



# RangeShifter

---

*Modelling eco-evolutionary dispersal dynamics &  
Investigating species' responses to environmental changes*

**Version 1.1 DRAFT**

**User Manual**

*Greta Bocedi*

*Stephen C.F. Palmer*

*Guy Pe'er*

*Risto K. Heikkinen*

*and Justin M. J. Travis*

---

April 2016



## How to use the RangeShifter manual

This manual serves as a reference guide and an introduction with tutorials for RangeShifter. The manual is split into three parts. The first main part (chapters [1](#) and [2](#)) introduces the conceptual basis of the RangeShifter package. The second main part (chapter [3](#)) provides a user guide, explaining how to use the software with a step-by-step guide to the different features of the program. This section is comprehensive, covering both standard and more advanced methods. The final section (chapter [4](#)) of the manual provides a set of tutorials designed to introduce the user to a broad range of the functionality that the package provides.

Different people have different learning styles, and this will likely influence the way in which you utilize the manual. While everyone is likely to eventually consult the range of material provided in the manual, different people will benefit more from starting in different places. Some of you will prefer to dive into the software at the first opportunity and will learn through so doing, consulting the manual as and when you run into difficulties or as and when you want to understand exactly what it is you are simulating. If this is your approach then you have a kinaesthetic learning style (you learn by doing) and you will probably want to start with the tutorials (chapter [4](#)), subsequently referring to the second section (chapter [3](#)) for help with using the software (we suggest you start at the Getting Started section) and dipping in and out of the first section as you want to find out more about the model concepts. Other amongst you will prefer to read through some material prior to opening the software and trying it out. For you, we recommend that you initially read the first part of the introduction and also the section from ‘Getting Started’. At the beginning of each tutorial we indicate to which earlier sections in the manual the tutorial relates, and you may want to read these before working through each tutorial, perhaps having the relevant sections in front of you as you work with the software. There may be yet more of you who would first like to read through all the concepts and the technical details before starting, in which case you are likely to read the manual more as a typical book, starting at the beginning and reading through to the end.



# Table of Contents

---

<b>1</b>	<b>Introduction</b>	<b>1</b>
<b>1.1</b>	<b>Background</b>	<b>1</b>
<b>1.2</b>	<b>Aim and purpose</b>	<b>5</b>
<b>1.3</b>	<b>Strengths and limitations</b>	<b>7</b>
<b>1.4</b>	<b>Changes in version 1.1</b>	<b>9</b>
<b>2</b>	<b>Concepts &amp; Methods</b>	<b>12</b>
<b>2.1</b>	<b>Model entities, state variables and scales</b>	<b>12</b>
2.1.1	Individuals	12
2.1.2	Populations	12
2.1.3	Landscape units	12
2.1.4	Spatial and temporal scales	13
<b>2.2</b>	<b>Model work flow / schedule</b>	<b>14</b>
<b>2.3</b>	<b>Landscape</b>	<b>16</b>
2.3.1	Imported landscape	16
2.3.2	Artificial landscape generator	16
2.3.3	Environmental gradient	17
2.3.4	Temporal environmental stochasticity	19
2.3.5	Local extinction probability	21
<b>2.4</b>	<b>Population dynamics</b>	<b>21</b>
2.4.1	Cell-based vs. patch-based model	22
2.4.2	Non-overlapping generations & no stage-structure	23
2.4.3	Overlapping generations & stage-structure	25
<b>2.5</b>	<b>Dispersal</b>	<b>35</b>
2.5.1	Emigration	36
2.5.2	Transfer	39
2.5.3	Dispersal kernels	39

---

2.5.4	Movement processes	42
2.5.5	Settlement	47
2.5.6	Dispersal mortality	50
<b>3</b>	<b>Using RangeShifter</b>	<b>51</b>
<b>3.1</b>	<b>Inputs</b>	<b>51</b>
3.1.1	Landscape	51
3.1.2	Species distribution	54
<b>3.2</b>	<b>The graphical user interface</b>	<b>55</b>
3.2.1	Main menu	55
3.2.2	Getting started	56
3.2.3	Setting the landscape	57
3.2.4	Importing a species distribution map	63
3.2.5	Environmental gradient	64
3.2.6	Setting the species parameters: population dynamics	65
3.2.7	Setting the species parameters: dispersal	73
3.2.8	Setting the simulation parameters	85
<b>3.3</b>	<b>Batch mode</b>	<b>100</b>
3.3.1	Control file	101
3.3.2	Parameter files	103
<b>3.4</b>	<b>Outputs</b>	<b>106</b>
3.4.1	Parameters	106
3.4.2	Species range	106
3.4.3	Occupancy	107
3.4.4	Populations	107
3.4.5	Individuals	108
3.4.6	Traits	110
3.4.7	Connectivity matrix	111

<b>4</b>	<b>Examples &amp; Tutorials</b>	<b>112</b>
<b>4.1</b>	<b>Exercise 1</b>	<b>112</b>
4.1.1	Species range expansion, long-distance dispersal and environmental stochasticity	112
<b>4.2</b>	<b>Exercise 2</b>	<b>118</b>
4.2.1	Landscape-scale connectivity, matrix permeability and dispersal behaviour	118
<b>4.3</b>	<b>Exercise 3</b>	<b>128</b>
4.3.1	Evolution of dispersal during range shifting	128
<b>4.4</b>	<b>Exercise 4</b>	<b>135</b>
4.4.1	Landscape-scale connectivity in batch mode	135
<b>5</b>	<b>References</b>	<b>142</b>

## Acknowledgments

We are grateful to all the colleagues and collaborators who provided help in testing and improving the software. This work was supported by the SCALES project (Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal, and Ecological Scales) funded by the European Commission as a Large-scale Integrating Project within FP 7 under grant 226 852 (Henle et al. 2012; [www.scales-project.net](http://www.scales-project.net)) and also by the Natural Environment Research Council, UK.



# 1 Introduction

---

## 1.1 Background

Multiple anthropogenic environmental drivers, including climate change and habitat loss and fragmentation driven by land-use changes, present major threats to species persistence (Parmesan et al. 1999; Warren et al. 2001; Davis & Shaw 2001; Travis 2003; Fahrig 2003; Parmesan & Yohe 2003; Thomas et al. 2004; Opdam & Wascher 2004; Fischer & Lindenmayer 2007; Lenoir et al. 2008; Araújo et al. 2011; Chen et al. 2011; Bellard et al. 2012). For conservation biology, developing strategies to mitigate the effects of environmental changes is a major challenge. There is increasing agreement that to manage biodiversity effectively facing these combined pressures, an integrated conservation approach is needed (Loss et al. 2011). This should include conservation of habitat area and quality (Hodgson et al. 2009, 2011), management for habitat connectivity (Krosby et al. 2010; Doerr et al. 2011; Hodgson et al. 2012), conservation genetics (Frankham 2009; Hoffmann & Sgrò 2011) and assisted colonization (Hoegh-Guldberg et al. 2008; Vitt et al. 2009; Willis et al. 2009a; Thomas 2011; Weeks et al. 2011).

Dynamic models of species' responses to environmental changes have the potential to become valuable tools for informing and effectively integrating these different management strategies. Such models should be based on solid ecological knowledge and understanding of species spatial dynamics produced by individuals' behaviours at local and landscape level, as well as on an understanding of the eco-evolutionary processes that shape species' ranges (Holt 2003; Norberg et al. 2012; Schurr et al. 2012; Thuiller et al. 2013; Travis et al. 2014). Although species may respond to environmental changes in many ways, the velocity and magnitude of current climate and habitat changes (Loarie et al. 2009) pose unprecedented challenges. Reduced gene flow across landscapes fragmented by land-use changes means that behavioural responses and micro-evolutionary processes are unlikely to be sufficient for local adaptation. Thus, geographical distribution changes will probably be one main type of the species' responses (Opdam & Wascher 2004; Huntley et al. 2010). However, the potential for species to expand their ranges into newly climatically-suitable regions will be inhibited by habitat fragmentation. Hence, understanding the synergy between climate change and habitat fragmentation and how species' interact with and move through the landscape is of primary importance. In particular, dispersal has been recognized as a crucial process that must be considered and better understood for making reliable projections of species' responses to

environmental changes (Hughes et al. 2003; Travis 2003; Kokko & López-Sepulcre 2006; Best et al. 2007; Brooker et al. 2007; McInerny et al. 2007; Mustin et al. 2009; Pöyry et al. 2009; Le Galliard et al. 2012a; Travis et al. 2014).

The past decade has seen an explosion of effort in trying to predict species' responses to environmental changes and their future distribution. The so-called 'climate envelope models' or 'species distribution models' (SDM) have been, and still are, the most used modelling methods (e.g. Thomas et al. 2004; Araújo et al. 2005; Thuiller et al. 2005, 2009). These are static statistical approaches that correlate the species' past and current distributions with multiple environmental variables in order to project the species' occurrence under future scenarios. Despite their massive use, the limitations of these methods are many, including the assumption that the observed species' ranges are at equilibrium with the environment, limited incorporation of demographic and dispersal processes, which ultimately affect the potential of species to track changing climates, and the lack of inter-specific interactions (Pearson & Dawson 2003; Guisan & Thuiller 2005; Heikkinen et al. 2006; Dormann 2007; Zurell et al. 2009; Sinclair et al. 2010; Dawson et al. 2011).

In the last few years, the limitations of SDMs in making reliable projections and management recommendations have been widely recognized, many authors advocating that key ecological processes, such as population dynamics and dispersal, be included in species' range models, moving towards the 'next generation of fully integrated dynamic models' (Thuiller et al. 2008, 2013; Engler & Guisan 2009; Franklin 2010; Gallien et al. 2010; Huntley et al. 2010; Higgins et al. 2012; Schurr et al. 2012). The integration of habitat suitability models with process based models will help to develop synthesis between the understanding of species-environment relationships derived from SDMs and the body of ecological and evolutionary theory that has developed recently focusing on eco-evolutionary dynamics of species' ranges (Dormann et al. 2012). This opens exciting new opportunities for improving our knowledge of how species' are likely to respond to potentially synergistic impacts of multiple environmental drivers, such as habitat fragmentation and climate change. Indeed, some progress has already been made towards the integration of SDM approaches and ecological theory and 'hybrid' models are starting to be developed (Keith et al. 2008; Anderson et al. 2009; Midgley et al. 2010; Zurell et al. 2012; Conklin et al. 2013). These models use the two methods sequentially by, for example, running dynamic models of varying complexity on the top of habitat suitability maps derived from SDMs. They are an interesting attempt to

integrate the two approaches, but their actual utility is source of current debate. While on the one hand some authors consider them as a step before the full integration of SDM and dynamic demographic models and in many cases the best we can do due to data limitations (Gallien et al. 2010), others argue that they incorporate the shortcomings of both approaches without overcoming them, and that, in some cases, they actually exacerbate the problems (Dormann et al. 2012; Schurr et al. 2012; Schymanski et al. 2013).

To make greater progress, we need models that take better advantage of the increased understanding that we have now gained relating to key processes, particularly movement and dispersal (e.g. Travis et al. 2014). Dispersal is typically treated extremely simplistically even in the recent models projecting future species ranges. This is a major drawback in many models (Travis et al. 2014), which is surprising when related to the substantial recent progress in understanding and modelling dispersal (Clobert et al. 2012; Travis et al. 2012). A useful approach for dispersal modelling is applying a framework which treats dispersal as three phases, emigration, transfer and settlement (Travis et al. 2012). This approach offers considerable potential for dynamic models exploring the response of species to multiple environmental drivers, as it allows for context-dependencies that may act on anyone of these stages to be represented. There is strong evidence that animal behaviours in each of these stages can be directly and/or indirectly impacted by climate (Travis et al. 2014). Some aspects of eco-evolutionary theory have been developed to account for these three phases of dispersal, and first demonstrations showing the importance of the three phases for range expansion dynamics have emerged, but the approach has not yet been used in an applied ecological or conservation biological context. Of particular importance for the transfer phase is the concomitant development of movement modelling alongside the much greater availability of data on animal movement trajectories. Coming from the growing field of movement ecology (Nathan et al. 2008; Jeltsch et al. 2013), there has been a recent call for integration of movement modelling and population dynamics (Morales et al. 2010). One reason to seek this integration is to increase our understanding and ability to manage how species will respond to environmental changes.

Clearly, increasing the degree of detail and realism a model incorporates provides substantial challenges in terms of parameterization, even when the number of additional of parameters is minimized. One important role that more complex models can play is to help identify those processes for which the inclusion of greater detail offers the most significant returns in terms

of reducing uncertainty in the outcomes. This can help the allocation of efforts on collecting empirical data which is critically important for model parameterization. It is timely that, at least for some processes, we now have improved technology that can aid in collecting the data required to estimate potentially key parameters. For example, in the case of dispersal, the ability to track animals at fine spatial and temporal resolution has advanced extremely rapidly (Cagnacci et al. 2010), providing the scope for directly estimating movement parameters of the transfer phase for an increasing number of species. However, we are unlikely ever to have the resources to collect high-quality data for all of the large number of species for which SDM approaches have been used to make range-shift projections. Thus, to run more complex models for large sets of species, alternative approaches to parameterization will be required. A promising approach is to use Bayesian methods to infer the parameter values for the demographic model using the same occurrence data that are used in SDMs (Pagel & Schurr 2012). For models where the representation of dispersal and demography is particularly complex, approximate Bayesian computation may offer a potential solution (Beaumont 2010).

Our belief is that the next decade will present opportunities for major advances in our understanding of, and abilities to predict, how species will respond to environmental change. This belief is due to the simultaneous advances that have been made across several different fields in the last decade. First, the species distribution modelling community has developed excellent data sets on the spatial and temporal distributions of species and sophisticated statistical methods for dealing with complex data (Thuiller et al. 2005; Elith & Leathwick 2009). Second, theory on ecological and evolutionary dynamics has advanced substantially, such that we now have greater insights into the processes which are likely to have a substantial impact on range dynamics (Holt 2003; Hastings et al. 2005; Excoffier et al. 2009; Sexton et al. 2009; Schurr et al. 2012). Third, rapid advances in technology mean that there are now more opportunities for obtaining estimates of key parameters required for modelling important eco-evolutionary processes (Broquet & Petit 2009; Cagnacci et al. 2010). Fourth, statistical approaches for linking dynamic models to different sources of data have been developed (and continue to develop rapidly) (Beaumont 2010; Hartig et al. 2011, 2012). To take advantage of these advances we require flexible dynamic modelling platforms which can represent the ecological and evolutionary processes that theory is highlighting as being important, and that can be parameterized using the increasingly available data. In essence, we need platforms that can readily be applied by multiple users; whereas there are various

widely-used and user-friendly packages for SDMs, there is currently a lack of availability of dynamic modelling platforms, especially in terms of incorporating complex dispersal and inter-individual variability. As dynamic modelling platforms are introduced, we envisage the rapid development of methods for integrating them with the inverse fitting approaches offered by Bayesian techniques such as approximate Bayesian computation. Thus dynamic modelling platforms can act as a vehicle for integrating several major disciplines, which together may offer huge potential for improving our ability to understand and manage biodiversity under multiple environmental drivers.

## **1.2 Aim and purpose**

The RangeShifter model has been developed in response to the recent calls for dynamic models of species' range dynamics and for models that integrate movement and spatial population dynamics. The overall aim is to provide a modelling platform that can be used for investigating species' ecological and evolutionary responses to environmental changes. It is a single species, spatially-explicit and stochastic individual-based model (IBM), built around the integration of two fundamental components: population dynamics and dispersal behaviour. It has been conceived as a flexible modelling platform to facilitate investigations of theoretical as well as applied questions at different spatial scales (from local to regional) and by considering different levels of details in the processes that are modelled.

Population dynamics (which can be represented at different levels of complexity from a simple non-overlapping generations and only-female population model to more complex sexual and stage-structured models) and dispersal (explicitly modelled in its three phases of emigration, transfer and settlement accounting for context-dependencies and sex/stage specificity) are played out on top of gridded multi-habitat landscapes. These landscapes can be real or artificial, and there is additionally the possibility of simulating environmental gradients and environmental stochasticity. Individuals are the basic entity of the model, and options for inter-individual variability in dispersal traits and their evolution is included. The simulation platform's modularity and flexibility make RangeShifter suitable for a variety of purposes.

There are two broad categories of questions for which we envisage RangeShifter being used. First, it can serve as a basis for developing new theory and testing hypothesis on eco-evolutionary dynamics of species' ranges as well as on how species respond at a more local scale to environmental pressures. Examples of typical questions that can be addressed are:

- What is the influence of individual heterogeneity in dispersal strategy on the persistence of populations occurring in complex landscapes?
- How does the level of habitat fragmentation and/or temporal environmental stochasticity influence the evolution of dispersal traits?
- Will our projections of species' range dynamics change when taking the possibility for 'evolutionary rescue' at macro-ecological scales into account?

Secondly, from the applied side, RangeShifter can be a tool for identifying obstacles to species' persistence and range shifts (e.g. lack of functional connectivity) and for exploring the relative effectiveness of alternative management interventions in different contexts, assisting the realization of integrated and dynamic conservation strategies. Importantly, it can be used as means for identifying data gaps, where lack of accurate estimates of particular parameters can be identified as crucial in understanding the responses of a particular system to environmental changes. Another useful aspect is the possibility of *in silico* testing of different methods, for example, in assessing functional connectivity or in designing networks of protected areas. By and large, RangeShifter can be employed both as a model for investigating general strategies and methods regarding conservation/management issues, as well as a tactical model specifically tailored for a particular species in a particular system.

