dispersal, but not enough to be considered a patchy population, which has unrestrained interpatch movement (Harrison and Taylor 1997). This suggests that IDH effects should be more frequent in early successional species with mid to high dispersal abilities.

Although the affinity for early-successional habitats was the main mechanism invoked in our study to explain the positive effect of intermediate disturbances, there may be other advantages arising from landscape dynamics. Loehle et al. (2007) and Zeigler and Fagan (2014) suggested that the creation and destruction of habitat patches would provide intermediate windows of connectivity, thus improving metapopulation persistence. This argument is also presented by Kun et al. (2009), highlighting the trade-off between the positive effect of these temporary stepping stones, and the negative effect of increasing the disturbance. In our case this effect might act in conjunction with the early successional preference and be much more reduced in mid

or late successional species, since extinction is higher in early successional patches for these species, thus reducing its potential as stepping stones.

4.3. Conservation implications

Although our study did not apply to any real species in particular, it provides some heuristic guidance towards metapopulation conservation. First and foremost, our study adds to the results of a relatively few other studies emphasising the importance of considering the rates of patch destruction and creation in dynamic landscapes (e.g. Loehle et al. 2007; Van Teeffelen et al. 2012; Zeigler and Fagan 2014). This is critical, because the persistence of most species clearly declines with increasing patch turnover rates, while others are benefited by such dynamism. Therefore, the optimal patch turnover to be maintained in a landscape should depend on the particular species or groups of species that are targeted for conservation.

Second, changes in habitat quality linked to successional dynamics also need to be considered in metapopulation modelling, because they strongly affect variation in metapopulation responses to patch turnover in relation to species habitat preferences. Specifically, it needs to be explicitly considered that a new patch may take several time units (e.g., years) to become progressively favourable for a late-successional species, or otherwise to become progressively unfavourable for an early-successional species. This was observed, for instance, during the process of vegetation succession after undergrowth removal in Mediterranean cork oak *Quercus suber* forests, where the abundance of some annual herb and butterfly species generally peaked just a few years after disturbance and then declined, whereas several birds and long-lived shrubs and trees took many decades to recover (Porto et al. 2011; Santana et al. 2011, 2012; Verdasca et al. 2012). Integrating patch turnover and successional habitat preferences may thus allow addressing the landscape persistence of these types of species in a metapopulation context.

Finally, we suggest that our approach based on the package MetLandSim (Mestre et al. 2016) should provide a relatively simple but powerful framework to address metapopulation conservation in real landscapes. This would require parameterising

the model with values estimated in the field from real metapopulations, which could then be used to simulate how persistence and patch occupancy is expected to vary as a function of different realistic scenarios of landscape dynamism. Although at present the package only allows for variation in patch turnover and total habitat amount, it should be relatively easy to incorporate other complexities such as variation in patch configuration (Vuilleumier et al. 2007), and in the spatial arrangement and intensity of disturbances (Johst and Drechsler 2003; Vuilleumier et al. 2007).

Acknowledgments

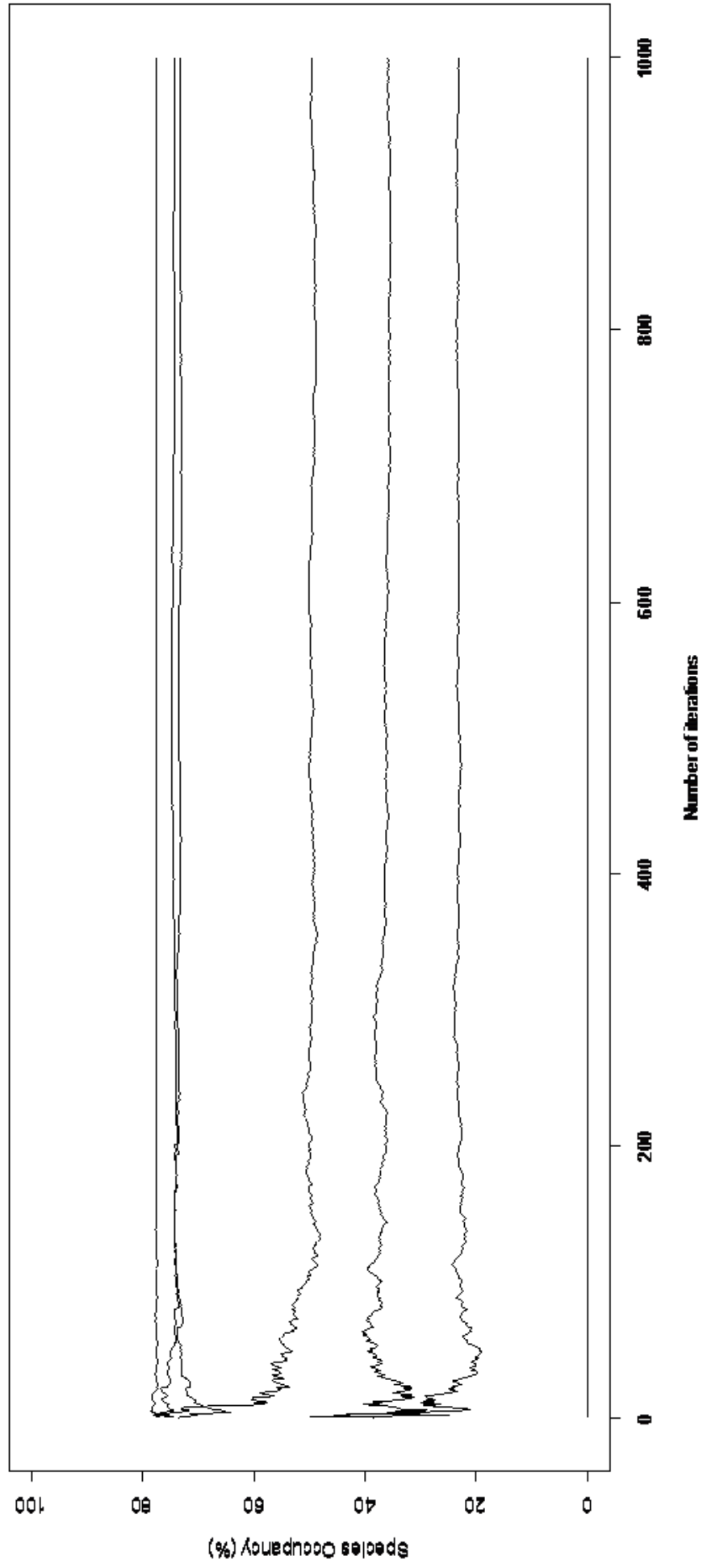
This study was funded by the Portuguese Foundation for Science and Technology through the fellowships to FM (SFRH/BD/73768/2010) and RP (SFRH/BPD/73478/2010 and SFRH/BPD/109235/2015) and the project NETPERSIST (PTDC/AAG-MAA/3227/2012). The EDP Biodiversity Chair supported PB. We are grateful to Bruno Silva (CIBIO-UE – University of Évora) for assisting in the setting up of the parallel multicore computing.