Note that we caution against the use of RangeShifter as a predictive model to be used for projecting where individual species will be under future climate change scenarios. We do not believe that dynamic modelling approaches have matured sufficiently to make robust projections of the future biogeographic ranges of species. Despite this note of caution, we believe that a bottom-up approach, where patterns emerge from processes, is the way that will critically help to improve our predictions on future species' distributions. We anticipate that ultimately much more robust estimates of species' future ranges will be provided by dynamic models such as RangeShifter than is possible using SDMs. However, in its present form, RangeShifter lacks two modules that would be crucial for that goal: inter-specific interactions and a functional relationship between demographic / dispersal parameters and climate variables, the integration of which will be a key target in the next generation version of the

platform. Despite this, we believe that RangeShifter already provides a platform that can significantly contribute to the understanding of which processes are important to consider in any future attempts to make species-specific projections.

### **1.3 Strengths and limitations**

Throughout the manual there are explicit and implicit references to the strengths and limitations of RangeShifter. However, it is useful to bring them together in one concise section. Thus, here we will summarize the strengths and limitations of the current version, RangeShifter 1.1. We anticipate that some of the limitations of this version will be addressed in future work, such that the same topics may become strengths in a future version.

The key strengths of RangeShifter, as we see them, are:

1. It provides a platform for rapidly transferring the development of eco-evolutionary theory towards applied questions. The software has deliberately been designed to facilitate pure theory development, but also to allow applied questions focusing on, for example, single species of conservation concern to be addressed. We hope RangeShifter can help to reduce the lag from theory development to its application (Benton et al. 2007).
2. RangeShifter provides an implementation of the new eco-evolutionary framework for modelling dispersal, and in so doing also tackles the challenge to integrate progress in movement ecology with spatial population dynamics (Morales et al. 2010; Travis et al. 2012). There are so far very few papers that model dispersal explicitly as a three-stage process and also very few that explicitly model movement behaviours during dispersal. Incorporating this complexity of movement is a major strength of RangeShifter, which helps to facilitate rapid increase of understanding about the causes and consequences of the complex three-phase dispersal strategies. In an applied context, this integration will also facilitate improvements in how we protect and manage habitat networks and landscapes for functional connectivity.
3. RangeShifter incorporates the possibility for sophisticated stage-structured population dynamics. This enables linking classical stage-structured matrix models with spatial dynamics. In particular we highlight two major advantages here. First, the adoption of the stage-structured modelling framework used in analytical matrix modelling allows for cross validation between the analytical and IBM approach. Second, RangeShifter

allows complex stage-structured population dynamics to be linked to sophisticated dispersal models and provides a platform to run them over complex landscapes.

4. RangeShifter provides a platform for simulating, at a broad range of spatial scales, species responses to alternative management strategies. It is an important advantage that the platform can be used for questions at the scales that most metapopulation models and population viability analyses (PVAs) have previously considered, but also can be used for the much larger spatial scales at which SDMs typically operate. This will facilitate the inclusion of those processes known to be influential at landscape scales into models informing management at much larger spatial extents.
5. RangeShifter has been designed with a user-friendly graphical user interface and runs under Microsoft Windows<sup>1</sup>. Thus, a flexible and sophisticated platform for simulating spatially-explicit eco-evolutionary dynamics is now available for potentially wide use. Until now, most IBMs used in ecology have been developed and used by individual ecologists with programming skills, whereas SDMs, matrix models, PVAs, metapopulation models, representation algorithms for spatial planning, etc. have been made available as user-friendly software packages designed for wider use.

The current limitations of RangeShifter, as we see them, are:

1. RangeShifter will be challenging to parameterize, especially when it is run for simulations incorporating substantial eco-evolutionary realism. Compared to some alternative models, it will often be much more parameter-hungry. However, methods are becoming available for direct and indirect estimation of parameters for moderately complex dynamic models (Beaumont 2010; Hartig et al. 2011; Dormann et al. 2012; Schurr et al. 2012) and we anticipate that the next five to ten years will see major progress in this field.
2. RangeShifter does not yet provide for functional relationships between its demographic or dispersal parameters and climate variables. When applying RangeShifter to study how species distributions will shift under climate change scenarios, this represents an important limitation. However, it is not unique to this software; indeed, the question of how to build these relationships and parameterize them is one of the most important currently being debated by the field. Technically, it will be relatively straightforward to add the linkage between life-history parameters

---

<sup>1</sup> Tested at the time of writing under Windows XP and Windows 2007

and climate variables when the methods have sufficiently matured to merit inclusion. RangeShifter can then provide an ideal platform for simulating the response of species to the synergistic impacts of climate and land-use changes.

3. RangeShifter does not include inter-specific interactions. There are many theoretical and applied questions for which inter-specific interactions may play an important role (Gilman et al. 2010; Hellmann et al. 2012; Singer et al. 2012; Urban et al. 2013; Wisz et al. 2013). However, the individual-based approach taken can be readily extended to run for multiple species simultaneously, and indeed, we have already explored methods for doing this in a theoretical exercise (Bocedi et al. 2013). During the two years 2013-2014, determining the ideal way to include both competitive and trophic interactions in RangeShifter is a major focus of work, and a working-group (funded by sDiv, Leipzig, Germany and Diversitas: see [link](#)) has this as a primary objective.
4. While RangeShifter can be run in batch mode, it has not yet been adapted to run on a cluster of processors. For some applications where, for example, considerable eco-evolutionary detail is desired in models run at large spatial extent, this will be an important future development. Currently the software is implemented to run in Microsoft Windows and this has major advantages in terms of usability (see point 5 above), but in the future a linux / unix version is likely to be desirable.
5. RangeShifter is a complex platform and provides substantial flexibility for the user. While this clearly is a strength it can also be a potential drawback. The danger is that some users will apply the software, generate and report results without fully understanding the assumptions that they are making as they set up their particular model. This is an inevitable risk with almost any modelling software, and we seek to minimize this risk by providing a comprehensive user manual. We have also introduced substantial internal checks in the software to catch some erroneous parameterizations. Additionally, we will run workshops introducing the user community to the software and, as far as is possible, will provide support to users.

## 1.4 Changes in version 1.1

As far as the user is concerned, the changes from v1.0 to v 1.1 appear limited, but internally the changes to the code are substantial, principally to prepare for future increased functionality, notably the modelling of species interactions and incorporation of explicit genetics. Users of v1.0 are therefore strongly encouraged to check that previous simulations produce similar results if run in v1.1 (note that they cannot be expected to be identical, as

RangeShifter is stochastic, and replicated simulations differ). Note that figures showing images from v1.0 have been retained in the manual if there has been no change in v1.1.

However, there are some functional changes introduced in v1.1, the principal ones being:

1. Although batch mode may still be invoked from the *File* sub-menu of the Main Menu screen, there is now a separate batch version of RangeShifter ([see 3.3](#)), which can be started, for example, by an automated scheduling routine. There is a new batch parameter BatchNum, which is used in all output file names, thereby enabling more than one batch within the same working directory to use the same range of simulation numbers without overwriting existing files.
2. The Landscape screen has been changed in several ways ([see 3.2.3](#)). When importing a raster landscape holding habitat codes, it is no longer necessary to specify the number of habitats or their code values prior to selecting the raster file. These data are now read directly from the file, after which the habitat codes table is displayed, and an option provided to change colours. For a patch-based landscape, the patch raster map selection dialogue is presented immediately after selecting the habitat raster map.
3. The habitat suitability option for an environmental gradient has been removed ([see 3.2.5](#)). The gradient is now applied on a scale of 0 to 1, where a value of 1 occurs at the gradient optimum, enabling it to be applied in similar fashion to habitats having different maximum carrying capacity or to population stages having different maximum fecundity.
4. The interpretation of minimum ages in a stage-structured population has been altered ([see 3.2.6](#)).
5. Two new options introduced for the Stochastic Movement Simulator ([SMS](#)) transfer model enable directional persistence to be determined over more than only the previous step and a dispersal bias away from the natal location to be applied.
6. Two new [initialisation rules](#) options are provided. The initial population density can be set to half carrying capacity. For a stage-structured population, there is an option to set up a quasi-equilibrium distribution of initial ages within a stage, which is based on the likely number of years an individual will remain in the stage and the (female) survival rate for the stage. This is useful for long-lived species which may spend many years in a sub-adult non-breeding stage; the more realistic initial distribution of

ages prevents an excessive rate of recruitment to the breeding population in the initial year(s) of the simulation, which in turn can lead to an initial surge in reproduction.

7. For a cell-based model, co-ordinates written to output files (except the range file) are now in terms of cell units (i.e. column and row number) rather than real-world co-ordinates in order to reduce the volume of data written to file. They may be converted to real-world co-ordinates by multiplying by the landscape resolution and adding the co-ordinates of the lower left corner (as specified in the header records of the raster input file)

## 2 Concepts & Methods

---

### 2.1 Model entities, state variables and scales

#### 2.1.1 *Individuals*

Individuals are the basic entities of the RangeShifter model. Each individual has a unique ID number and is defined by the following state variables:

- status (alive or dead; dispersal mode: resident, dispersing or settled)
- initial (natal) and current location
- sex (in the case of sexual models)
- age and stage (in the case of stage-structure models)
- dispersal traits (in the case of inter-individual variability; these can include: emigration probability or emigration reaction norm to density, mean dispersal distance or step length and correlation)

#### 2.1.2 *Populations*

Populations are defined by the individuals occupying either a single cell or a single patch (for cell- vs. patch-based models [see 2.4.1](#)) and they represent the scale at which individuals interact and density dependencies act. Populations are characterized by their size and location and, where applicable, by the number of individuals of each sex and/or the number in each stage class.

#### 2.1.3 *Landscape units*

The model runs over grid-based maps. Depending on the settings of a particular modelling exercise each cell stores a particular land-cover type (which can be breeding habitat for the species or otherwise), proportions of different land-cover types or habitat qualities ([see 2.3](#)). Each cell is defined as suitable or not suitable for a species based on the presence/absence of habitat, and it is characterized by a species' local carrying capacity (or nature of demographic density dependence in the stage-structured version) and by the species presence. Depending on the setting, additional state variables are: cost of movement through the cell (see 2.5.4, [SMS](#)), local deviation from a large-scale environmental gradient ([see 2.3.3](#)), local extinction probability and an environmental noise value  $\varepsilon$  in case of local environmental stochasticity ([see 2.3.4](#)).

If the model is run as patch-based, the patch is a higher-level entity composed of a group of adjacent cells ([see 2.4.1](#)). A single patch is characterized by a unique ID number, the number of cells that it contains, a list of these cells' coordinates and its maximum and minimum x and y coordinates. In the patch-based model, species' presence, species' local carrying capacity (or demographic density dependence) are characteristics of the patch and not of the single cell.

#### **2.1.4 Spatial and temporal scales**

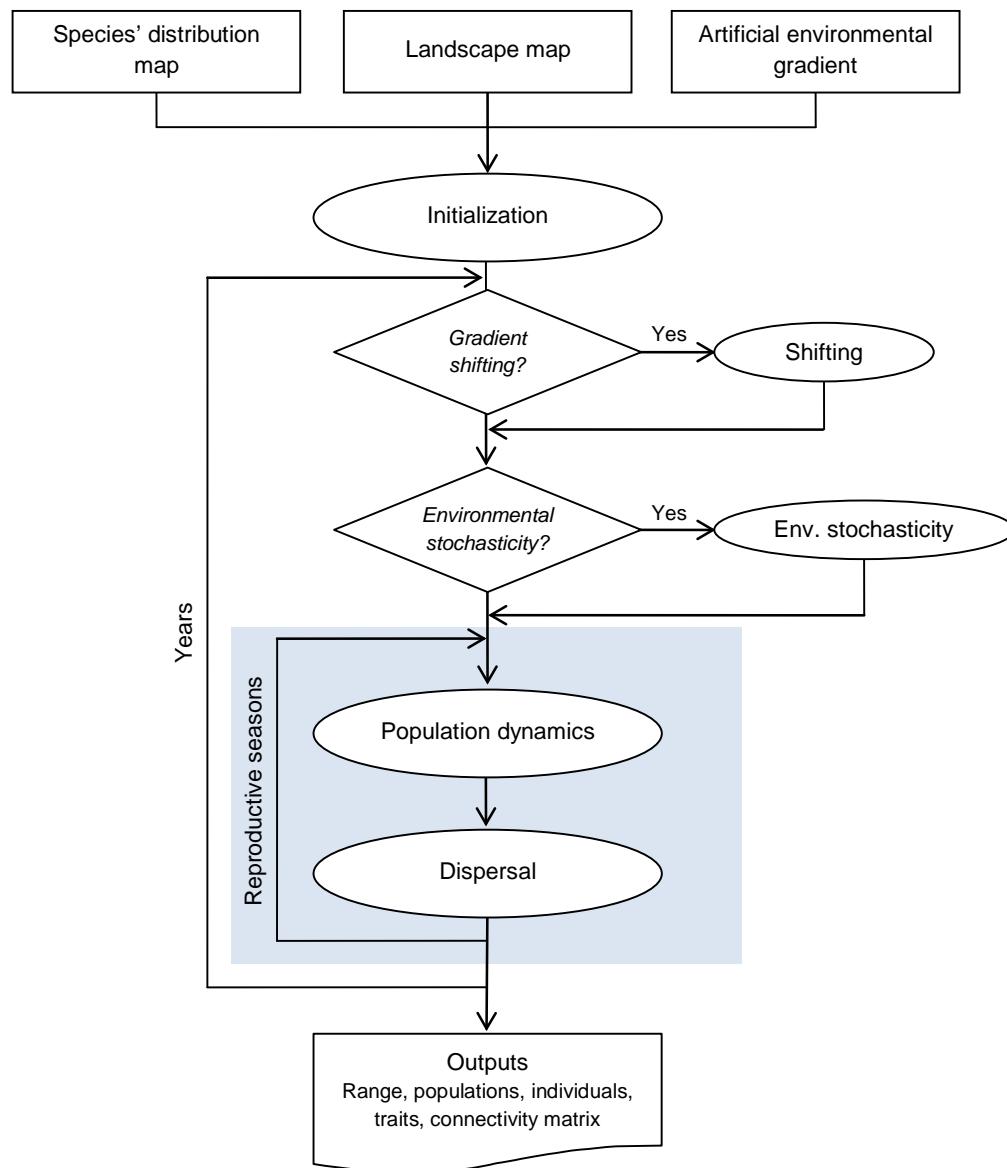
The cell size (resolution) is specified by the user in meters. It is important to note an essential difference in spatial scale between the cell-based and the patch-based version. In the cell-based model, the cell resolution represents the spatial scale at which the two fundamental processes of population dynamics and dispersal happen. This means that all the density-dependencies in the model (reproduction, survival, emigration, settlement, etc...) act at the cell scale and the same scale is used as a single step unit for discrete movement models. In the patch-based version, two spatial scales are simultaneously present: the cell scale, which in this case is used just for the transfer phase of dispersal (movements) and the patch scale, at which the density-dependences are acting. The choice of type of model and cell resolution (as well as the definition/scale of patches) is of fundamental importance because, depending on the system and on the question being tackled, it can systematically bias the outcomes of the model (Bocedi et al. 2012b).

The spatial extent that the software is able to handle is variable, and depends on the cell resolution, the amount of information related to each cell and the amount of random-access memory (RAM) available in the computer used to run the program. As an example, when we run models similar to that presented in Tutorial 1 for the extent of Great Britain at 1km resolution, we are able to simulate up to 10 million individuals on a laptop with 4GB of available RAM. Note however that these are simple individuals, each storing limited information, and that substantially fewer individuals could be simulated on the same machine were they holding more information about themselves (e.g. on their dispersal strategies, etc).