Supplementary Material #1

Evolution of the simulation stability with the number of iterations

In order to evaluate the stability of the output with the number of iterations used, simulations were first ran with 1000 iterations for 10 randomly selected species at the higher (20%) landscape dynamism, which is the scenario presumably yielding higher perturbations. The final landscape occupation by each species was then assessed using a cumulative higher number of iterations. This process was repeated 10 times per species, and suggested that 500 interactions are sufficient to produce stable results (Fig. A1).

Figure A1 – Final occupancy of ten randomly selected species at the more dynamic landscape scenario (20%), according to the number of iterations.



R Script for the virtual scenarios simulation

```
#####  
#                               R SCRIPT FOR RUNNING THE SIMULATIONS                               #  
#####  
  
#Loading MetaLandSim  
library(MetaLandSim)  
  
#####  
##                               Used Packages                               ##  
#####  
  
#Loading packages  
library(parallel)  
library(foreach)  
library(doParallel)  
  
#Citation details  
citation (package = "parallel")  
citation (package = "foreach")  
citation (package = "doParallel")  
citation(package = "base", lib.loc = NULL)  
  
#####  
##                               Creating parameter data frame                               ##  
#####  
  
#Control column  
clock <- rep(c(1:18),each=12)#Each scenario  
  
#Species parameters  
par_a <- rep(rep(c(0.02, 0.004, 0.001),6),12)  
par_y <- rep(rep(c(5,10, 20),each=3,2),12)  
A_MIN_SPECIES1 <- rep(rep(c(0.05, 0.1),each=9),12)  
par_x <- rep(rep(1,18),12)  
par_e <- A_MIN_SPECIES1^par_x  
  
#Landscape and simulation parameter columns  
PAR1_SPAN1 <- rep("stoc", 216)  
  
PAR2_SPAN1 <- rep(rep(c(0, 5, 10, 20),3),each=18)  
PAR3_SPAN1 <- rep(rep(c(0, 5, 10, 20),3),each=18)  
NPATCH1 <- rep(rep(c(100, 200, 400),each=4),each=18)#number of patches  
  
PAR4_SPAN1 <- rep("NULL",216)#parameter 4 for the span function  
PAR5_SPAN1 <- rep("NULL",216)#parameter 5 for the span function  
METHOD_SPECIES1 <- rep("percentage",216)#method for populating the  
landscape  
PARAM_SPECIES1 <- rep(50,216)#parameter for the species function  
NSEW_SPECIES1 <- rep("none",216)#where to start populating the  
landscape  
AREA_M1 <- rep(0.5, 216)#mean area  
MAPSIZE1 <- rep(3163,216)#dimension of the landscape  
SPAN1 <- rep(100,216)#number of time steps of each simulation  
ITER1 <- rep(500,216)#number of iterations of each simulation  
AREA_SD1 <- rep(0.2,216)#area sd  
MDST1 <- rep(10, 216)#minimum distance between  
KERN <- rep("op1",216)#kernel function
```

```

CONN <- rep("op2",216)#connectivity function
COLNZ <- rep("op1",216)#colonization function
EXT <- rep("op1",216)#extinction function
BETA1 <- rep("NULL",216)
B <- rep(1,216)
C1 <- rep(1,216)
C2 <- rep("NULL",216)
Z <- rep("NULL",216)
R2 <- rep("NULL",216)
dispersal <- 1/par_a
succ <- rep("early",216) #successional preference (run all the code
three times: to "early", "mid" and "late" successional preference)

#Creating the data frame
simulation1 <- data.frame(clock, par_a, par_y, par_x, par_e, MDST1,
NPATCH1, AREA_M1, AREA_SD1, MAPSIZE1, SPAN1, ITER1, PAR1_SPAN1,
PAR2_SPAN1, PAR3_SPAN1, PAR4_SPAN1, PAR5_SPAN1, NSEW_SPECIES1,
PARM_SPECIES1, METHOD_SPECIES1, KERN,CONN, COLNZ, EXT, BETA1, B,C1,
C2, Z, R2, dispersal, succ)

#Delete the individual data frame columns
rm("clock", "PAR1_SPAN1", "PAR2_SPAN1", "PAR3_SPAN1", "PAR4_SPAN1",
"PAR5_SPAN1", "A_MIN_SPECIES1", "NSEW_SPECIES1", "PARM_SPECIES1",
"METHOD_SPECIES1", "MAPSIZE1", "SPAN1", "ITER1", "NPATCH1", "AREA_M1",
"AREA_SD1", "MDST1", "KERN", "CONN", "COLNZ", "EXT", "BETA1", "B",
"C1", "C2", "Z", "R2", "dispersal", "par_x", "par_e", "par_y",
"par_a", "succ")

#####
##      Parallel computing related code      ##
#####

#### Function used to clean memory after disconnecting the cluster
unregister <- function() {
  env <- foreach:::foreachGlobals
  rm(list=ls(name=env), pos=env)
}

#### Number of processors
N_cpu <- 5

#### Creating and registering a cluster with a given number of
clusters
cl <- makeCluster(N_cpu)
registerDoParallel(cl, cores = N_cpu)

#####
##      Preparing data for simulation loop      ##
#####

#Species
par2_2 <- list()

for(i in 1:18){

  df1 <- create.parameter.df(alpha=as.numeric(simulation1[i,2]),
x=as.numeric(simulation1[i,4]),