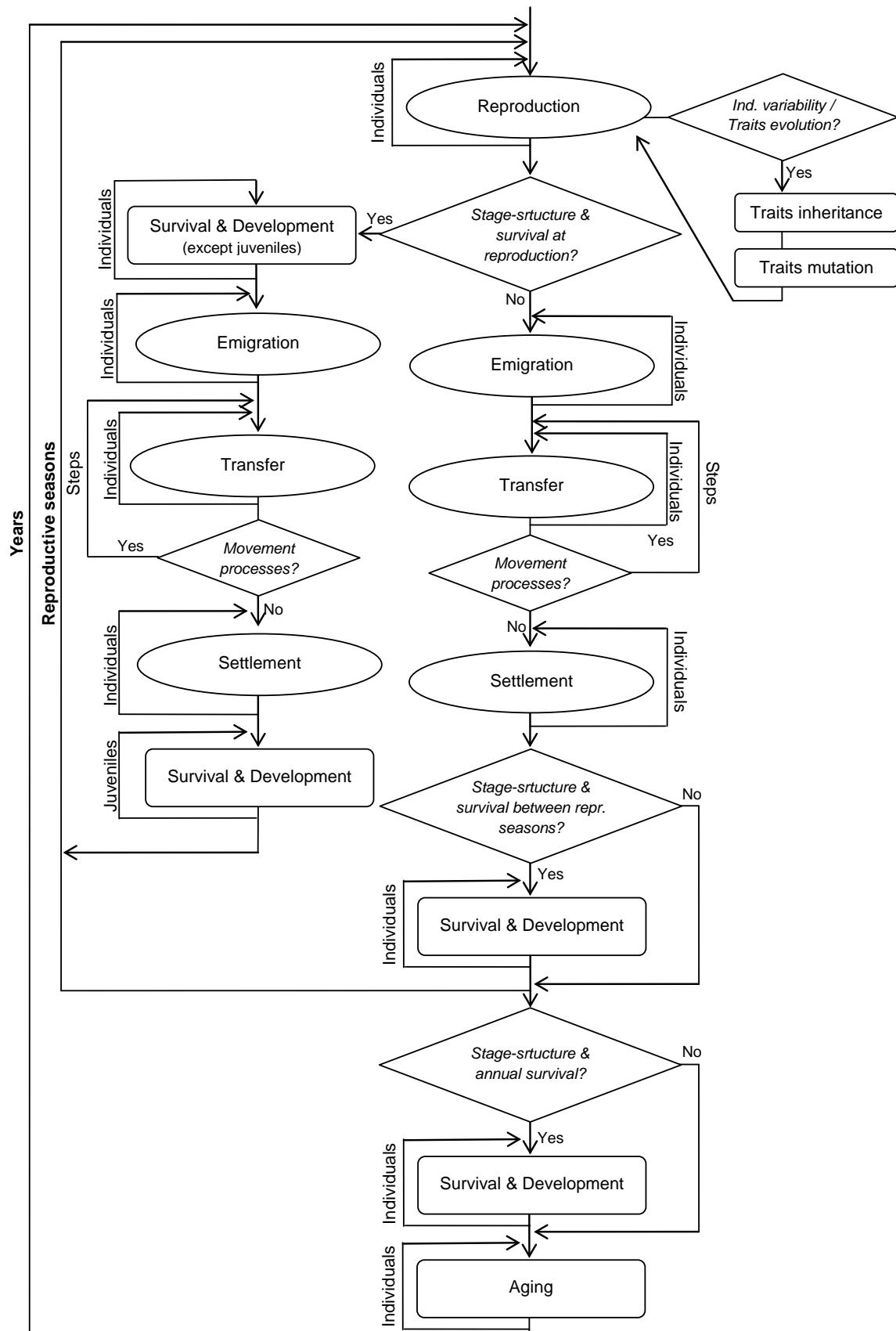
The user also defines the temporal scales. There are three distinct temporal scales. The highest-level one has years as units and represents the scale at which variations in the abiotic environment are modelled (RangeShifter does not explicitly model within-year variability in conditions). The intermediate scale is the species' reproductive season. The model can be used to simulate the case where there is only one reproductive season per year but it is also

possible to simulate situations where there more than one per year or only one every  $N$  years. A single reproductive event is always followed by dispersal (see [section 2.5](#) for more details). Finally, the smallest time scale is represented by the number of steps that emigrants take during the movement phase of dispersal. This can be determined by a maximum number of steps, per-step mortality or both ([see 2.5.4](#)).

## 2.2 Model work flow / schedule



**Figure 2.1.** General model workflow and schedule. The core of the model, highlighted in blue, is expanded in the flow chart in Figure 2.2.

**Figure 2.2.** Flow chart of the core model.

## 2.3 Landscape

### 2.3.1 Imported landscape

The model can be run on real landscape maps that can be imported into RangeShifter provided that they are files in the standard ArcGIS raster export format ([see 3.1.1](#)).

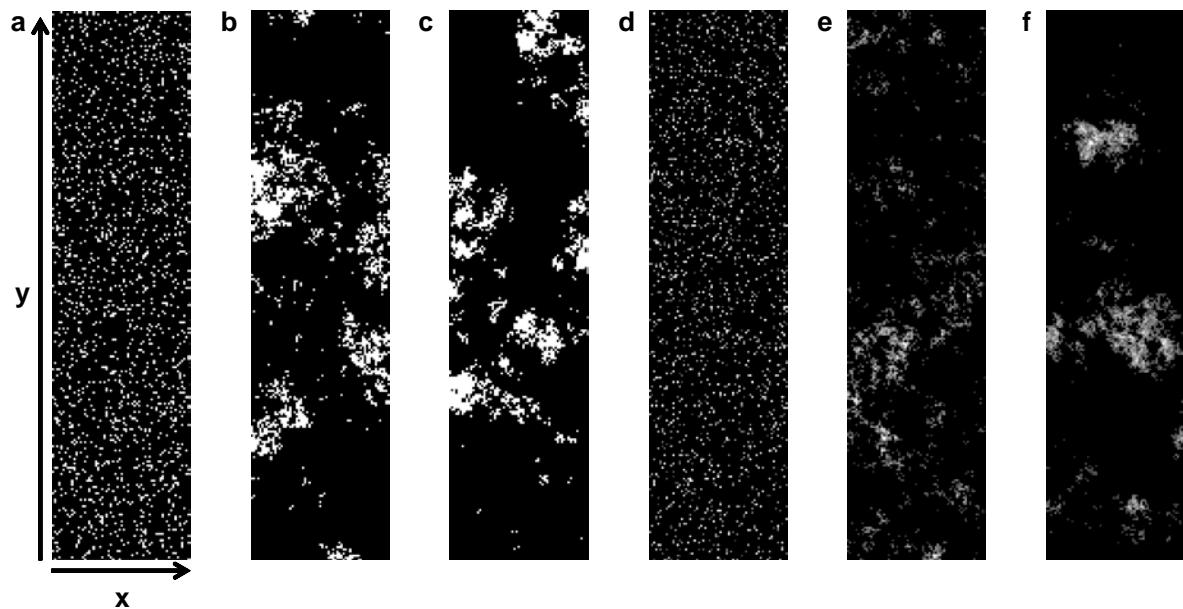
### 2.3.2 Artificial landscape generator

For theoretical studies which might be related to fundamental questions in eco-evolutionary dynamics or strategic questions concerning conservation ecology, it is often desirable to use artificial landscapes.

RangeShifter can import artificial landscape that have been generated by other generators (e.g. Qrule, Simmap, Dinamica, G-RaFFE – see review by Pe'er et al. 2013), or can use an embedded landscape generator for producing single-habitat neutral landscapes. Landscapes generated using the embedded algorithm can be completely random, where each cell has a certain probability of being a habitat, or fractal. To generate fractal landscapes, the midpoint displacement algorithm (Saupe 1988) is applied, adapted to allow for the generation of elongated landscapes (useful for theoretical studies on range shifting and environmental gradients; Figure 2.3). Landscape structure is determined by two parameters: the proportion of landscape occupied by suitable habitat ( $p$ ) and the degree of spatial autocorrelation (Hurst exponent,  $H$ ) which ranges from  $> 0.0$  (low autocorrelation but still not completely spatially independent) to  $< 1.0$  (high autocorrelation, i.e. high habitat aggregation). The resulting landscape can be discrete and binary, or continuous. In the first case, the cell is either suitable (with 100% habitat cover) or not; in the second case, each cell is given a continuous value describing the percentage of habitat cover within a cell. Note that more complex algorithms are available for providing fractals where setting  $H = 0.0$  results in no spatial autocorrelation (see Chipperfield et al. 2011). For applications where this is a required property, we recommend users import landscapes generated by these alternative algorithms.

This fractal method has proven useful as a null model to investigate population responses to landscape changes such as habitat loss and fragmentation (With & King 1999; Plotnick & Gardner 2002). Fractal landscapes are characterized by possessing greater structure than a completely random landscape, but less than a completely deterministic one (With 1997) – but note that the spatial structure of landscapes fragmented by human activities is often not

fractal in nature and, depending upon the research question, other landscape generators may be more appropriate (Pe'er et al. 2013).



**Figure 2.3.** Examples of artificial landscapes generated with RangeShifter. (a-c) Discrete landscapes: white = suitable habitat; black = unsuitable habitat. (d-f) Continuous landscape: black = unsuitable habitat; grey scale = percentage cover of suitable habitat, from 1% (dark grey) to 100% (white). (a,d) Random landscapes. (b,e) Fractal landscapes for which  $H = 0.1$ . (c,f) Fractal landscapes for which  $H = 0.3$ . In all cases the proportion of cells with habitat cover greater than zero is 0.1.

### 2.3.3 Environmental gradient

In modelling species' distribution and responses to environmental changes it is often important to consider environmental gradients, i.e. gradients in one or more abiotic and/or biotic variables that affect the ecology of species and their evolutionary dynamics (Travis & Dytham 2012).

Often species' ranges are structured along gradients and gradients are thought to be one of the contributing factors in determining species' range limits (Holt 2003; Holt et al. 2005; Thomas 2010; for reviews: Gaston 2009; Sexton et al. 2009). The ecology of a species', including for example vital rates and competitive abilities, can change along environmental gradients. Often the most suitable conditions are found at the core of a species' range and gradually decline along the gradient until the environment is no longer suitable for the species. The nature of the gradient can impact the dynamics, potentially leading to different responses to environmental changes (Brooker et al. 2007; Mustin et al. 2009). Moreover, populations along gradients can show adaptation to local conditions (Hereford 2009; Franks & Hoffmann

2012), which, in interaction with other factors such as inter-specific interactions, can determine complex dynamics and responses to climate change (Atkins & Travis 2010; Bocedi et al. 2013; De Block et al. 2013; Kubisch et al. 2013).

From the evolutionary point of view, environmental gradients often generate selection gradients. In the last few years, a few studies have investigated the evolution of dispersal along gradients in stationary ranges (Dytham 2009; Kubisch & Poethke 2011) and during range expansion (Kubisch et al. 2010) or range shifting (Henry et al. 2013). Different types of gradients determine the relative advantage of different dispersal strategies leading to different strategies becoming spatially structured along the gradient. During range shifting, evolving dispersal strategies are likely to interact with the ability of the species to adapt locally, determining obscure outcomes (Bridle & Vines 2007; Phillips 2012; Schiffers et al. 2013).

In RangeShifter, it is possible to superimpose an artificial gradient on top of the landscape map (this being either real or artificial). Gradients are implemented for cell-based models only; in the current version it is not possible to use gradients with patch-based models. The gradient must be imposed along the north-south ( $y$ ) axis and the conditions for the species decline linearly with distance from an optimum location. Three of the four types of gradients used in recent studies (Dytham 2009; Kubisch et al. 2010; Henry et al. 2013) are implemented in RangeShifter: decreasing carrying capacity ( $K$ ), decreasing growth rate ( $r$ ) (or fecundity ( $\phi$ ) in the case of stage structured models), and increasing local extinction probability. Gradients are implemented following the method of Travis & Dytham (2004) which combines linear variability with local heterogeneity. If  $E$  is one of the gradient variables listed above, the value of  $E$  for a cell with  $x$  and  $y$  coordinates is given by the following equation:

$$e_{(x,y)} = 1.0 - |y - y_{opt}| / G + U(-1.0, 1.0)f \quad \text{eqn. 1}$$

$$\text{and} \quad E_{(x,y)} = E_{opt} * e_{(x,y)} \quad \text{for } K \text{ and } r$$

$$E_{(x,y)} = 1.0 - e_{(x,y)} + E_{opt} \quad \text{for extinction probability}$$

where  $E_{opt}$  is the value of the variable at the gradient optimum for the species,  $|y - y_{opt}|$  is the distance from the cell to the optimum and  $G$  is the gradient steepness.  $e_{(x,y)}$  is constrained to be  $\geq 0.0$ ; any negative value is set to zero. A random number between -1.0 and 1.0 gives the local quality of the cell and the scaling factor  $f$  determines the magnitude of local variation relative to the gradient value.

For example, consider a gradient in carrying capacity with  $K_{opt} = 100$  individuals/ha. The following table shows the value of  $K$  for a cell that is 10 cells away from the species' optimum when varying  $G$  and  $f$ :

<b>G</b>	<b>f</b>	<b>K</b>
0.01	0.0	90
0.01	0.01	$89 \leq K \leq 91$
0.01	0.1	$80 \leq K \leq 100$
0.05	0.0	50
0.05	0.01	$49 \leq K \leq 51$
0.05	0.1	$40 \leq K \leq 60$

The gradient in fecundity  $\phi$  applies to the fecundity of each stage.

It is also possible to simulate the shifting of the gradient. Here the position  $y$  of the species' optimum is shifted northwards at a given rate  $v$ .

#### 2.3.4 Temporal environmental stochasticity

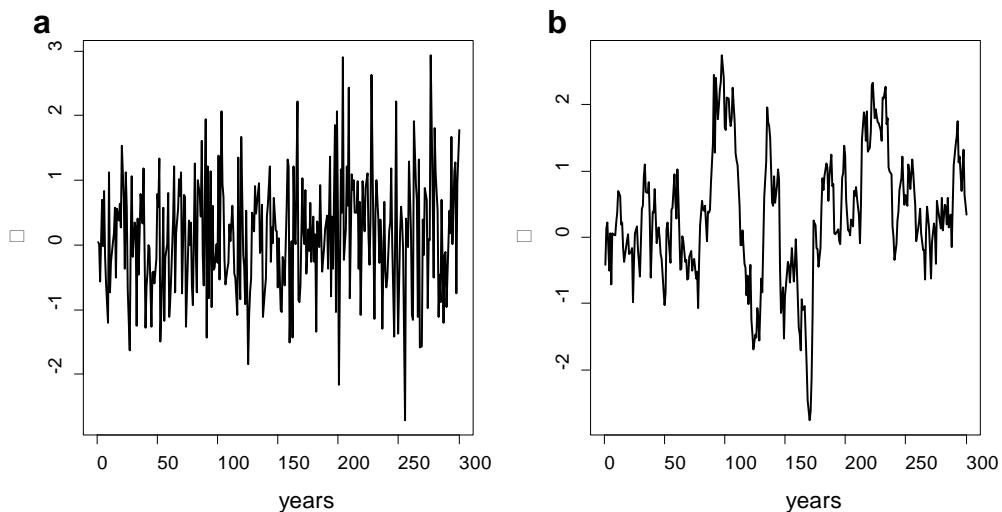
Temporal environmental stochasticity is a ubiquitous and fundamental factor affecting both ecological and evolutionary processes acting at all levels of biological organization, from individuals to ecosystems (Vasseur & Yodzis 2004; Ruokolainen et al. 2009). Importantly, it has been demonstrated to interact with the density dependence of a species' demography to influence population dynamics profoundly, and, as consequence, extinction risk (Ruokolainen et al. 2009). In particular, in unstructured populations, red noise (low frequency fluctuations) is predicted to increase extinction risk, especially in a population having under-compensatory dynamics (Ripa & Lundberg 1996; Johst & Wissel 1997; Greenman & Benton 2005; Schwager et al. 2006; Heino et al. 2009; Fowler & Ruokolainen 2013). This body of theory has focused on local populations, and there has been much less effort devoted to understanding how inter-annual variability influences species' large-scale responses to climate change. One recent model shows that red noise can increase species' regional extinction risks under periods of climate change (Mustin et al. 2013). By incorporating inter-annual variability, RangeShifter provides an ideal platform for generating improved knowledge relating to eco-evolutionary responses to environmental changes in the presence of inter-annual variability.

There is evidence that inter-annual variability in weather is increasing and is expected to increase further and also to redden under climate change (Easterling 2000; Coumou & Rahmstorf 2012; Hansen et al. 2012). Despite its importance as a selective pressure and in determining a species' extinction risk, especially for small fragmented populations already stressed by anthropogenic disturbances, environmental stochasticity has rarely been included in models that try to make predictions regarding species' future distribution and persistence (McLaughlin et al. 2002; Verboom et al. 2010).

In RangeShifter, environmental stochasticity is implemented using a first order autoregressive process to generate time series of the noise value  $\varepsilon$  (Ruokolainen et al. 2009):

$$\varepsilon_{t+1} = \kappa \varepsilon_t + \omega_t \sqrt{1 - \kappa^2} \quad \text{eqn. 2}$$

where  $\kappa$  is the autocorrelation coefficient and  $\omega$  is a random normal variable drawn from  $N(0, \sigma)$ . Changing  $\sigma$  changes the amplitude of the fluctuations. The spatial scale of the variation can either be global (a single time series for the entire landscape) or local (each cell fluctuates independently), and is always applied on a yearly basis (Figure 2.4). Different degrees of spatial autocorrelation are not implemented in the current version.



**Figure 2.4.** Exemplary time series of the noise value  $\varepsilon$ . (a) Temporal autocorrelation coefficient,  $\kappa = 0.0$  (white noise). (b)  $\kappa = 0.9$  (red noise). In both cases,  $\sigma = 1.0$ .

The noise can affect either the species' demographic density-dependence ( $K$  or  $1/b$ ; [see section 2.4](#)), its growth rate ( $R$ ) or, in stage structured models, fecundity ( $\phi$ ), through the following equations:

$$K_{x,y,t} = K_{x,y,0} + K * \varepsilon_t \quad (K \text{ becomes } 1/b \text{ for stage-structure}) \quad \text{eqn. 3}$$

$$R_{x,y,t} = R_{x,y,0} + R * \varepsilon_t \quad (R \text{ becomes } \phi \text{ for stage structure}) \quad \text{eqn. 4}$$

where  $x$  and  $y$  are the cell coordinates and  $K$  (or  $1/b$ ) and  $R$  (or  $\phi$ ) are respectively the local carrying capacity (or nature of demographic density-dependence) and growth rate (or fecundity) in absence of stochasticity. In the absence of an environmental gradient,  $K_{x,y,0}$  (or  $1/b_{x,y,0}$ ) and  $R_{x,y,0}$  (or  $\phi_{x,y,0}$ ) are equal to  $K$  (or  $1/b$ ) and  $R$  (or  $\phi$ ). In the presence of an environmental gradient,  $K$  (or  $1/b$ ) and  $R$  (or  $\phi$ ) are the gradient value at the cell location.