```

```

                                y=as.numeric(simulation1[i,3]),
e=as.numeric(simulation1[i,5]))

  par2_2[[i]] <- df1
}

#Landscape and simulation
par3_2 <- list()

for(i in 1:18){

  pal <- par2_2[[i]]

  simulation2 <- simulation1[simulation1$par_a==pal[1,1] &
simulation1$par_x==pal[2,1] &
                                simulation1$par_y==pal[3,1] &
simulation1$par_e==pal[4,1], ]

  df2 <-
data.frame(simulation2[,6],simulation2[,7],simulation2[,8],simulation2
[,9],simulation2[,10],simulation2[,11],

simulation2[,12],simulation2[,13],simulation2[,14],simulation2[,15],si
mulation2[,16],simulation2[,17],simulation2[,18],simulation2[,19],

simulation2[,20],simulation2[,21],simulation2[,22],simulation2[,23],si
mulation2[,24],simulation2[,25],simulation2[,26],simulation2[,27],

simulation2[,28],simulation2[,29],simulation2[,30],simulation2[,31],si
mulation2[,32])

  name_2 <-
names(simulation1[c(6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21,22,23,
24,25,26,27,
                                28,29,30,31,32)])

  names(df2) <- name_2

  par3_2[[i]] <- df2
}

#clean environment
rm(df1)
rm(pal)
rm(simulation2)
rm(df2)
rm(name_2)
rm(i)

#####
##           Running the simulation           ##
#####

cluster_6 <- system.time(
  result1 <- foreach(i = 1:length(par2_2), .packages =
c("MetaLandSim"))
    %dopar% {
      try({

```

```

df3 <- par2_2[[i]]
df4 <- par3_2[[i]]

ms1_2 <- manage_landscape_sim(par_df = df4, parameters_spm =
df3)

save(ms1_2, file = paste('result','_', i ,'.RData',sep=''))

return(ms1_2)

  })
}
)

#####
##          Saving global loop output          ##
#####

save(result1, file = "total_sim_output.RData")

#####
##          Disconnect cluster          ##
#####

stopCluster(cl) # stoping cluster
unregister() # clean memory
registerDoSEQ() # Return to sequential computing

```

Global Outputs

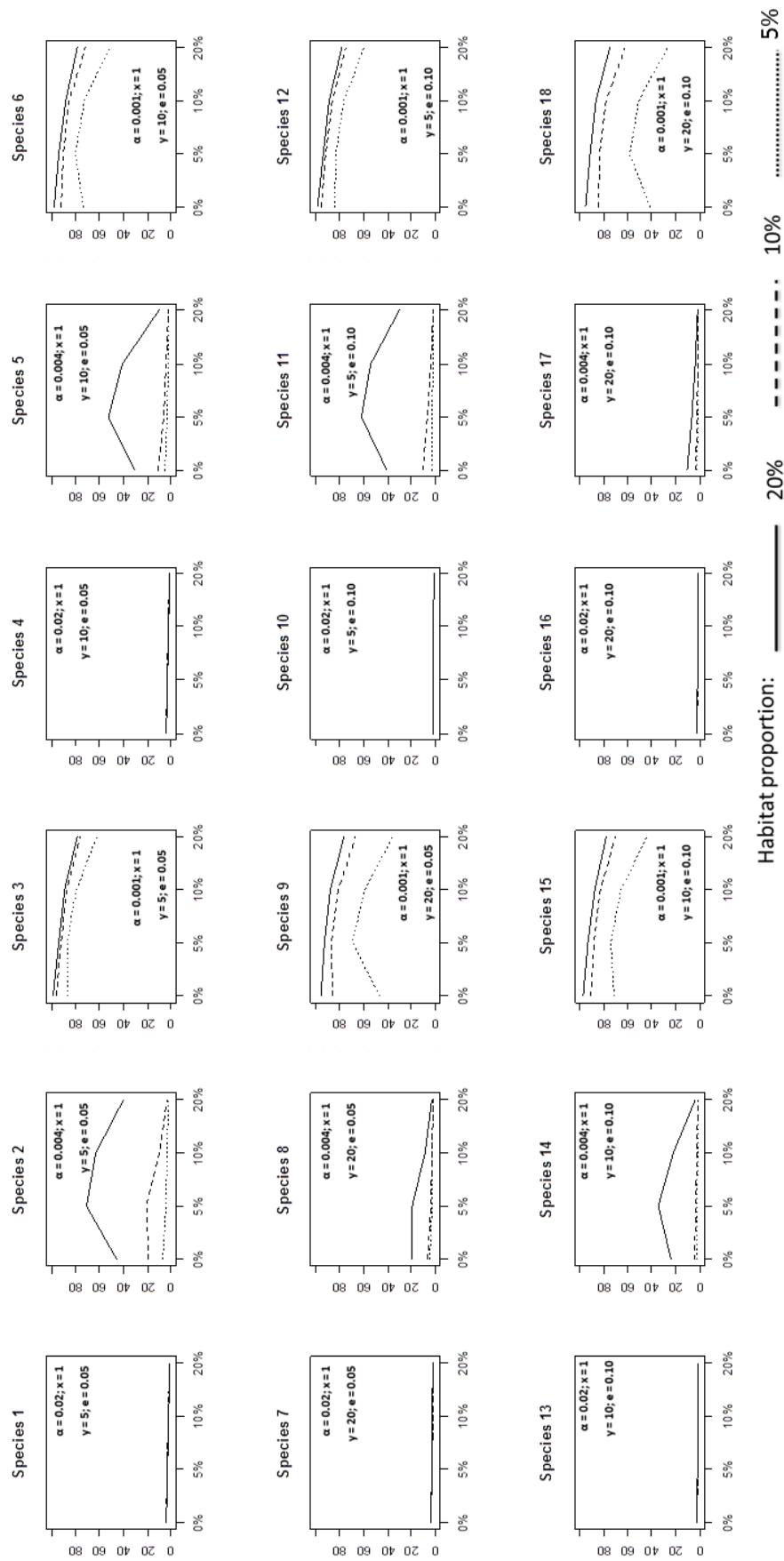


Figure A2 – Early successional metapopulation density after 100 time steps in each scenario of habitat availability (5%, 10% and 20%) and landscape dynamics (0%, 5%, 10%, 20%) considered in the study. To each virtual species: metapopulation density (% - y axis) and landscape dynamics (% - x axis).

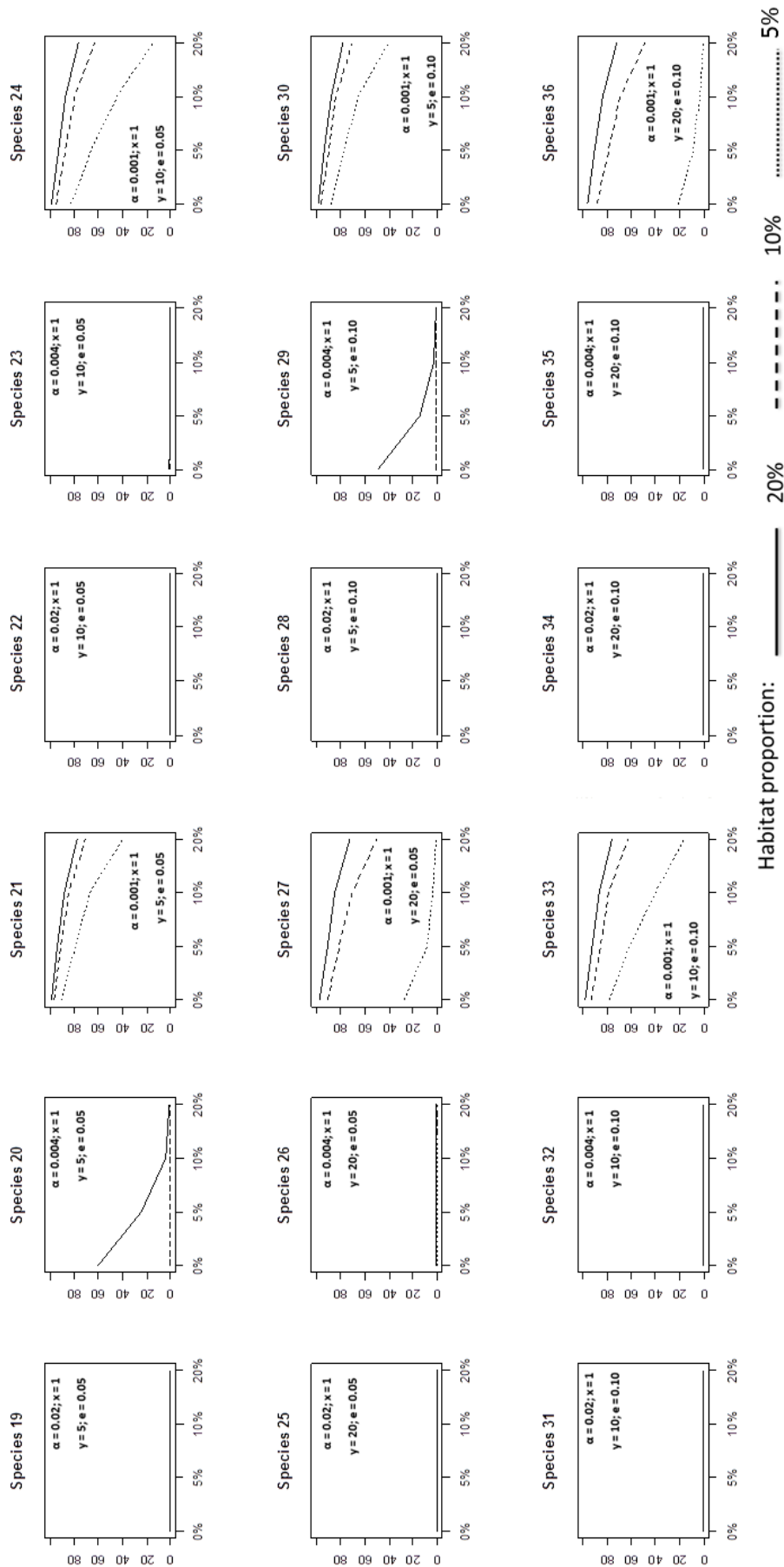


Figure A3 – Mid successional metapopulation density after 100 time steps in each scenario of habitat availability (5%, 10% and 20%) and landscape dynamics (0%, 5%, 10%, 20%) considered in the study. To each virtual species: metapopulation density (% - y axis) and landscape dynamics (% - x axis).