### 2.3.5 Local extinction probability

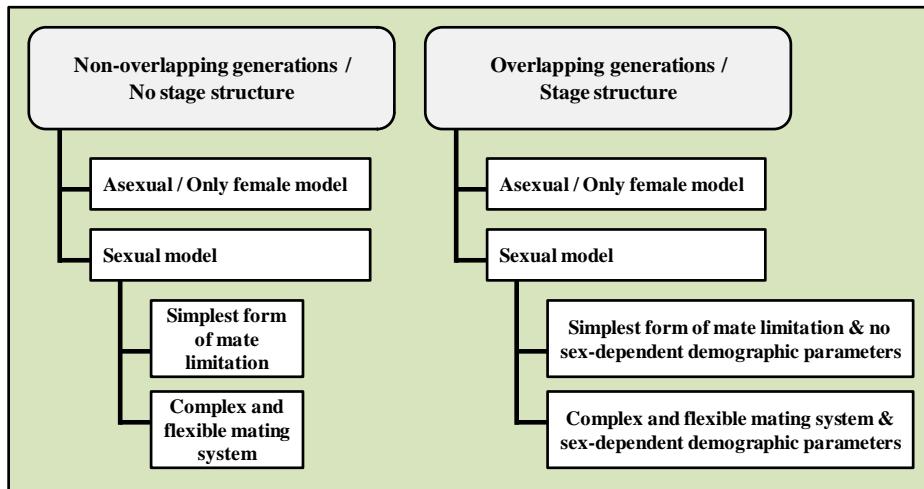
Alternatively, or additionally, to temporally auto-correlated environmental stochasticity, RangeShifter implements random local extinction probability. In each year, every population has an identical probability of going extinct. This does not affect the demographic parameter but simply kills-off the local population. Note that local extinction probability is applicable only in the case of cell-based models.

## 2.4 Population dynamics

Demographic stochasticity is fundamentally important for the dynamics of populations that are naturally small or have declined to low abundances owing to anthropogenic pressures. Additionally, inter-individual variability within populations can have a major influence on dynamics. Modelling stochastic events that happen to individuals is crucial for avoiding systematic overestimation of population viability or rate of spread (Clark et al. 2001; Kendall & Fox 2003; Robert et al. 2003; Grimm & Railsback 2005; Jongejans et al. 2008; Travis et al. 2011). Thus, population dynamics in RangeShifter were constructed to be fully individual-based and stochastic. Each reproductive individual produces a discrete number of offspring sampled from a Poisson distribution with a mean that is influenced by the species' demographic parameters and the local population density.

As RangeShifter has been designed for modelling a variety of species with different life-history traits, a range of different population models can be chosen, depending on the species

being modelled and on the available information (Figure 2.5). In all cases demographic stochasticity is implemented.



**Figure 2.5.** Schematic of the population models possible within RangeShifter.

#### 2.4.1 Cell-based vs. patch-based model

RangeShifter can be run as a cell-based or patch-based model (Bian 2003). It should be noted that the selection between cell-based or patch-based model is of fundamental importance for population dynamics calculations because it influences the spatial extent at which density dependence operates. In both cases, the landscape is represented as a grid with cells belonging to a particular habitat type, holding proportions of different habitats or being assigned a habitat quality index. However, when RangeShifter is run using the cell-based setting, the cell is the scale at which processes such as population dynamics and dispersal act. The individuals present in a cell define a distinct population, and density-dependencies for reproduction, emigration and settlement all operate at this scale. Even in the case where two habitat cells are adjacent, they still hold separate populations. In contrast, in the patch-based model, population dynamics happen at the patch level, a patch being an assemblage of landscape cells of potentially different habitat types. Patches are not defined automatically by RangeShifter. Rather, the user is required to define which cells belong to which patch, taking into account the ecological understanding of the study species. Density-dependencies regarding reproduction, development, survival, emigration and settlement will depend on the density of individuals in a patch. However, discrete step-wise movements during the transfer phase will always use the cell as the resolution at which steps occur, thus retaining important information about the landscape heterogeneity.

The choice between cell- and patch-based modelling can be of crucial importance. While a cell-based model provides an excellent abstraction of space for many theoretical studies, for some applied studies it may be insufficient. This is because the misrepresentation of population dynamics and dispersal (in terms of the scale at which they operate) can lead to substantial biases in projections regarding, for example, rate of range expansion and population persistence (Bocedi et al. 2012b). Ideally, the scales at which population dynamics and dispersal processes are modelled (by choosing the cell resolution or by defining the patches) should be those that are relevant for the species. Importantly, the patch-based implementation allows separating the scales used for population dynamics and movements. In this case, the landscape can be modelled at very fine resolution in order to capture the features that are likely to influence movements (e.g. narrow linear features) without constraining the local population dynamics to operate at too small a scale.

#### **2.4.2 Non-overlapping generations & no stage-structure**

This is the appropriate way to model species that have discrete generations. At each generation the life cycle comprises: reproduction, death of the adults and offspring dispersal (in that order). These discrete generation models can be applied to asexual species, species for which it is assumed that females play the dominant role in spatial dynamics and for species for which it is considered crucial to model both sexes explicitly.

##### *Asexual / only-female models*

Recruitment is determined by a stochastic, individual-based formulation of Maynard-Smith and Slatkin's (1973) population model, where the number of offspring produced by a single individual in the cell (or patch)  $i$  at time  $t$ , is drawn from the following distribution:

$$\text{Poisson} \left( \frac{R_{i,t}}{1 + |R_{i,t} - 1| * \left( \frac{N_{i,t}}{K_{i,t}} \right)^{b_c}} \right) \quad \text{eqn. 5}$$

Here,  $R_{i,t}$  is the maximum growth rate (obtained at very low density only) and  $K_{i,t}$  is the carrying capacity. Both  $R_{i,t}$  and  $K_{i,t}$  can vary in space and time, depending on the model setting.  $b_c$  is the competition coefficient which describes the type of density regulation, providing the possibility for under-compensatory ( $b_c < 1$ ), compensatory ( $b_c = 1$ ) or over-compensatory ( $b_c > 1$ ) dynamics.

### *Sexual models*

In this second class of models, individuals are explicitly characterized by their sex. The proportion of each sex in the population is controlled by setting the proportion of males. There are two types of possible sexual sub-models.

1. *Mating system is simplest form of mate limitation.* Each female individual is assumed to mate, as long as there is at least one male in the population. As for the asexual case, the Maynard Smith and Slatkin model is used to determine the expected number of offspring produced by each female. To maintain equivalence between the asexual and sexual versions,  $R_{i,t}$  is multiplied by 2 (Lindström & Kokko 1998):

$$\text{Poisson} \left( \frac{2 * R_{i,t}}{1 + |R_{i,t} - 1| * \left( \frac{N_{i,t}}{K_{i,t}} \right)^{bc}} \right) \quad \text{eqn. 6}$$

2. *Mating system is more complex and flexible.* Here, the mating system is explicitly modelled through a mating function (Lindström & Kokko 1998; Legendre 2004; Bessa-Gomes et al. 2010), where the number of mated females  $c$  is given by:

$$c = \min \left( 1, \frac{2hm}{f+hm} \right) f \quad \text{eqn. 7}$$

where  $f$  and  $m$  are the numbers of potentially reproductive females and males, respectively, and  $h$  is the maximum harem size, i.e. the maximum number of pair bonds that a male can establish.  $h = 1$  corresponds to monogamy,  $0 < h < 1$  to polyandry and  $h > 1$  to polygyny.

Each potentially reproductive female has a probability of reproducing  $p_r$ , given by:

$$p_r = \frac{c}{f} \quad \text{eqn. 8}$$

A Bernoulli trial,  $Bern(p_r)$ , determines if the female reproduces or not. Hence, the specification of the mating system determines the probability for each female to reproduce. However, no explicit pair bonds are formed, and in the cases where traits inheritance is involved ([see 2.5](#)), the father (of all the offspring produced by a single female in a single reproductive event) is selected randomly from the males in the population. An explicit and more comprehensive treatment of mating systems from the social and genetic point of view

will be addressed in future releases of the software. For females that reproduce, the number of offspring is determined through eqn. 5.

### 2.4.3 Overlapping generations & stage-structure

This is the appropriate choice for species in which generations can overlap and individuals can be classified in different stages (e.g. immature vs. breeding individuals) differing in their demographic parameters. Individuals are characterized by their age and stage. Each stage has a certain fecundity, survival and probability of developing to the next stage. The parameters are provided through classical transition matrices (Caswell 2001). However, in RangeShifter, these are not solved analytically as is typical for matrix models but, instead, the parameters are applied stochastically in an individual-based fashion. We believe that presenting the demographic parameters in the standard matrix notation will ease parameterization, as most population modellers are used to matrix models and, additionally, the number of parameters is kept to the minimum. It has the further important benefit of helping bridging the gap between analytical models and IBMs, the joint use of which has considerable potential, especially for improving modelling for conservation (Travis et al. 2011).

In RangeShifter, it is possible to have one or more reproductive seasons per year, or a reproductive event once every few years. At each reproductive season, two parameters control the likelihood that each individual / female reproduces:

1. First, it is determined whether a reproductively mature female is a potential reproducer. The user specifies a minimum interval before an individual, that has already reproduced, is able to reproduce again. Only those mature individuals that are either yet to reproduce, or last reproduced more than this number of reproductive seasons previously, are potential breeders.
2. Potential breeders all reproduce with set probability. Note that this probability is different from the probability of reproducing  $p_r$  given in eqn. 8. The latter will be additionally applied only in the case of more complex modelling of the mating system and it is determined by the number of reproductive males and females present in the cell/patch.

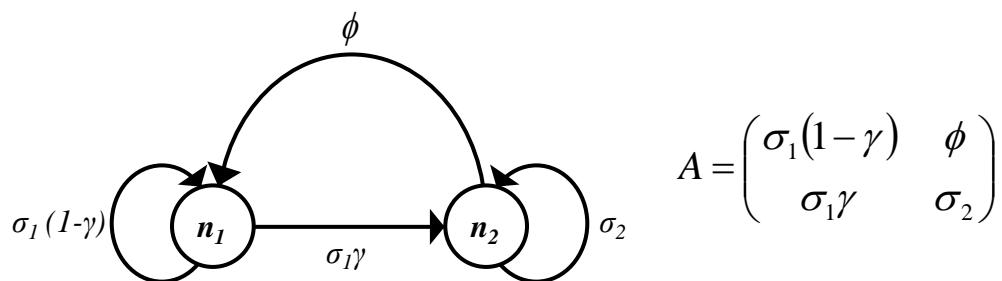
For example, if every female invariably reproduces every season, the probability of reproduction will be 1.0 and the reproduction interval 0. Alternatively, every female can have a probability of reproducing  $<1.0$ , but no minimum interval between subsequent

reproductions (to achieve this, reproduction interval is 0). As a further example, every female can have a probability of reproducing  $<1.0$  and a minimum interval between subsequent reproductions  $\geq 1$ .

Setting the number of reproductive seasons per year to 1 does not necessarily mean that all reproductive individuals are reproducing once every year. For example, let's imagine a hypothetical species where individuals can reproduce only once every three years. In this case we would set the number of seasons between subsequent reproductions to 2 and the probability of reproducing either to 1 (every three years the individual deterministically reproduces) or to less than one (after a gap of two reproductive seasons, an individual has a certain probability of reproducing that is applied each reproductive season until it reproduces again, at which point it has two seasons in which it has zero probability of reproducing). Therefore, every year each individual will reproduce or not depending on the time since last reproduction and on the reproduction probability. Of course, regardless of the temporal pattern of reproduction, the success of the reproductive attempt will still be subject to demographic stochasticity, and in some cases no offspring can result. Note that as RangeShifter is currently implemented, reproductive attempts that result in zero offspring still count in terms of an individual having to wait for the chance to reproduce again.

#### *Asexual / only-female models*

As for the non stage-structured models, these are provided for asexual species or for sexual species where it is assumed that only females determine the population dynamics and there are always enough males to fertilize all the females (Caswell 2001) (Figure 2.6).



**Figure 2.6.** Example of a two stage model and corresponding transition matrix  $A$  (re-drawn from Neubert & Caswell, 2000).  $n_1$  and  $n_2$  are the number of individuals in the two stages (e.g., immatures and adults),  $\gamma$  is the probability of developing from stage 1 to stage 2,  $\sigma_1$  and  $\sigma_2$  are the survival probabilities of the two stages and  $\phi$  is the fecundity of stage 2. In a female-only model,  $\phi$  represents the number of female offspring per female.

A common mistake in building a transition matrix is made when offspring produced at year  $t$  develop to the next stage in the same year (Caswell 2001: pg. 60-62). To avoid this problem without losing the offspring stage, and hence the chance for simulating post-natal dispersal, we require an additional explicit juvenile stage (stage 0). Juveniles have to develop to stage 1 in the same year they are born. It is important to note that juvenile mortality can be accounted for in two ways. Either it is included in adult fecundity  $\phi$  (by appropriately reducing its value), and  $\sigma_0\gamma_{0-1}$  is equal to 1.0. This is how it is typically accounted for in matrix models. Or, alternatively,  $\phi$  is equal to the true maximum fecundity and  $\sigma_0\gamma_{0-1}$  is less than 1.0. Only the first approach allows straightforward direct comparison with standard analytical matrix models. In RangeShifter, the matrix  $A$  in Figure 2.6 becomes:

$$A_2 = \begin{pmatrix} 0 & 0 & \phi \\ 1.0 & \sigma_1(1-\gamma) & 0 \\ 0 & \sigma_1\gamma & \sigma_2 \end{pmatrix}$$

A major difference between projection matrices and our individual-based model is that in the first, the three processes of reproduction, survival and development happen simultaneously while, in the second, they are explicitly modelled in sequence. The sequence of these events and the time of the dispersal phase in relation to them can change the actual dynamics and density-dependencies in both population growth and dispersal. At the beginning of each year, reproduction is always the first process to be modelled. After reproduction there are three choices:

1. Survival and development of all the stages (apart from stage 0) which occur simultaneously with reproduction; dispersal; survival and development of stage 0; aging; end of the year.
2. Dispersal; survival and successive development of all the stages; aging; end of the year.
3. Only for species having multiple reproductive seasons in a year: dispersal and then survival and development of all stages happen at the end of every reproductive season (i.e. more than once per year); aging; end of the year.

Option 1 gives results that are comparable with the analytical solution of the matrix (see Boxes 1, 2 and 3). The choice will depend on the biology of the species. If the main mortality happens overwinter, option 2 might be more appropriate.

The parameters in the matrix are used in a stochastic way at the individual level. Hence, each female at stage  $s$ , if it reproduces, produces a number of offspring given by  $\text{Poisson}(\phi_s)$ , while Bernoulli trials  $\text{Bern}(\sigma_s)$  and  $\text{Bern}(\gamma_s)$  determine if that individual/female survives or not and if it survives, if it develops to the next stage or not.

### *Sexual models*

Using stage-structure models in RangeShifter it is possible to consider sexes either implicitly or explicitly.

1. *Mating system is simplest form of mate limitation & demographic parameters are not sex-specific.* The model structure is the same as described above in this section. Individuals are defined by their sex and the sex is acknowledged also in the dispersal process and transmission of alleles. In this case,  $\phi$  refers to the number of offspring (males and females) per female.
2. *Mating system is flexible & demographic parameters are sex-specific.* As for the non stage-structured models (2.4.2), the mating system is explicitly modelled and a female's probability of reproducing is given by eqns. 7 and 8. Additionally, the demographic parameters are sex-dependent. The example two-stage matrix (Figure 2.6) is modified as follows (Caswell & Weeks 1986; Lindström & Kokko 1998):

$$A = \begin{pmatrix} \sigma_{1m}(1-\gamma_m) & \sigma_{1f}(1-\gamma_f) & \phi_m & \phi_f \\ \sigma_{1m}\gamma_m & 0 & \sigma_{2m} & 0 \\ 0 & \sigma_{1f}\gamma_f & 0 & \sigma_{2f} \end{pmatrix}$$

$\gamma_m$  and  $\gamma_f$  are the probability of developing from stage 1 to stage 2 of males and females respectively,  $\sigma_{1m}$ ,  $\sigma_{1f}$ ,  $\sigma_{2m}$  and  $\sigma_{2f}$  are the two sexes' survival probabilities at each stage and  $\phi_m$  and  $\phi_f$  are their fecundities. In the classical matrix modelling framework,  $\phi_m$  and  $\phi_f$  are derived from a birth function, which takes into account the number of males and females, the harem size and the clutch size (Caswell & Weeks 1986; Caswell 2001). In RangeShifter, the mating and the birth processes are modelled explicitly and separately in an individual-based manner; therefore, the fecundity parameter utilized is the same as in the non sex-specific model, as the differences between sexes are already accounted for during the mating process (i.e. number of offspring per female). What the user still needs to determine before

running structured explicit mating system models in RangeShifter is at which stages males are reproductive (see section [3.2.6](#) for details on how to compile the sex-specific transition matrix).

As for the asexual model, we have to add an explicit juvenile stage to the matrix. The above matrix  $A$  becomes:

$$A_2 = \begin{pmatrix} 0 & 0 & 0 & 0 & \phi_m & \phi_f \\ 1.0 & 0 & \sigma_{1m}(1-\gamma_m) & 0 & 0 & 0 \\ 0 & 1.0 & 0 & \sigma_{1f}(1-\gamma_f) & 0 & 0 \\ 0 & 0 & \sigma_{1m}\gamma_m & 0 & \sigma_{2m} & 0 \\ 0 & 0 & 0 & \sigma_{1f}\gamma_f & 0 & \sigma_{2f} \end{pmatrix}$$

### Density dependence

Density-dependence can act on each of the three demographic phases of reproduction, survival and development (Box 1). Moreover, the strength of density-dependence can be uniform for all stages or stage-dependent. Even greater complexity can be incorporated with different stages contributing differently to density-dependence.

1. *Density-dependence in reproduction.* Following Neubert & Caswell (2000), density-dependence in fecundity is implemented as an exponential decay:

$$\phi_i = \phi_{0,i} * e^{-bN_t} \quad \text{eqn. 9}$$

where  $\phi_i$  is the fecundity of stage  $i$ ,  $\phi_{0,i}$  is its maximum fecundity at low densities,  $b$  is the strength of density dependence and  $N_t$  is the total number of individuals in the local population at time  $t$ .

In the case of stage-specific density dependence, eqn. 8 is modified as follows (Box 3):

$$\phi_i = \phi_{0,i} * e^{-b \sum_{j=1}^S \omega_{ij} N_{j,t}} \quad \text{eqn. 10}$$

where,  $\phi_i$ ,  $\phi_{0,i}$  and  $b$  are as in eqn. 9,  $S$  indicates the number of stages and  $\omega_{ij}$  is contribution of stage  $j$  to the density dependence in the fecundity of stage  $i$ . Hence, the total number of individuals  $N_t$  in eqn. 9 becomes a weighted sum of the number of individuals in each stage (e.g. Caswell et al. 2004).

2. *Density-dependence in survival.* As for fecundity, density-dependence in survival is implemented as an exponential decay:

$$\sigma_i = \sigma_{0,i} * e^{-C_\sigma * b N_t} \quad \text{eqn. 11}$$

where  $\sigma_i$  is the survival probability of stage  $i$ ,  $\sigma_{0,i}$  is its survival probability at low densities,  $b$  is the strength of density dependence and  $N_t$  is the total number of individuals in the local population at time  $t$ . To allow for the possibility of having different strengths of density-dependence in different processes, we introduce the coefficient  $C_\sigma$ , which scales the strength of density dependence in survival relative to the strength of density dependence  $b$  in fecundity (Box 2).

In the case of stage-specific density-dependence, eqn. 11 becomes (Box 3):

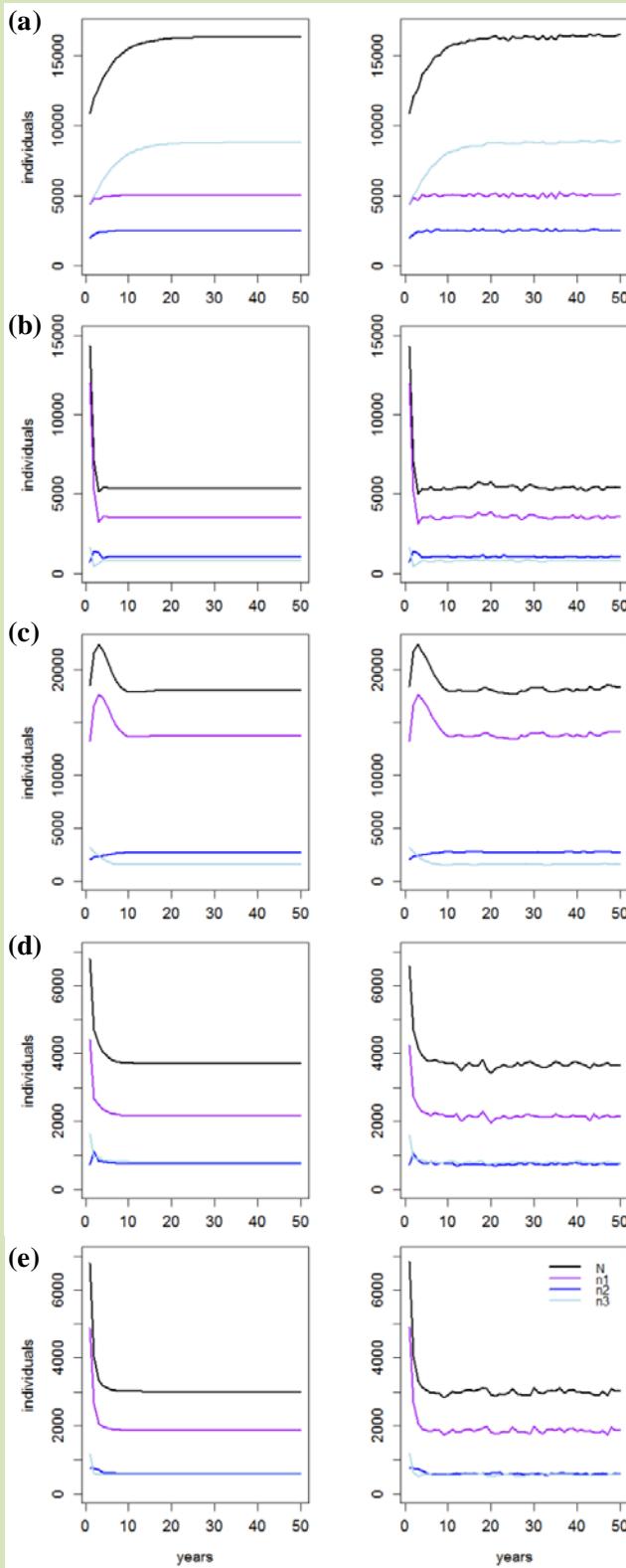
$$\sigma_i = \sigma_{0,i} * e^{-C_\sigma * b \sum_{j=1}^S \omega_{ij} N_{j,t}} \quad \text{eqn. 12}$$

3. *Density-dependence in development.* The same method is used as in 2. The non stage-specific density-dependence in development probability is implemented as:

$$\gamma_i = \gamma_{0,i} * e^{-C_\gamma * b N_t} \quad \text{eqn. 13}$$

where  $\gamma_i$  is the development probability of stage  $i$ ,  $\gamma_{0,i}$  is its development probability at low densities,  $b$  is the strength of density dependence and  $N_t$  is the total number of individuals in the local population at time  $t$ . The coefficient  $C_\gamma$  scales the strength of density dependence in development relative to the strength of density dependence  $b$  in fecundity. Stage-specific density-dependence in development probability thus becomes:

$$\gamma_i = \gamma_{0,i} * e^{-C_\gamma * b \sum_{j=1}^S \omega_{ij} N_{j,t}} \quad \text{eqn. 14}$$

**Box 1. Examples of stage-structured population dynamics incorporating density dependence.**

In all examples, the parameter  $b$  (see eqn. 9-14) is set to 1/10,000. No maximum age is included. The model is run for a single closed population (no dispersal) and initialised as following:  $N_0 = 0$ ,  $N_1 = 4,000$ ,  $N_2 = 3,000$  and  $N_3 = 3,000$ .

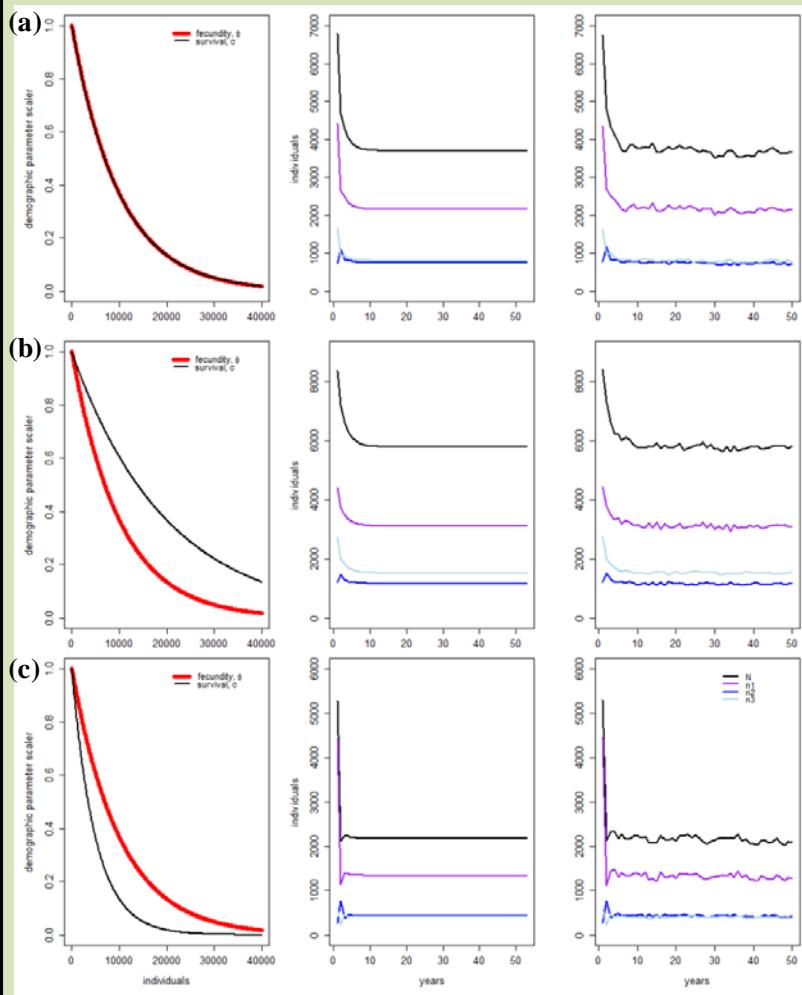
$$A = \begin{pmatrix} 0.0 & 1.5 & 2.5 \\ 0.5 & 0.0 & 0.0 \\ 0.0 & 0.7 & 0.8 \end{pmatrix}$$

$$A_2 = \begin{pmatrix} 0.0 & 0.0 & 1.5 & 2.5 \\ 1.0 & 0.0 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.0 & 0.0 \\ 0.0 & 0.0 & 0.7 & 0.8 \end{pmatrix}$$

Here, we illustrate population trajectories obtained from a stage-structured population model. We vary the processes upon which density dependence acts but, in all five examples, the transition matrix  $A$  (shown above) is the same.  $A_2$  is the modified matrix used in RangeShifter (note the additional juvenile stage). In each row, the left panel shows the deterministic realisation of the model over 50 years, while the right panel shows a stochastic realisation obtained with RangeShifter. In the examples, the density dependence is acting on (a) fecundity, (b) survival, (c) development, (d) fecundity and survival and (e) fecundity, survival and development. Note that the equilibrium population sizes and the stable stage distributions differ between the different cases. In RangeShifter, survival and development for all stages but stage 0 happen simultaneously with reproduction. Juvenile survival and development happen at the end of the year. To match with the deterministic solutions, survival and development of stage 0 must be density-independent, and stage 0 must not contribute to the density dependence on the other stages. Hence, for survival and development, the following stage weights  $\omega_{ij}$  (see eqn. 12 and 14) apply (note that  $i$  refers to the column and  $j$  to the row).

	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>
<b>0</b>	0	0	0	0
<b>1</b>	0	1	1	1
<b>2</b>	0	1	1	1
<b>3</b>	0	1	1	1

**Box 2. Examples of stage-structured population dynamics incorporating density dependence with different strengths in fecundity and survival.**



$$A = \begin{pmatrix} 0.0 & 1.5 & 2.5 \\ 0.5 & 0.0 & 0.0 \\ 0.0 & 0.7 & 0.8 \end{pmatrix}$$

$$A_2 = \begin{pmatrix} 0.0 & 0.0 & 1.5 & 2.5 \\ 1.0 & 0.0 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.0 & 0.0 \\ 0.0 & 0.0 & 0.7 & 0.8 \end{pmatrix}$$

Here, we illustrate population trajectories from a stage-structured population model. Between simulations, we vary the strength of density dependence acting upon fecundity and survival. The transition matrix  $A$  is the same for the three examples and it is reported above.  $A_2$  is the modified matrix used in RangeShifter (note the additional juvenile stage 0). Survival and development for all stages but juveniles happen at the same time as reproduction. Survival and development of stage 0 happen at the end of the year.

The same stage weights  $\omega_{ij}$  for survival, as in Box 1, are applied. The parameter  $b$  (see eqn. 9-12) is set as  $1/10,000$ . No maximum age is included. The model is run for a single closed population (no dispersal) and initialised as following:  $N_0 = 0$ ,  $N_1 = 4,000$ ,  $N_2 = 3,000$  and  $N_3 = 3,000$ . In each row, the middle panel shows the deterministic realisation of the model over 50 years, while the right panel shows a stochastic realisation obtained with RangeShifter. In the three models, fecundity and survival for each stage ( $\phi_s$  and  $\sigma_s$ ) are given by:

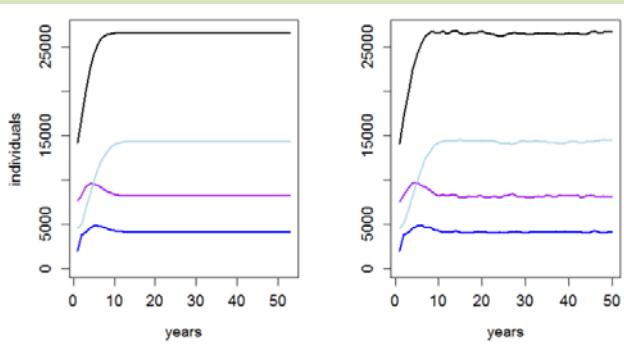
$$\phi_s = \phi_0 * e^{-bN} \quad \text{and} \quad \sigma_s = \sigma_0 * e^{-C_\sigma * bN} \quad (\text{eqn. 9 and 11}).$$

The left hand panels in each row show the shape of density dependence ( $e^{-bN}$  and  $e^{-C_\sigma * bN}$ ) in fecundity (red line) and survival (black line). **(a)** The shape of density dependence is the same for both fecundity and survival (cf. Box 1, fig. d). **(b)** Density dependence is stronger on fecundity than survival,  $C_\sigma = 0.5$ . **(c)** Density dependence is stronger on survival than on fecundity,  $C_\sigma = 2.0$ . Note that the equilibrium population sizes and the stable stage distributions differ between the different cases.

**Box 3. Examples of stage-structured population dynamics incorporating stage-specific density dependence.**

Here, we illustrate population trajectories from the stage-structured population model already shown in Boxes 1 and 2. Between simulations, we vary the strength of density dependence acting upon fecundity and survival. Additionally, different stages are affected differently in their demographic parameters by each stage's density. The transition matrices  $A$  and  $A_2$  are the same for the three examples and are reported on the right. The parameter  $b$  (see eqn. 9-14) is set as 1/10,000. No maximum age is included. The model is run for a single closed population (no dispersal) and initialised as following:  $N_0 = 0$ ,  $N_1 = 4,000$ ,  $N_2 = 3,000$  and  $N_3 = 3,000$ . In each figure, the left panel shows the deterministic realisation of the model over 50 years, while the right panel shows a stochastic realisation obtained with RangeShifter.

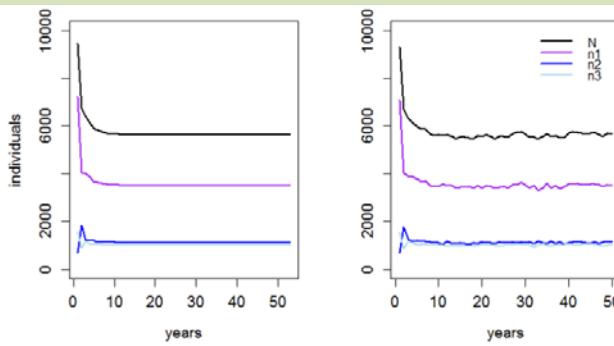
**(a)** Density dependence is acting on both fecundity and survival, with  $C_\sigma = 1.0$ . The fecundity of different stages is affected differently by each stage's density. The stage weights  $\omega_{ij}$  (see eqn. 10) are reported in the table on the right (note that  $i$  refers to the column and  $j$  to the row). In particular the effect of stage 3 on fecundities of both reproductive stages is double the effect of stage 2. Density dependence in survival is not stage-specific.



Stage weights for fecundity:

	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>
<b>0</b>	0	0	0	0
<b>1</b>	0	0	0	0
<b>2</b>	0	0	0.5	0.5
<b>3</b>	0	0	1	1

**(b)** Density dependence is acting on both fecundity and survival, with  $C_\sigma = 2.0$ . Both fecundity and survival of different stages are affected differently by each stage's density. The stage weights  $\omega_{ij}$  (see eqn. 10 and 12) are reported in the tables on the right.