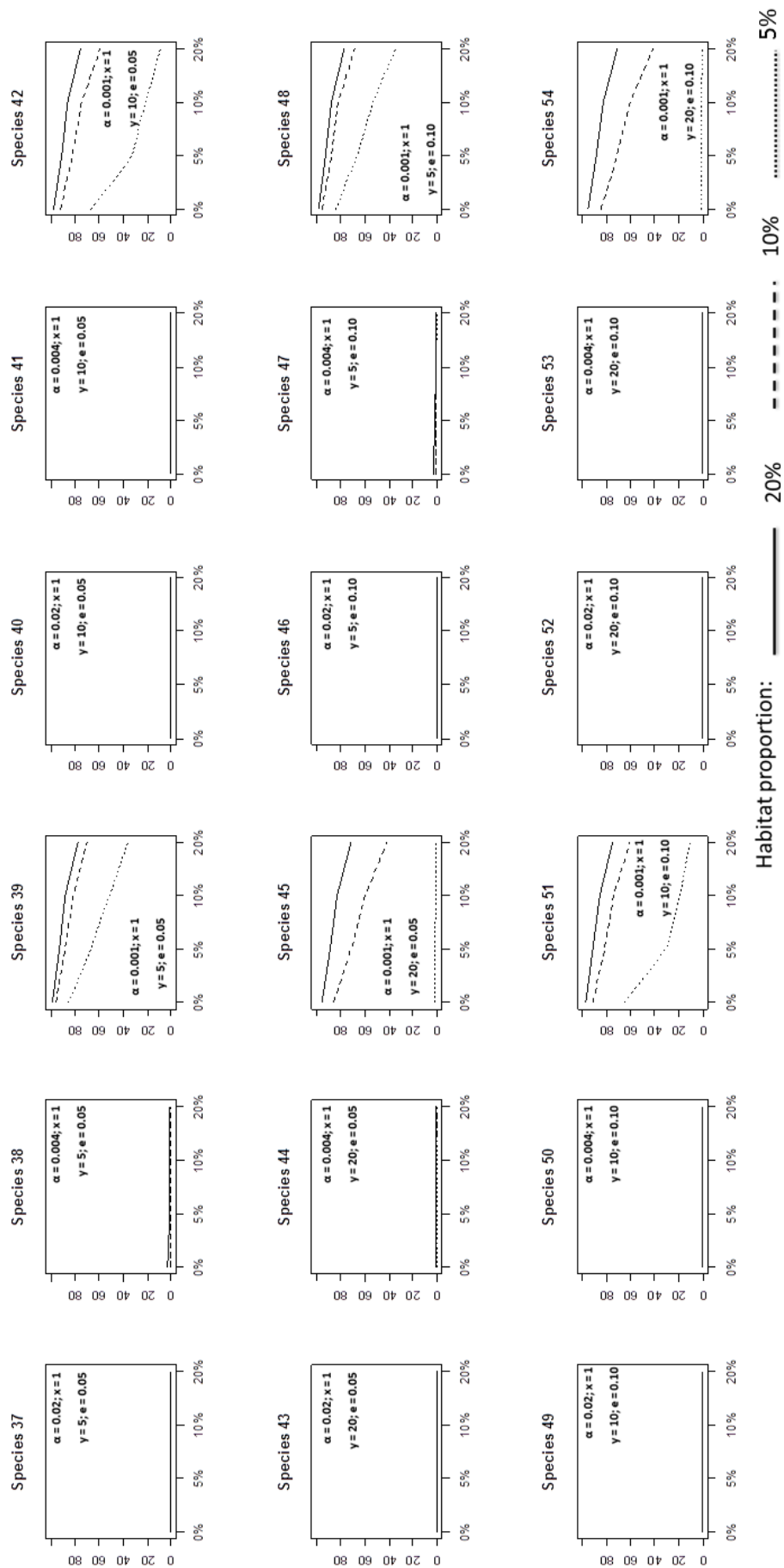


Figure A4– Late successional metapopulation density after 100 time steps in each scenario of habitat availability (5%, 10% and 20%) and landscape dynamics (0%, 5%, 10%, 20%) considered in the study. To each virtual species: metapopulation density (% - y axis) and landscape dynamics (% - x axis).

Chapter 6

Conclusion

It is widely acknowledged that climate change is currently affecting biodiversity (Parmesan, 2006; Parmesan and Yohe, 2003; Walther et al. 2002). The response of a species to climate change is extinction, adaptation or range shift (Parmesan, 2006). Range shifts, which are the main research focus of this thesis, raise a lot of questions regarding landscape and biodiversity management. The species range moves, allowing it to follow the climatic envelope with the ideal conditions for its persistence (Walther et al. 2002; Parmesan and Yohe, 2003; Parmesan, 2006). Frequently the species range shifts poleward (e.g. northward in the northern hemisphere) (e.g. Parmesan, 2006), but this raises an important question: will the landscape allow such a shift? This question brings us to the second point relevant to this thesis: landscape connectivity and its impact on species range expansion (Saura et al. 2014).

The combination of both landscape and climate change poses major threats to the persistence of species (Hof et al. 2011; Opdam and Wascher 2004; Travis 2003), raising questions about the best conservation policies to slow down the ongoing biodiversity crisis.

The aim of this work, which uses the Cabrera's vole (*Microtus cabreræ*, Thomas, 1906) as model species, was to offer new approaches to improve Ecological Niche Models (ENM) and to consider simultaneously landscape and climate changes in projections of future species distribution, linking metapopulation dynamics at the landscape scale and species range shifts at regional and geographical scales.

1. Summary of the main findings

1.1. Potential future changes in the Cabrera's vole range

Previous knowledge about the Cabrera's vole distribution in Portugal and its environmental drivers (Mira et al. 2008) showed that the species prefers regions of intermediate annual rainfall, low to medium humidity and slightly acidic soils. Here, a much larger dataset was used, which resulted from i) updated data in Portugal after the paper by Mira et al. (2008), ii) inclusion of data from Spain, allowing a complete cover of all the species range (the Iberian Peninsula) and iii) additional data obtained during the field work, resulting in new locations of the species in 19 10x10 km square grids. The new models showed that the more suitable areas for the species have a precipitation around 50 mm during the warmest quarter of the year and in the wettest month, a mean diurnal temperature ranging between 10 and 12°C, a mean temperature of wettest quarter below 15°C, and a minimum temperature of the coldest month between -5°C and 0°C. This suggests that the Cabrera's vole is strongly influenced by precipitation and temperature (avoiding areas with excessive rain or high temperatures).

Araújo et al. (2011b), in a work about the impacts of climate change on Iberian vertebrates, revealed that the distribution range of the Cabrera's vole would probably suffer a northward shift, as generally expected for species in this hemisphere (Parmesan and Yohe, 2003). Here, as shown in the second chapter, a slight northward shift is also apparent, although the prevalent pattern is the fragmentation of the regions with climatic suitability. Additionally, chapter four considered three connectivity scenarios in the projection of the species future potential range. In this chapter the combined effects of landscape and climate changes on species persistence were evaluated. The projection of the ENM into the future, using two climatic scenarios developed in chapter two, showed the impact of climate change on species persistence, by depicting the geographical areas with ecological suitability for the species (Mestre et al. 2015). However, the species might not have the ability to colonize all the areas with higher suitability, due to the low species dispersal ability, landscape permeability and the existence of barriers to dispersal (Peterson et al. 2011). The spatially explicit dispersal model (SEDM), produced by MetaLandSim (Mestre et al. 2016), showed the probabilities of species future occurrence considering

its dispersal ability in three realistic scenarios of landscape connectivity (high, medium and low). Overall, results suggested that the species future distribution will be reduced, particularly under the low connectivity scenario. This decreases even more the suitable regions for Cabrera's voles, by considering the accessibility to every portion of the Iberian Peninsula. Chapter four thus allowed responding to the main research question raised by the thesis, regarding the combined effects of climate and landscape change on the future distribution of Cabrera's voles. By moving from a model solely based upon ecological variables (Chapter two) to one considering also reachability (Chapter four) we are shifting from "Ecological Niche Model" to "Species Distribution Model".

Generally, it can be concluded that Cabrera's vole will be very much affected by climatic variables (Mestre et al. 2015), since it depends upon habitats that occur in moisty soils (Santos et al. 2006). Currently, the species avoids the regions of the Iberia Peninsula that are dryer or that have higher levels of precipitation (Mira et al. 2008; Mestre et al. 2015). Furthermore, the fourth chapter also showed that landscape configuration and the species dispersal limitations might reduce even more the potential future distribution of the species (Mestre et al. *submitted*). This is particularly evident if we consider the low connectivity scenario which should greatly limit the species ability to expand its range.

1.2. Landscape dynamics and metapopulation density

The fifth chapter (fourth paper, submitted) builds on the second, by using MetaLandSim to simulate metapopulation dynamics on changing landscapes. It focuses on landscape-level changes and its effects on species persistence. In this chapter, a set of 54 virtual species, encompassing a variety of different metapopulation parameters and three successional preferences (early, mid, and late successional species), was used to evaluate the effects of habitat amount and patch turnover on population persistence. The main objective of this paper was to characterize the species and landscapes types that promote occupancy peaks at intermediate levels of landscape dynamics. It was expected to uncover species traits that would maximize occupancy of the landscape at intermediate levels of dynamism in a way consistent with the

“Intermediate Disturbance Hypothesis” (IDH) developed by Grime (1973). The virtual landscapes upon which the simulations were made encompassed several levels of proportion of suitable habitat (5, 10 and 20%) and landscape dynamics (0, 5, 10, and 20%).

Globally, a decreasing metapopulation density with higher landscape dynamics was found, as predicted. However, species preferring early successional stages were shown to be more resilient than species with medium and high successional preferences. Furthermore, our result also demonstrated that species with higher dispersal ability have higher metapopulation density at the end of the simulations.

The more relevant result, however, was the identification of the virtual species typology that exhibits an occupation pattern consistent with IDH-like responses to landscape dynamics. Generally, species with early successional habitat preference and under particular levels of patch turnover (5%) showed this type response. Regarding habitat amount and species dispersal, which were also highly relevant, those with mid to high dispersal abilities in landscapes with a proportion of at least 20% of suitable habitat and those with high dispersal ability with lower habitat cover (5%) showed IDH-like responses to landscape dynamics. So, it appears that there is some interaction between dispersal ability and habitat proportion in determining the maximum metapopulation density at intermediate levels of landscape dynamics.