Stage weights for fecundity:

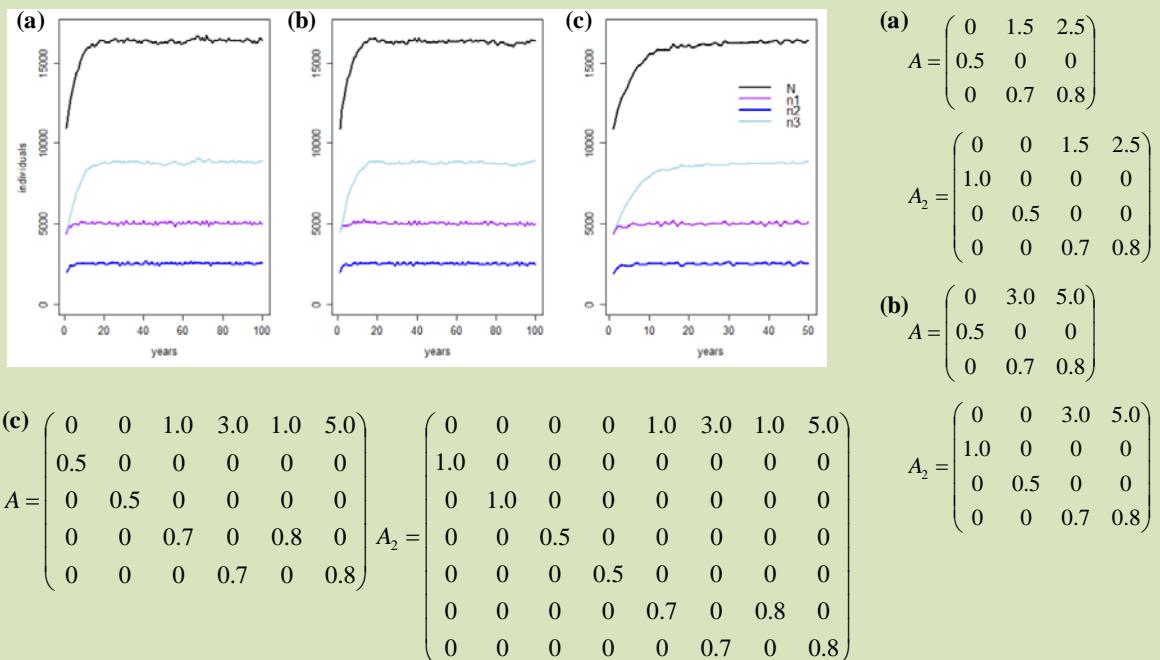
	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>
<b>0</b>	0	0	0	0
<b>1</b>	0	0	0	0
<b>2</b>	0	0	0.7	0.7
<b>3</b>	0	0	1	1

Stage weights for survival:

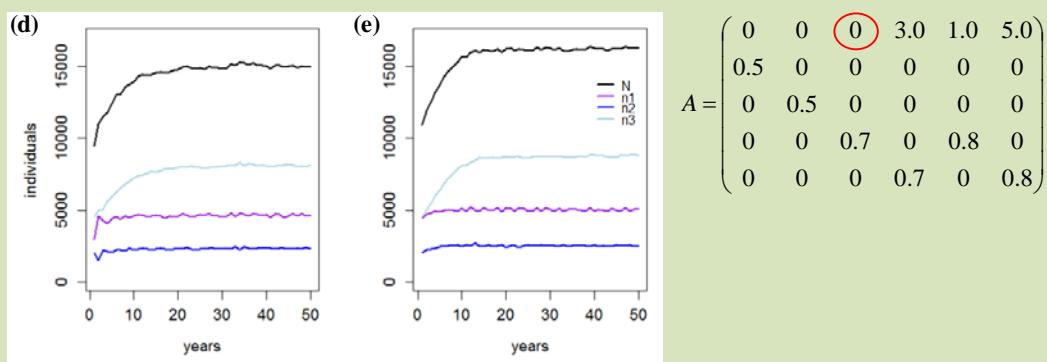
	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>
<b>0</b>	0	0	0	0
<b>1</b>	0	0.2	0.2	0.2
<b>2</b>	0	0.5	0.5	0.5
<b>3</b>	0	1	1	1

**Box 4. Examples of stage-structured population dynamics for asexual / only female models and sexual models.**

Here, we illustrate how equivalent population trajectories are obtained from three different types of models: (a) asexual / only female model, (b) sexual model with no explicit mating system nor sex dependent demographic parameters and (c) sexual model with explicit mating system and sex dependent demographic parameters. To obtain equivalent dynamics, the fecundities in the sexual models need to be doubled.  $A_2$  is the modified matrix used in RangeShifter (note the additional juvenile stage). In (c) the matrix  $A$  and  $A_2$  have been modified (c.f. Caswell & Weeks 1986; Lindström & Kokko 1998) to be used in an individual based way: fecundity of males are set either to zero or to one to denote which of the stages is reproductive. The number of offspring is determined by the females fecundity which represent the number of males and females offspring produced per female. The proportion of offspring of different sexes is given by the sex ratio. In (c) the maximum harem size  $h$  is 1. For all three models, density dependence is acting only on fecundity without differences between stages ( $b = 1/10,000$ ). No maximum age is included. The model is run for a single closed population (no dispersal) and initialised as following:  $N_0 = 0$ ,  $N_1 = 4,000$ ,  $N_2 = 3,000$  and  $N_3 = 3,000$ .



Figures (d) and (e) are showing the population trajectories for a sexual model with explicit mating system and sex dependent demographic parameters. The model has the same parameters of (c) except for the fact that males in stage 2 are not reproductive. (d) and (e) differ for the maximum harem size: (d)  $h = 1$ ; (e)  $h = 5$ .



## 2.5 Dispersal

Dispersal is defined as movement leading to spatial gene flow, and it typically involves three phases: emigration, transfer and settlement (Stenseth & Lidicker 1992; Clobert et al. 2001, 2009, 2012; Bowler & Benton 2005; Ronce 2007). The key role of dispersal in species persistence and responses to environmental change is increasingly recognized (Travis et al. 2014). Moreover, the importance of modelling dispersal as a complex process, explicitly considering its three phases, each of which has its own mechanisms and costs, has been recently highlighted (Bonte et al. 2012; Travis et al. 2012, 2014). The implementation of the dispersal process in RangeShifter is based on these recent frameworks and the substantial dispersal theory that has been developed so far (Clobert et al. 2012). Due to the recognized complexity of the process and its multi-causality, building this into models is not a simple task, nor is it to collect data that enable such models to be parameterized for applied questions. RangeShifter provides a platform that facilitates future theory development and aims to motivate greater collection of detailed dispersal data in the field. Importantly, RangeShifter incorporates the potential evolution of several key dispersal traits. Below, we first describe how heritability and evolution work (as that is consistent across traits acting at the three dispersal phases) before providing details on each of those phases.

### *Dispersal traits, genetic architecture and evolution*

RangeShifter v1.1 incorporates the possibility for inter-individual variability in different dispersal traits and a simple adaptive genetic module to simulate heritability and evolution of traits. An explicit, complex and more realistic genetic module is beyond the scope of the first version of the program. When inter-individual variability in dispersal traits is modelled, whether or not these traits are evolving, each individual carries alleles coding for each varying trait. If the reproductive model is asexual or female only, the species is assumed to be haploid and single loci code for each trait. Alleles assume continuous values assuming a continuum-of-alleles model (Hoban et al. 2011; Scheiner et al. 2012). Offspring inherit their alleles from their single parent/mother, and the phenotype is given directly by the genotype. In the case of sexual models, the species is assumed to be diploid with a single locus with ‘infinite’ alleles coding for each trait. Offspring inherit one random allele from the mother and one from the father. The phenotype is given by the arithmetic mean of the two alleles, and the heritability is assumed to be equal to one. No dominance is modelled, and loci for different traits are assumed to be unlinked. More details about each individual trait are given in the following paragraphs.

When traits vary between individuals, they can also be allowed to evolve. When an individual is born, each of its alleles can independently mutate with a set probability. In the case of mutation, a number drawn from the uniform distribution  $U(-\mu, \mu)$  is added to the trait value, where  $\mu$  is the mutation size set for the trait. A different mutation size  $\mu$  can be set for each trait.

### **2.5.1 Emigration**

Emigration is the first phase of dispersal, and can be passive (e.g. a seed released from the mother plant in such a way that it will be transported away from its natal patch) or active (e.g. an animal moving away from its natal patch). Whether the emigration is passive or active, it can be either independent of the local conditions or it can be context-dependent. Emigration itself can be a complex process determined by multiple proximate and ultimate causes. Multiple emigration strategies can be present across the species' range, inside a single population or even within the same individual in form of plastic emigration behaviour.

In the past thirty years, the theory on emigration, as well as the collection of empirical evidence, has advanced substantially, moving from considering single fixed strategies to accounting for context dependencies, plasticity and inter-individual variability in emigration strategies. For example, there is general understanding and agreement on how evolving emigration strategies are affected by environmental variability (Comins et al. 1980; McPeek & Holt 1992; Denno et al. 1996; Travis 2001; Friedenberg 2003; Bach & Ripa 2007) and habitat fragmentation (Travis & Dytham 1999; Heino & Hanski 2001; Mathias et al. 2001; Bonte et al. 2006; Schtickzelle et al. 2006; Baguette & Van Dyck 2007; Zheng et al. 2009a; Hanski & Mononen 2011). Similarly, much work has been conducted to understand the role of density dependence in emigration (Travis et al. 1999; Metz & Gyllenberg 2001; Poethke & Hovestadt 2002; Matthysen 2005; Kun & Scheuring 2006; Chaput-Bardy et al. 2010; De Meester & Bonte 2010). Of more recent development is theory on how range shifting and climate change affects the evolution of emigration (Travis & Dytham 2002, 2012; Simmons & Thomas 2004; Duckworth 2008; Travis et al. 2009; Kubisch et al. 2010) and how conversely, context-dependent emigration can affect species range shift (Kubisch et al. 2011; Altwegg et al. 2013). Yet, many questions remain relatively unexplored including, for example, the role of information acquisition and associated costs (Cote & Clobert 2007; Armsworth 2008; Clobert et al. 2009; Enfjäll & Leimar 2009; Bocedi et al. 2012a; Fellous et al. 2012; Chaine et al. 2013), the emergence of plastic strategies vs. behavioural syndromes

(Ronce & Clobert 2012), the interaction between evolving emigration strategies and the other phases of dispersal (Travis et al. 2012) and trade-offs and interactions with other life history traits (Ronce et al. 2000; Travis et al. 2010).

Within RangeShifter, the three phases of dispersal are modelled explicitly. Concerning emigration, some of the basic understanding described above is incorporated in a flexible way, allowing the implementation of different strategies. Emigration is modelled as the probability that an individual will leave its natal patch during the present year (or season). Note that in a stage-structured population, if a stage having non-zero  $d$  can last for more than one year, an individual has multiple opportunities to emigrate, each with probability  $d$ , and hence the realised overall emigration rate will be larger than  $d$ . The emigration probability  $d$  can be density-independent, and hence constant, or density-dependent. The latter is given by the following function, introduced by Kun and Scheuring (2006) (Figure 2.7):

$$d = \frac{D_0}{1 + e^{-\left(\frac{N_{i,t}}{K_{i,t}} - \beta\right)\alpha}} \quad \text{eqn. 15}$$

Here,  $D_0$  is the maximum emigration probability,  $\beta$  is the inflection point of the function and  $\alpha$  is the slope at the inflection point. We are aware that different functions have been proposed for density dependent emigration (Poethke & Hovestadt, 2002; Hovestadt *et al.* 2010). We chose this one because it is a flexible function that allows for modelling a range of different reaction norms, as well as their emergence through evolution. In the case of density-dependent emigration, we assume individuals to have full knowledge of the population density and habitat quality in their natal patch. Information acquisition is not explicitly modelled in RangeShifter.

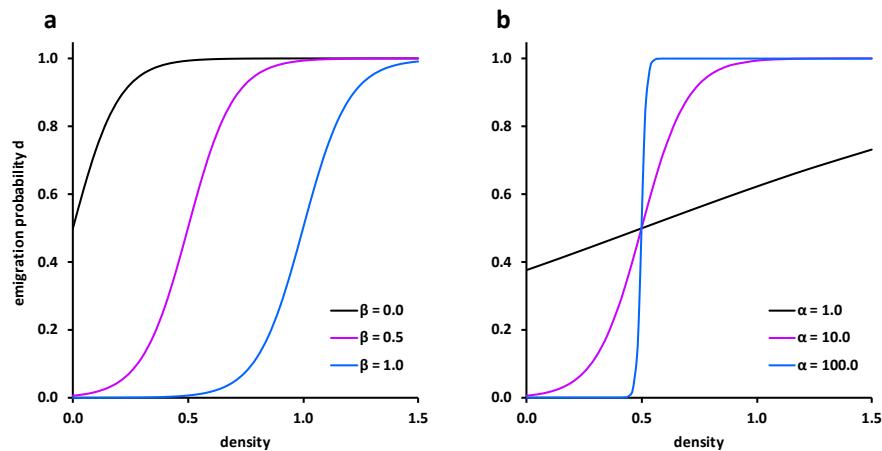
In the case of stage-structured models, eqn. 15 is modified as follows:

$$d = \frac{D_0}{1 + e^{-(bN_{i,t} - \beta)\alpha}} \quad \text{eqn. 15a}$$

where  $b$  represents the strength of density dependence used for the population dynamics.

The emigration probability can be the same for every individual or vary between individuals. In the latter case, individuals carry either one allele (two in the case of diploid genotype) determining the density-independent  $d$ , or three alleles (six in the case of diploid genotype)

coding for  $D_0$ ,  $\beta$  and  $\alpha$ . For a diploid genotype, the phenotypic value is simply the mean of the two alleles.



**Figure 2.7.** Density-dependent emigration probability. (a) Effect of changing the function's inflection point ( $\beta$ ) for  $\alpha = 10.0$  and (b) its slope ( $\alpha$ ) at the inflection point for  $\beta = 0.5$ . Density refers either to  $N/K$  for non stage-structured models, or to  $bN$  for stage-structured models.

Emigration and, more generally, dispersal are often sex-biased (Greenwood 1980; Lawson Handley & Perrin 2007). Sex-biased dispersal can evolve under the interaction of multiple selective pressures, such as availability of resources or mates, inbreeding avoidance or kin competition/cooperation, which act differently on the two sexes depending on the mating and social systems (Perrin & Mazalov 1999, 2000; Gros et al. 2008, 2009; Bonte et al. 2009; Guillaume & Perrin 2009). A unifying theory on the evolution of such complexity has yet to be achieved. Moreover, sex-biased dispersal has recently been demonstrated to affect the speed of species' range expansion (Miller et al. 2011; Miller & Inouye 2013). In RangeShifter, it is possible to model sex-specific emigration strategies, as well as sex-specific transfer and settlement. In each of these cases, the number of loci is doubled, one set coding for the trait in females and the other for the trait in males.

As well as being sex-biased, dispersal can be stage-biased, meaning that only certain stage or age classes disperse. When modelling stage-structured populations in RangeShifter, it is possible to model stage-specific emigration allowing different stages to have different emigration parameters. However, the current version does not accommodate inter-individual variation in emigration strategies when they are stage-dependent.

### 2.5.2 Transfer

Transfer, or transience, is the second phase of dispersal, and consists of the movement of an individual starting from when it departs from its natal patch and ending with settlement or mortality. The main components of this phase are the individual movement ability and navigation capacity in response to the characteristics of the environment. The interaction between these components and their associated costs will determine the distance moved, the movement path and the chance of surviving the transfer phase.

Understanding and modelling how species move is not a simple task, and, perhaps more than for the other phases of dispersal, much effort has been spent in two separate and not always interacting fields: dispersal ecology (Clobert et al. 2012) and movement ecology (Nathan et al. 2008). While the former seeks to understand movements as a part of the dispersal process and has often described transience with phenomenological dispersal kernels (but see recent developments in fitting mechanistic kernels: (Schurr 2012)), the latter is more focused on understanding the mechanisms of the movement process itself, even though recent emphasis has been put on the consequences of movements for population dynamics (Morales et al. 2010). Modelling dispersal in IBMs needs to draw from both fields.

Depending on the information available for a given species and the level of detail that is considered important to represent in models (which will depend on the aim and the scale of the model), there are two main methods to model the transfer phase: phenomenological dispersal kernels or mechanistic movement processes. Versions of both methods are incorporated in RangeShifter.

### 2.5.3 Dispersal kernels

Dispersal kernels are statistical distributions that are largely used to describe dispersal distances. For a comprehensive review about theory and empirical estimation of dispersal kernels we refer to Clobert et al. (2012), Part IV.

Dispersal kernels have been largely used in dispersal ecology both for describing dispersal patterns and for theoretical studies, as well as in metapopulation theory. Recently they have been incorporated in species distribution models (Travis et al. 2014), either at population or individual level (Keith et al. 2008; Anderson et al. 2009; Engler & Guisan 2009; Willis et al. 2009b; Mitikka et al. 2010; Boulangeat et al. 2012; Pagel & Schurr 2012; Schurr et al. 2012). The main assumption behind dispersal kernels is that the principal determinant of the

probability of an individual dispersing to a particular site is the distance from the starting location. However, it is well recognized and supported by data (Hovestadt et al. 2012; Baguette et al. 2013), that in most cases realized kernels are the results of multiple factors, such as the interaction between individual movement capacity and landscape structure, making Euclidean distance a poor predictor of dispersal. Dispersal kernels are not a fixed characteristic of the species, but are likely to vary between and within populations depending upon landscape structure and the history of movement rule evolution (Van Dyck & Matthysen 1999; Hanski et al. 2004; Merckx & Van Dyck 2006; Fahrig 2007; Ovaskainen et al. 2008b; Stevens et al. 2010; Wang et al. 2011). Dispersal kernels can vary through time (Schtickzelle et al. 2012), and there can be considerable variability between individuals, sexes and stage classes (Delgado et al. 2010; Turlure et al. 2011; Benton & Bowler 2012; Matthysen 2012).

Particular emphasis has been placed during the last decade on rare long-distance dispersal events, which have been found fundamental for explaining phenomena such as rate of species' range shifting in response to past and present climate change (Clark et al. 1998; Nathan et al. 2011; Lesser & Jackson 2013) and connectivity of isolated populations (Johst et al. 2002; Baguette 2003; Muñoz et al. 2004). These events are difficult to capture and model with traditional kernels. Therefore, fat-tailed kernels and mixed kernels have started to be used (Bullock & Clarke 2000; Clark et al. 2001; Hovestadt et al. 2011; Fronhofer et al. 2013).

As for emigration, movement abilities and strategies are under multiple selective pressures and can evolve separately. As a result, the realized dispersal kernels will themselves evolve (Hovestadt et al. 2012). Theory of the evolution of dispersal distances in relation to kin-competition and parent-offspring competition (Murrell et al. 2002; Rousset & Gandon 2002; Dytham & Travis 2006; Starrfelt & Kokko 2010), landscape structure (Hovestadt et al. 2001; Bonte et al. 2010; Travis et al. 2010; North et al. 2011), environmental gradients and range expansion (Hughes et al. 2007; Phillips et al. 2008, 2010; Dytham 2009; Boeye et al. 2013; Henry et al. 2013) has started to be developed (although not to the extent of emigration theory), but empirical work in this topic is still in its infancy (e.g. Bitume et al. 2013).