The results of Kun et al. (2009) suggest IDH effects on species with limited dispersal abilities. However, the habitat available in these simulations was 40 and 60% of the landscape. This supports the idea that IDH effects should in part result from the interplay between habitat availability and species dispersal, being evident in species with long dispersal distances when habitat amount is small, and for species with low dispersal distances when habitat amount is high.

These species, which benefit from some degree of spatial dynamics, will not be negatively affected by landscape change, if it is kept below a given threshold. All the virtual species that showed IDH-like responses peaked metapopulation density at around 5% of landscape dynamics. Above this threshold the metapopulations tended to have a gradually lower density. Thus, when considering expansion of the range, the species with medium to high dispersal ability, that thrive in landscapes with dynamics around 5% might be considered pioneers that will expand easily into new available

habitats. However, if the landscape dynamics is over this threshold, then expansion into new regions will be impaired, making it difficult to follow the suitable climatic envelope.

1.3. Methodological insights

This thesis provides some innovative approaches. First of all is the approach taken to answer the research question in chapter two. In this chapter a step-by-step method was implemented in order to combine ecological niche modelling, field work and non-invasive genetics. Rather than only projecting the species potential future distribution, the objective was to do so effectively, gathering the best information provided by ecological niche modelling, field work and non-invasive genetics. A first ecological niche model (ENM1) was calibrated using all the occurrence data in Iberian Peninsula previously known for the species. Then, at the range margins defined by ENM1, field work was conducted in order to evaluate the species presence in 40 10x10 km square grids (20 inside the predicted range and 20 outside of it). Non-invasive genetics was used to confirm the species occurrence, since several species have similar presence signs (particularly *Microtus agrestis*, and to some extent *Arvicola sapidus* juveniles). Finally, with the new occurrences (19) and the previous dataset (391) a new ecological niche model (ENM2) was calibrated. Both ENM1 and ENM2 were projected into the future to three periods (2020, 2050 and 2080) and two IPCC climate scenarios (A1b and B2).

Although this is not an entirely new approach, since it draws from Guisan et al. (2006), it focuses more on sampling the range margins given by the first ENM. This option, to carry out the field work near the species projected range margins which were expected to represent also the ecological margins, is very relevant, since it aims to capture the extreme values of the species ecological niche, clarifying its boundaries. The second chapter confirms that the *Microtus cabreræ* range (geographical space) is a balanced representation of the environmental space (or ecological niche) of the species, since the additional field work at the range margins only slightly changed the species responses to extreme values of some ecological variables, suggesting that the species geographical distribution is limited by ecological, not geographical, factors. It succeeds in demonstrating that sampling areas close to the geographic limits of the range (but,

more importantly, which are in the limits of the species ecological distribution) enables the prediction of the species presence at areas with extreme values of its bioclimatic niche. It is important to mention here that the limits of the geographic range might not coincide with regions where the species is at its ecological extremes. This is due to the fact that there is not a direct translation between the geographic and ecological space due to effects of dispersal barriers, source-sink dynamics and/or species poor dispersal ability (Peterson et al. 2011). This improved modeling approach enables the refinement of the knowledge about a species' ecological niche, improving current and future model projections. Thus, by combining modelling, field sampling and non-invasive genetics, one can obtain a more reliable image of the future potential distribution, contributing to more informed conservation policies.

The MetaLandSim R package (Mestre et al. 2016), which provided tools for the following chapters, was a major output of this thesis. This package can be thought of as a virtual environment and a scenario-producing tool. It can be used at two scales: landscape (habitat network level) and biogeographic (species range level).

It is considered that landscape scale is the one where metapopulational dynamics take place, and MetaLandSim simulates these dynamics in changing landscapes, based upon Stochastic Patch Occupancy Models (SPOM) (e.g. Hanski, 1994, 1999). This is an innovative approach, since existing software packages simulate metapopulational dynamics in static landscapes (see supplementary material for comparison). Given the degree of human intervention, but also natural processes, landscapes are not generally static. Chapter five provides a good demonstration of the package usability at the landscape scale.

The biogeographic scale encompasses the full range of the focal species. At this scale the species distribution is determined by climatic variables, large scale barriers (e.g. mountain chains, rivers) and the species ability to expand its range (Peterson et al. 2011). MetaLandSim uses a simple upscaling approach to simulate such a range expansion. The algorithm implemented is based on the expansion of the species through several contiguous landscape units (square areas with landscape graphs), until the time steps considered for simulation are over. Within each landscape unit metapopulational dynamics are simulated resorting to SPOMs to emulate the natural processes. The transition rule between landscape units has been improved since the

publication of the paper. The transition from one landscape unit to the next is allowed when (and if) one patch located in an area strip delimited by the landscape unit adjacent margin and half of the mean dispersal ability for the species is occupied. If this occupation takes place, then the species will expand to the next landscape unit, where it occupies all patches in an area strip delimited between the adjacent margin and half the mean dispersal ability of the species in a proportion identical to the previous landscape. The repetition of such simulations allows the conception of a dispersal kernel which, in turn, is used to produce the dispersal model (DM), resulting from the evaluation of the species capacity to expand through successive landscape units. This DM can be coupled with an ecological niche model (ENM) in order to capture both the species ability to disperse and the climatic suitability. The first of these factors is influenced by the intrinsic dispersal ability of the species and by the landscape configuration. MetaLandSim allows a variety of connectivity, dispersal kernels, colonization, and extinction functions.