In RangeShifter, two types of kernels have been implemented: negative exponential and a mixed kernel given by two different negative exponentials. Here, kernels are considered as ‘distance kernels’, i.e. the statistical distribution of the probability that an individual will move a certain distance (Hovestadt et al. 2012; Nathan et al. 2012). These kernels are

specifically used for the transfer phase, meaning that they do not incorporate information on the emigration or settlement probabilities, which are modelled independently. Therefore, dispersal kernels are applied only to dispersing individuals and not normally to the entire population. However, the program allows a particular setting where emigration and transfer are not explicitly separated but are both modelled through the kernel (as described below).

We are aware that there are many possible statistical distributions that have been fitted to dispersal data, which in many cases perform better than the negative exponential (Nathan et al. 2012). However, the negative exponential is still commonly used, has been found useful for describing dispersal patterns of certain organisms and the combination of two different negative exponentials has been demonstrated to be a valuable method for discerning between common short-distance and rare long-distance dispersal (Hovestadt et al. 2011). Moreover, providing an exhaustive choice of different kernels is beyond the current scope of this program, but it would be technically easy to implement a different shape kernel for future versions if needed.

#### *Negative exponential*

If the individual disperses, the distance and the movement direction are determined in continuous space. The distance is drawn from a negative exponential distribution with a given mean  $\delta$ , and the direction is selected randomly from a uniform distribution between 0 and  $2\pi$  radians. If the arrival point lies beyond the boundary of the landscape, distance and direction are re-drawn. The individual is displaced from a random point (using continuous coordinates) inside the natal cell to the arrival cell where the model switches back to discrete space (Bocedi et al. 2012b). If the arrival point is inside the natal cell, individual starting position, distance and direction are re-sampled until the individual leaves the natal cell. In the case of patch-based models, the individual is assumed to disperse from a random point in the patch and this position, the dispersal distance and direction are drawn until the individual leaves the patch. In order to separate emigration and transfer explicitly, and to avoid potential infinite re-sampling, the program requires the mean of the kernel to be greater or equal the cell resolution. This condition is relaxed only in the special case where emigration probability is set to be density-independent and the kernel is applied to the entire population without re-sampling (the ‘use full kernel’ option). Individuals which draw a short movement distance do not leave the natal cell/patch and implicitly become sedentary, and therefore the kernel itself defines the proportion of individuals which emigrate. When this option is selected, the

emigration probability for those stages/sexes which disperse should be set to 1.0; otherwise, only a proportion of such individuals would use the kernel to determine whether or not they emigrate.

#### *Mixed kernel*

The distance an individual moves is sampled from a mixed kernel given by the combination of two negative exponentials with different means  $\delta_1$  and  $\delta_2$ , occurring with probability  $p$  and  $1-p$  respectively (Hovestadt et al. 2011). Otherwise, the conditions for the single kernel apply.

For both types of kernel, inter-individual variability is possible. Individuals will carry either one allele for  $\delta$  or three alleles for  $\delta_1$ ,  $\delta_2$  and  $p$ , which they inherit from the parents. Dispersal kernels can also be sex-dependent. In the case of inter-individual variability, individuals will carry either two alleles (female  $\delta$  and male  $\delta$ ) or six alleles (female and male  $\delta_1$ ,  $\delta_2$  and  $p$ ). Finally, dispersal kernels can be stage-specific. In this case, inter-individual variability is not implemented.

When inter-individual variability is implemented, the dispersal kernel parameters can evolve. As for the emigration traits, each trait ( $\delta$  for the negative exponential or  $\delta_1$ ,  $\delta_2$  and  $p$  for the mixed kernel) can mutate independently according to a given mutation probability. In the case of mutation, a number drawn from the uniform distribution  $U(-\mu, \mu)$  is added to the trait value, where  $\mu$  is the mutation size specific for the trait. When dispersal kernels are sex-specific, alleles for male and female traits can mutate independently. In the case that the dispersal kernel is applied to the entire population (i.e. density-independent emigration probability of 1.0), the mean dispersal distance can evolve down to zero (i.e. evolution for no dispersal). In all other cases where emigration and transfer are modelled separately, the mean dispersal distance has a lower limit to which can evolve equal to the landscape resolution.

#### **2.5.4 Movement processes**

It is increasingly acknowledged that individual movements within and between habitat patches, and consequently also population dynamics, are strongly affected by the behavioural and physical traits of individuals and by the landscape structure and composition (Morales & Ellner 2002; Hawkes 2009; Stevens & Coulon 2012; Baguette et al. 2013). This has led to the development of mechanistic models where movement behaviour and its interaction with the environment is explicitly described (Nathan et al. 2008; Revilla & Wiegand 2008; Morales et al. 2010; Palmer et al. 2011; Pe'er et al. 2011). The classical method to represent individuals'

movements mechanistically is to use a random walk (Codling et al. 2008), or its diffusion approximation, assuming that individuals are moving randomly in a homogeneous landscape and that they are all following the same rules. From this basis, there have been recent developments in diffusion models for including landscape heterogeneity and some behavioural responses, like reaction to habitat boundaries, directly derived from empirical data through state-space models (Ovaskainen & Cornell 2003; Ovaskainen 2004; Ovaskainen et al. 2008a; Patterson et al. 2008; Zheng et al. 2009b; Ovaskainen & Crone 2010). Yet, these models do not account for individual variability or for many behavioural components including memory, perceptual range and movement modes. Despite this simplicity, diffusion models, and especially their recent developments, can still be satisfactory at large temporal and spatial scales and serve as a null hypothesis against which to test more complex movement models. Moreover they can provide basis for building blocks for population dynamics models.

Mechanistic IBMs allow extending the “random paradigm” by incorporating behavioural elements that are likely to be crucial in affecting species’ spatial dynamics (Lima & Zollner 1996; Baguette & Van Dyck 2007; Knowlton & Graham 2010; Shreeve & Dennis 2010). These elements can be assigned into six main categories: (i) the switching between different movement modes [for example foraging within the home range vs. dispersal (Fryxell et al. 2008; Delattre et al. 2010; Pe’er et al. 2011)]; (ii) the individuals’ perceptual range (Zollner & Lima 1997, 2005; Gardner & Gustafson 2004; Olden et al. 2004; Vuilleumier & Metzger 2006; Vuilleumier & Perrin 2006; Pe’er & Kramer-Schadt 2008; Palmer et al. 2011); (iii) the use of information in movement choices (Clobert et al. 2009) and the memory of previous experience (Smouse et al. 2010); (iv) the influence of habitat fragmentation and matrix heterogeneity on movement behaviours (Ricketts 2001; Vandermeert & Carvajal 2001; Schtickzelle & Baguette 2003; Revilla et al. 2004; Wiegand et al. 2005; Fahrig 2007; Dover & Settele 2008); (v) the individual responses to habitat boundaries (Schultz & Crone 2001; Morales 2002; Merckx et al. 2003; Ovaskainen 2004; Stevens et al. 2006a; Pe’er et al. 2011); and (vi) the period of activity (Revilla et al. 2004) and the time scale of movements (Lambin et al. 2012).

A general framework for a mechanistic representation of movements has been outlined by Nathan et al. (2008), who identified four basic components: the internal state of the individual (why does it move?), its motion capacities (how does it move?), its navigation capacities

(when and where does it move?) and external factors that affect the movement. This framework allows us, starting from individual movements, and taking into account individual variability, to predict movement patterns over large temporal and spatial scales and potentially to scale up to populations, communities, ecosystems and to multi-generation / evolutionary processes (Holyoak et al. 2008). The ultimate limitation is likely to be the quantity and the type of data needed to parameterize this /these kind of models; therefore, the challenge is to understand which level of detail is needed to make reliable projections in different contexts and for different purposes (Lima & Zollner 1996; Morales et al. 2010).

Movement behaviours during the transfer phase are a core component of the dispersal strategy of an individual, and therefore they come under selection and they can evolve (Merckx et al. 2003; Fahrig 2007; Hawkes 2009; Travis et al. 2012). Ultimately, it is the evolution of movement behaviours that leads to what we consider the evolution of dispersal kernels. A handful of theoretical studies have so far explored the evolution of movement rules. For example, it has been shown how the landscape composition and configuration, in interaction with the ecology of the species, can affect the evolution of movement patterns, such that the greater the costs of dispersal the more highly correlated are the emerging walks (Heinz & Strand 2006; Bartoń et al. 2009). Moreover, straighter movement paths (Phillips et al. 2010) and riskier strategies seem to be selected during range expansion in such a way that the rate of expansion is maximized at the expense of the survival probability of the single individual (Bartoń et al. 2012)

RangeShifter v1.1 has two types of movement models implemented: the Stochastic Movement Simulator (SMS, Palmer et al. 2011), and a correlated random walk (CRW). These two movement models are fully individual-based and explicitly describe the movement behaviour of individuals with a level of detail, and hence parameters, which is probably close to the most parsimonious for a mechanistic movement model. However, they facilitate considerably increasing the complexity and realism with which the transfer phase is modelled. More detailed and species-specific movement models are beyond the scope of RangeShifter but they could be added relatively easily in the future versions for more specific purposes.

#### *Stochastic Movement Simulator, SMS*

SMS is a stochastic individual-based model where organisms move through grid-based, heterogeneous landscapes. The model uses similar cost surfaces as the least cost path (LCP)

(Adriaensen et al. 2003; Chardon et al. 2003; Stevens et al. 2006b; Driezen et al. 2007), but it relaxes two of the main assumptions/limitations of the latter. Firstly, individuals are not assumed to be omniscient, but move according to what they can perceive of the landscape within their perceptual range. Secondly, individuals do not know *a priori* their final destination, which is a reasonable assumption for dispersing individuals. Here, the core components of SMS are briefly described, but we refer to Palmer et al. (2011) for a complete description of the method.

SMS uses cost maps where a relative cost to movement is assigned to each habitat type. Costs are integer numbers and represent the cost of moving through a particular land cover relative to the cost of moving through breeding habitat (conventionally set to a cost of 1). Individuals take single cell steps basing their decisions on three parameters: their perceptual range (PR), the method used to evaluate the landscape within their perceptual range and their directional persistence (DP), which corresponds to their tendency to follow a correlated random walk. The PR is defined by a number of cells. At each step, the individual evaluates the surrounding habitat in order to determine the effective cost of taking a particular step to each of the eight neighbouring cells. The effective cost is a mean of the cost of the neighbouring cell and the surrounding cells beyond it within the PR, and is calculated by one of three possible methods:

1. *Arithmetic mean.*
2. *Harmonic mean.* The reciprocal of the arithmetic mean of the reciprocals of the observations (cell costs). This method increases the detectability of low cost cells but performs less well than the arithmetic mean in detecting high cost cells. Therefore, the choice between the two depends on whether the main driver of the animal movement is selecting for good habitat or avoiding costly habitat.
3. *Weighted arithmetic mean.* The cost of each cell is weighted by its inverse distance from the individual (which is assumed to be in the centre of the current cell).

The effective cost of each neighbouring cell is weighted by the DP, which is lowest in the direction of travel. RangeShifter v1.1 provides two new additional SMS features not previously available. First, DP can be calculated over more steps than just the previous one (up to a maximum of 14), controlled by the memory size parameter (Palmer et al. 2014; Aben et al. 2014). Increasing the memory size means that an individual retains for longer its tendency to move in a certain direction, and hence paths tend to become somewhat smoother. Second, there is an option to include goal bias, i.e. a tendency to move towards a particular destination, which is implemented in a similar way to DP (Aben et al. 2014). However, as

dispersers in RangeShifter are naïve and have no goal, it may be applied only in the ‘negative’ sense of moving away from the natal location (goal type = 2), i.e. as a dispersal bias (but note that care should be taken, as it is time-independent, and even relatively small increases above the minimum of 1.0 can substantially influence path characteristics). The reciprocals of the product of effective cost, DP and dispersal bias, scaled to sum to one, give the probabilities that the individual will move to each neighbouring cell. All the dispersing individuals move simultaneously, i.e. at each time-step they all make one move. In the case of patch-based models, the individual is forced to leave the natal patch by increasing its DP ten-fold until it has taken a number of steps (equal to twice the perceptual range) outside the natal patch. As currently implemented in RangeShifter, SMS does not allow inter-individual variability, sex / stage specificity or evolution of traits.

#### *Costs estimation*

Critical for the outcomes of SMS are the relative costs assigned to the different habitats (as is also the case for the LCP approach). Despite being important, often these costs are based on expert opinion rather than on real data. Promisingly, methods for estimating costs experimentally or in the field are being developed (Verheyen et al. 2003; Stevens et al. 2004, 2006a; Spear et al. 2010; Stevens & Coulon 2012).

#### *Correlated random walk, CRW*

RangeShifter implements a simple correlated random walk without any bias. This model is implemented in continuous space on the top of the landscape grid. Individuals take steps of a constant step length (metres); the direction is sampled from a wrapped Cauchy distribution having a correlation parameter  $\rho$  in the range 0 to 1 (Zollner & Lima 1999; Bartoń et al. 2009). As for SMS, all individuals take each step simultaneously. In the case of patch-based models,  $\rho$  is automatically set to 0.99 until the individual steps outside the natal patch, after which the value of  $\rho$  set by the user is restored.

Step length and  $\rho$  can vary between individuals and can evolve. In this case, each individual carries two alleles (four for diploid genotypes) coding for the two traits. These can mutate independently with a given mutation probability. As for the other evolving traits, when a mutation occurs a number drawn from the uniform distribution  $U(-\mu, \mu)$  is added to the trait value,  $\mu$  being the mutation size specific for the trait. There is no sex- or stage-specific CRW implemented.

### 2.5.5 Settlement

Settlement, or immigration, is the last phase of dispersal, when the organism stops in a new cell or patch of breeding habitat. This phase is determined by a suite of strategies, behaviours and reaction norms that lead individuals to the decision to stop in a particular place. Habitat selection, mate finding and density dependence are probably three of the main processes involved, but not the only ones. Like emigration, settlement is a complex process affected by multiple criteria including inter-individual variability and context dependencies. It can be influenced by the causes and mechanisms of the previous phases of dispersal (Clobert et al. 2009) and it has associated specific costs (Bonte et al. 2012), which can also feed back to the previous phases (Le Galliard et al. 2012b).

As for the previous phases, the use of different sources of abiotic and biotic information is likely to be crucial in the settlement decision, for which evidence is now accumulating. For example, studies have demonstrated that in some species, dispersing individuals exhibit a preference for habitat that is similar to the natal one, philopatry being a stronger predictor of habitat preferences for settlement than intrinsic habitat quality (Haughland & Larsen 2004; Stamps & Blozis 2006; Stamps et al. 2009). Conspecific density and performance have also been demonstrated to be important cues for settlement decisions (conspecific attraction), because they can provide a rapid approximation of the habitat quality (Stamps 1998; Doligez et al. 2004; Cote & Clobert 2007; Fletcher 2007; Vercken et al. 2012; Clotuche et al. 2013).

From the theoretical point of view, much work has been done on habitat selection during settlement decisions and its consequences for species' population dynamics and spatial genetic structure. The basic assumption is that individuals are expected to select habitat patches where their expected fitness is greater than the one expected in the natal patch, weighted by the costs of searching (Ruxton & Rohani 1998; Stamps 2001; Baker & Rao 2004; Stamps et al. 2005; Armsworth & Roughgarden 2008; Bonte et al. 2012). Recently the idea of 'matching habitat choice' has been proposed, for which individuals aim to settle where the environment best matches with their phenotype. This process, expected to be more important for species with limited phenotypic plasticity, can have important implications for processes such as local adaptation, adaptive peak shifts and evolution of niche width, and speciation (Edelaar et al. 2008). Other factors affecting settlement such as density dependence (Poethke et al. 2011), conspecific attraction (Fletcher 2006) or mate finding

(Gilroy & Lockwood 2012), their evolution and their consequences on species' responses to environmental changes, have been much less theoretically investigated.

RangeShifter incorporates some basic settlement rules, whose level of complexity varies depending on the movement model utilized for the transfer. In any case, dispersing individuals are not allowed to settle in their natal cell/patch.

#### *Settlement with dispersal kernels*

When using dispersal kernels, individuals are displaced directly from the starting location to the arrival location. The suitability of the arrival cell or patch determines whether the disperser is successful or not. For species with non-overlapping generations, where individuals have only one chance to disperse and reproduce, the model has two options if the arrival cell is unsuitable: the individual either dies or it can move to one of the eight neighbouring cells in the case that at least one of them is suitable. In the latter case, if more than one of the neighbouring cells is suitable, the individual is placed in one of them chosen randomly. For patch-based models, if the arrival patch is unsuitable, the individual either dies or can move to a randomly chosen neighbouring suitable patch, provided that the new patch is only one cell apart from the arrival patch. For species with overlapping generations, where individuals can disperse over multiple seasons, there are two additional options. First, if the arrival cell/patch is unsuitable, the individual can stay there waiting until the next dispersal event when it will disperse again according to the set kernel. Second, if both the arrival cell/patch and all eight neighbouring cells, or all eventual neighbouring patches, are unsuitable the individual can wait in the arrival cell/patch before moving again at the next dispersal event.

The arrival cell/patch is considered suitable if it contains breeding habitat. Additionally, sexual species may be required to find a mate, i.e. there has to be at least one individual of the opposite sex present for the cell/patch to be considered suitable for settlement.