Chapter four is a good example of the applicability of MetaLandSim at the biogeographical scale. It demonstrated how joining the ENM and the SEDM produced by MetaLandSim, promotes the creation of a more accurate projection of species potential future distribution. This followed a scenario-building strategy by creating projections for 2050 and 2080 in two climatic scenarios (A1b and B2) and three landscape connectivity scenarios (high, medium, low). It provided a clear demonstration of the package use in producing SEDMs to limit the potential future species distribution considering reachability. Furthermore, MetaLandSim provides the critical link between landscape-level processes, such as landscape change, and biogeographical-level processes, such as the effect of climate on species range.

MetaLandSim is, in effect, a virtual environment, encompassing landscapes and species and allowing the implementation of virtual ecological experimentation in landscape ecology, a field that due to the spatial and temporal scales frequently considered is difficult to approach using traditional experimental techniques (Ims, 2005; Zurell et al. 2009).

2. Follow-up research

These modelling-based approaches are interesting in itself but, most importantly, they should have relevance for designing species conservation policies. The modelling outputs offer a valuable tool in informing conservation practitioners concerned with landscape and climate change impacts on biodiversity. Future research has to be concerned with continuously improving the estimates of future distribution and the integration of scales. This relates with several practical aspects of the design of conservation areas and connectivity corridors. Modelling is fundamental in answering questions related with, for instance, the size and number of areas and the location of connectivity corridors. It also relates with the question of which are the more adequate conservation policies considering the knowledge we have on the species biology and ecology (Alagador et al. 2014 and 2016; Ovaskainen, 2002b). It is fundamental to know the species spatial strategy to decide which is the adequate size of a reserve, the number of reserves and the maximum distance amongst them. This is where tools such as MetaLandSim might be very useful. Then, having the outputs of these modelling approaches, conservation practitioners should decide which are the optimal conservation strategies to the species, considering its spatial strategy and environmental preferences.

Furthermore, it might be relevant to evaluate if the current distribution of Cabrera's vole is affected by interactions with competing species and to what extent these could affect model projections (Araújo and Luoto, 2007; Wisz et al. 2013). Additionally, in what way can these interactions be evaluated and incorporated into the ENM procedure? This is also part of a much needed continuous effort to improve the modelling procedures, which should produce accurate results without making the whole process too complex. Modelling should be understood by the user and it should not be seen as a black box process.

Regarding the more theoretical questions addressed here, particularly in the fifth chapter, where virtual species are used to evaluate the Intermediate Disturbance Hypothesis how can we move to more realistic models, including, for instance, patch configuration (Vuilleumier et al. 2007), and/or the spatial arrangement and intensity of disturbances (Johst and Drechsler, 2003; Vuilleumier et al. 2007)?

Also, several additional improvements might be made to MetaLandSim. Amongst the most relevant are the consideration of spatial variation in the suitability of the landscape matrix and the development of more robust parameter estimation methods for the SPOM (e.g. adapting the functions of Risk et al. 2011).

Here the matrix was considered homogeneous, which is far from reality, but is a needed simplification. Models are a simplified representation of real world that should allow the user to understand which variable is causing an effect. For the purposes of the fifth chapter the matrix was not highly relevant, as the focal question concerned habitat patch dynamics. Introducing matrix heterogeneity would cause unnecessary noise, which would make the output more difficult to understand. However, several other research questions, related specifically with matrix permeability and heterogeneity, might be posed (e.g. Revilla et al. 2004 and Ricketts, 2001).

In what concerns the parameters estimation, MetaLandSim has a very simple approach, which is not ideal. However the focus of the package has been to act as a virtual environment where several competing scenarios might be simulated. The user has other available tools which make it possible to estimate the species SPOM parameters outside of MetaLandSim (e.g. Moilanen, 1999 and Ter Braak and Etienne, 2003). However, in an effort to make the package more complete, the parameter estimation utilities should be improved. This would not take an enormous amount of effort, since robust R functions are already available in the supplementary material of the package by Risk et al. (2011). These functions should be adapted to the package objects structure, and incorporated into MetaLandSim.

Other smaller improvements might also be made to the package, such as for example the consideration of real landscapes with the actual patch shape. Currently MetaLandSim considers landscapes to be graphs, e.g. nodes (habitat patches) which are interconnected. Differently from the traditional graph approach, however, these nodes only have a binary relation (connected/not connected) for graphical representation; the simulations procedure considers inter-node distance as a proxy for connectivity. But, since the habitat patches are circles in this graph-like landscape, the inter-node distance is dictated by the radius and Euclidian distance. To better approach real landscapes, MetaLandSim should account for patch shape. This has two practical consequences: i) the inter-node distance has to account for patches shape

and ii) the graphical representation has to depict the true patch shape. This might be useful if, rather than simulating on virtual landscapes, the user wants to simulate metapopulation dynamics on real landscapes, or if the user needs to derive connectivity metrics for a real landscape. Some users of MetaLandSim have expressed their interest in such an improvement.

In conclusion, this thesis was able to answer the proposed research questions regarding Cabrera's vole future potential distribution and to develop some new approaches to incorporate dispersal and landscape connectivity into the projections. Additionally it lays out future paths for research, which will certainly contribute to the improvement of modelling and simulation procedures, and to provide more accurate results for informed conservation policies.

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Scientific work

(2010-2016)

Publications included in the thesis

Mestre, F.; Pita, R.; Mira, A. & Beja, P. (*submitted*). **“Metapopulations, patch turnover and successional dynamics: When does intermediate disturbance favours species persistence?”** Submitted to *Oikos*.

Mestre, F.; Risk, B.; Mira, A., Beja, P. & Pita, R. (*submitted*). **“A metapopulation approach to predict species range shifts under different climate change and landscape connectivity scenarios”**. Submitted to *Ecological Modelling*.

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