#### *Settlement with movement processes*

If individuals are dispersing by one of the two movement processes implemented (SMS or CRW), at each step (made simultaneously) they each evaluate their current cell or patch for the possibility of settling. This allows for the implementation of more complex settlement rules. The simplest one is that the individual decides to stop if there is suitable habitat; this is

in any case a necessary condition. Additionally, the settlement decision can be density-dependent. The individual has a probability,  $p_s$ , of settling in the cell or patch  $i$ , given by:

$$p_s = \frac{S_0}{1+e^{-(\frac{N_i}{K_i} - \beta_s) * \alpha_s}} \quad \text{eqn. 16}$$

Here,  $N_i$  and  $K_i$  are the number of individuals and the carrying capacity of the cell/patch  $i$ ,  $S_0$  is the maximum settlement probability,  $\beta_s$  is the inflection point and  $\alpha_s$  is the slope of the function. Sexual species may also be required to find a mate in order to settle. As for settlement with kernels, this requirement is satisfied if there is at least one individual of the opposite sex in the cell/patch. Density-dependence and mating requirements can also be combined together to determine the settlement decision.

In the case of stage-structured models, eqn. 16 becomes:

$$p_s = \frac{1}{1+e^{-(bN_i - \beta_s) * \alpha_s}} \quad \text{eqn. 16a}$$

where  $b$  represents the [strength of density dependence](#) used for the population dynamics.

To avoid having individuals moving perpetually because they cannot find suitable conditions to settle, the model requires a per-step mortality ([see 2.5.4](#)) or a maximum number of steps, or both, to be set. The maximum number of steps defines the maximum time length of the transfer period. This could be calculated combining the average time taken for each step (which can be derived from tracking data on maximum distances covered in a given time and considering the cell resolution or the step length for discrete and continuous models respectively) and the time available for individuals to disperse (Kramer-Schadt et al. 2004). When an individual reaches the maximum number of steps, it stops where it is regardless of the suitability of the location; in the case of annual species this results in automatic death if the individual stops in unsuitable habitat. For species that can disperse over multiple seasons, the model requires a maximum number of steps per dispersal event; on reaching that limit, the individual will stop where it is and the next season, if still alive, it will move again.

An additional rule that can be set constitutes a minimum number of steps that each individual must take before settlement can take place. This is useful for simulating situations where animals, in a ‘dispersal mode’, will keep moving and not consider settling even if suitable conditions are available (e.g. Bartoń et al. 2012).

Settlement rules, whether the transfer is modelled with kernels or with movement processes, can be sex- or stage-specific or both. Inter-individual variability and trait evolution are not implemented in the current version of Range Shifter.

### **2.5.6 Dispersal mortality**

Dispersal is often a costly process for an organism (Bonte et al. 2012) and, in some cases, a dispersing individual may suffer mortality. Obtaining a sensible representation of dispersal requires that these mortality costs are described appropriately and, for this, it is important to recognize how dispersal mortality is incorporated in RangeShifter.

First, dispersal mortality can arise as a result of individuals failing to reach suitable habitat. For example, when a simple dispersal kernel is used with no possibility for individuals to search for locally-suitable habitat, mortality occurs to all individuals that arrive in unsuitable habitat. The same is true when a movement model is used for the transfer phase; some individuals may fail to find suitable habitat before they use up a maximum number of movement steps. In this first case, dispersal mortality clearly depends upon the proportion of suitable habitat in the landscape and will increase as the availability of habitat declines.

A second source of dispersal mortality can be specified by the user. In the case of the dispersal kernel, either a constant or a distance-dependent (i.e. individuals that travel further are more likely to die) probability of mortality can be incorporated. The latter may be thought to represent the increased energetic, time or attritional costs that longer-distance dispersers will experience (Bonte et al. 2012). Where movement rules are used, a per-step probability of mortality can be included and again, this can be useful for representing mortality risks that increase with distance or time spent travelling. Additionally, where movement across a complex landscape is modeled more explicitly, it is possible that the per-step mortality varies according to the nature of the local environment and the possibility for including this additional detail is provided in RangeShifter.

We note here that the total dispersal mortality experienced will be the sum of the mortalities due to the two sources identified above and, in parameterising the model, it will be important to recognize this such that dispersal mortality is not double-accounted.

### 3 Using RangeShifter

---

RangeShifter is a standalone application coded in C++ and downloadable as an executable file running under Microsoft Windows. The program is implemented with a user-friendly graphical user interface (GUI). Opening the executable will always start the GUI. From there, the user can decide whether to run the software in batch mode (hence without interacting further with the GUI, but see also [section 3.3](#)) or through the GUI. Using the GUI has some advantages (Grimm & Railsback 2005), especially for the novice user. It is very useful for exploring the model and its different components, and understanding how it works. Observing the simulation developing through the dynamic visualisation options can help in identifying mistakes in the parameterization and in interpreting the results. Furthermore, the GUI is extremely valuable for communicating the model and its results, especially to researchers who are not modellers or not familiar with the approach, and also to the general public (Turner et al. 1995). Finally, the GUI can be very useful for teaching purposes, both for demonstration in lectures and for practical classes.

In this chapter, we will describe how to use RangeShifter. We will start by describing the type of inputs required. We will then describe in detail the main components of the software through the GUI, continue with instructions on how to use the program in batch and finally illustrate the outputs of the model.

#### 3.1 Inputs

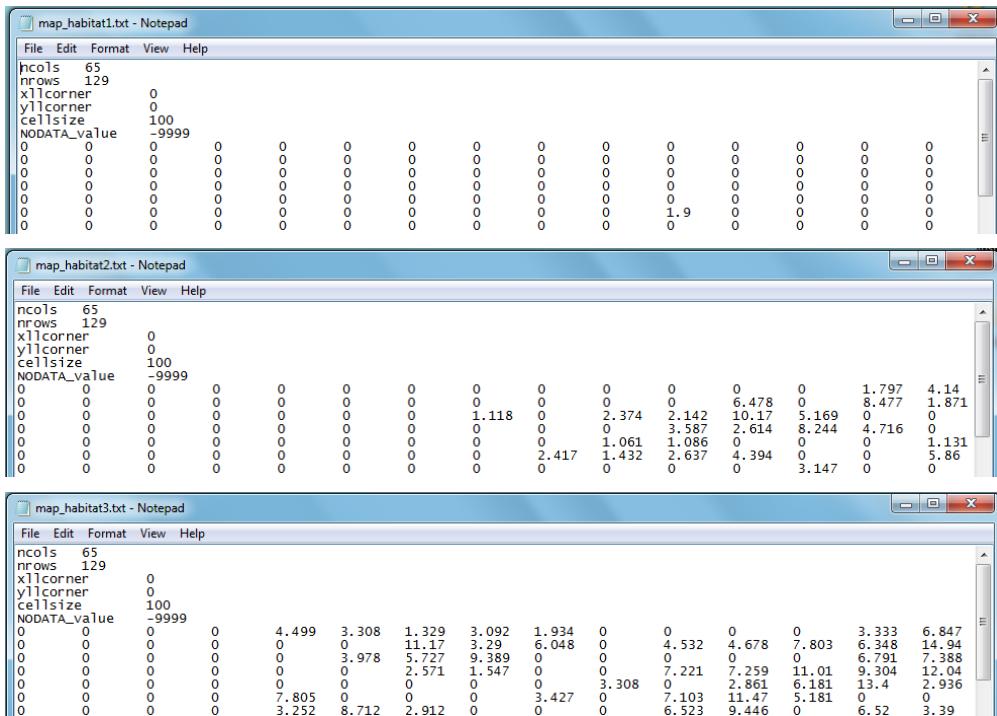
##### 3.1.1 *Landscape*

RangeShifter requires every input map to be a text (\*.txt) file in ArcGIS raster export format, which has the following six header lines:

ncols	Number of columns
nrows	Number of rows
xllcorner	x coordinate (longitude) of the lower-left corner
yllcorner	y coordinate (latitude) of the lower-left corner
cellsize	Resolution (meters)
NODATA_value	Value for cells having missing data (usually -9999)

The rest of the file is a grid containing a value for each cell, one line per row. RangeShifter can read-in three different types of habitat maps ([see also 3.2.3](#)):

1. **Raster with habitat codes.** In this option each habitat, or land-cover type, has a unique integer code. Each cell in the file contains a single habitat code and 100% coverage is assumed for the cell. The landscape is therefore composed of discrete habitat cells. For an example of the file format, see the landscape file provided for the first tutorial ([section 4.1](#)). In the batch mode, the codes are required to be sequential integers starting from 1.
2. **Raster with habitat percentage cover.** A single cell in the landscape can contain different habitats in different proportions. In this case, RangeShifter requires a raster file for each habitat type. A given habitat file stores the percentage cover of that habitat for each cell (Figure 3.1). Percentage is represented with continuous numbers. **Note that RangeShifter requires the decimal point “.” as decimal separator.** The total coverage of a cell must be less or equal to 100.0; if less, the remaining coverage is considered generic non-habitat. Note that this option is available only if using the program via the GUI, and not in batch mode. However, for use in batch mode, the landscape can be prepared at pre-processing time by combining the percentage of the different habitats (possibly in a weighted way) to give, for each cell, an overall habitat quality ranging from 0 to 100 (see below, “Raster with habitat quality”).
3. **Raster with habitat quality.** Each cell in the landscape is assigned a continuous quality value between 0.0 and 100.0. There are no explicit habitat or land-cover types. This allows integrating different methods for calculating the habitat suitability for a given species. For example, qualities can result from different methods of suitability modelling, which incorporate multiple variables like habitat types, elevation, climate, etc. In the current version of the program, a straight-line relationship between carrying capacity and quality is assumed. Therefore, the quality should be scaled accordingly in case of a curvilinear relationship.



**Figure 3.1.** Example files for a landscape represented with the percentage cover of three habitat types.

### *Patch-based model*

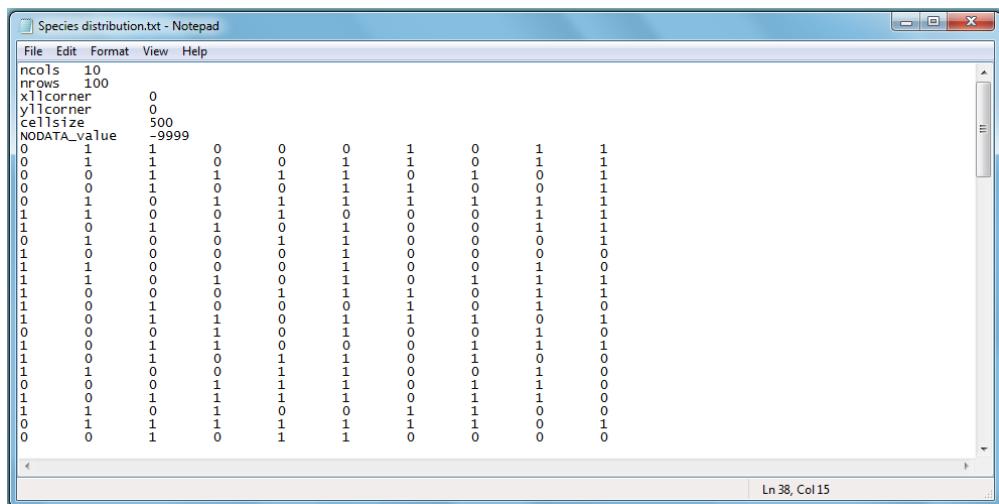
The program can be run as a patch-based model ([see 2.4.1](#)) on the same habitat map described above. An additional file is required: a raster map of the same landscape, where each cell contains the ID number of the patch to which it belongs. Each patch must have a unique positive integer ID. The ID of every cell that does not belong to a patch must be zero. Note that a single patch is the unit at which the density dependence in the population dynamics acts. Therefore, a patch can be discontinuous, i.e. it can contain cells that do not belong to the patch if they are assumed not to affect the dynamics, or on the other hand, patch cells that are not physically contiguous to the rest of the patch cells. For an example of the two files, see the input files provided for the second tutorial ([section 4.2](#)).

### *Costs layer*

When using SMS as the movement model (see [2.5.4](#) and [3.2.7](#)), RangeShifter requires habitat costs or resistance to movement. These can be set manually or imported as a raster map. The map has to match the landscape raster in extent, coordinates and resolution, and each cell contains a cost value. Importing a cost layer is the only option when the landscape comprises habitat coverage or quality. Moreover, using a costs layer allows for costs to be a function of multiple variables instead of a simple value associated to the habitat type.

### 3.1.2 Species distribution

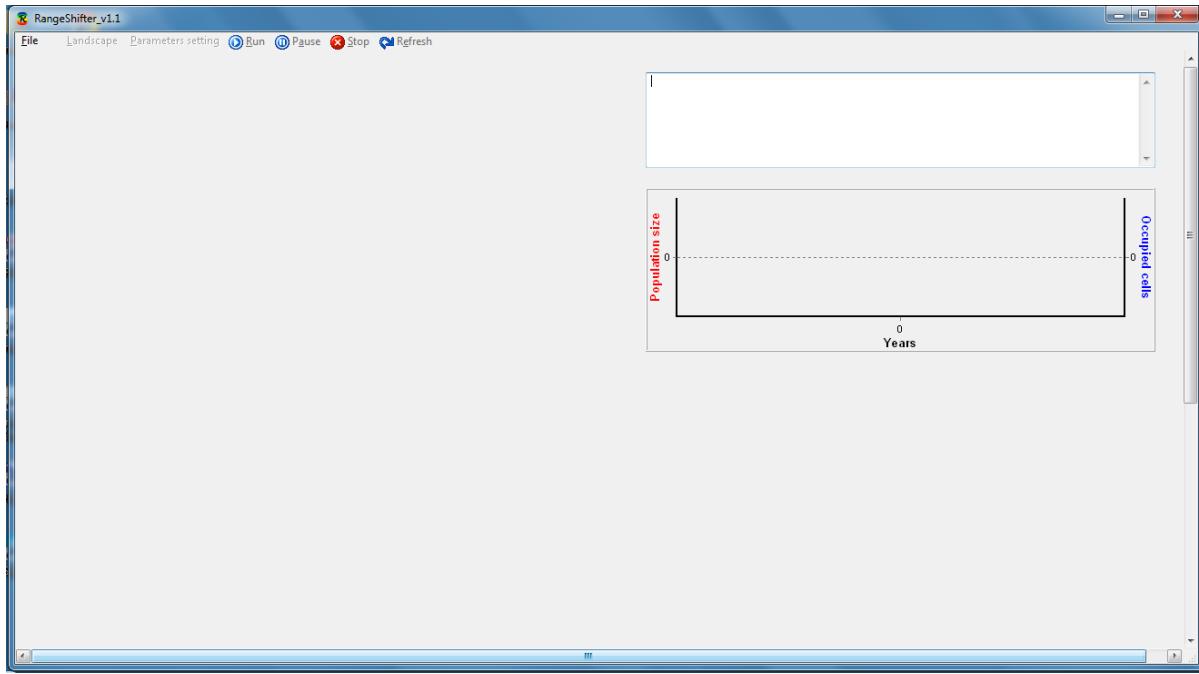
A species distribution map can be overlaid on top of the habitat map. The map must be in raster format and be aligned with the landscape map, i.e. the coordinates of the lower-left corner must be the same (Figure 3.2). The extent of the map does not have to be necessarily the same as the landscape. The resolution can be the same or coarser, provided that it is a multiple of the landscape resolution. For example, if the landscape cell size is 250m, the species distribution can be at the resolution of 250m, 500m, 750m, 1000m etc. Each cell of the species distribution map must contain either 0 (species absent or not recorded) or 1 (species present).



**Figure 3.2.** Example of a species distribution file

The current version of RangeShifter does not provide the possibility of using batches of species distribution maps through the GUI. However, it is possible to specify multiple distribution maps for each simulation in batch mode ([see 3.3](#)).

## 3.2 The graphical user interface



**Figure 3.3.** The RangeShifter graphical user interface.

### 3.2.1 Main menu

The Main Menu comprises three drop-down menus (**File**, **Landscape** and **Parameter setting**) and four buttons (**Run**, **Pause**, **Stop** and **Refresh**) (Figure 3.3).

1. **File** sub-menu.
  - a. **Set Directory**. Allows setting the working directory for the project.
  - b. **Batch Mode**. To run the model in batch mode, disregarding the GUI.
2. **Landscape** sub-menu.
  - a. **Import Raster**. To load landscape and species distribution maps.
  - b. **Generate Artificial Landscape**. To open the artificial landscape generator.
  - c. **Environmental Gradient**. Allows generating an artificial environmental gradient on top of the landscape.
3. **Parameter setting** sub-menu.
  - a. **Species**. To set the species parameters.
  - b. **Simulations**. To set the simulation parameters.
4. **Run**. This button starts the simulation (for both batch and non-batch versions).
5. **Pause**. Allows pausing the model while it is running. Pressing Run will continue the simulation. This option is not active when the model is running in batch mode.

6. **Stop.** Allows interrupting the simulation before it is completed. If running the program via GUI, the program can be refreshed for further use without the need to restart it. If running in batch mode the program must be closed.
7. **Refresh.** Allows refreshing the simulation when completed or manually stopped.

**Note:** If, when the simulation is run, an error message “External exception EFACE” appears, it is because the number of individuals in the simulated population has exceeded the amount of computer memory available to store them. In this situation, click *OK* on the message window, then *Stop* and *Refresh* the simulation. Check the parameter values (particularly the fecundity and carrying capacity) and correct them if necessary. If they are correct, then it is not possible to run the simulation as specified. A possible solution might be to reduce the extent of the landscape. If the message persists even if you have changed the parameters, it may necessary to close RangeShifter and restart it.

### 3.2.2 Getting started

Open RangeShifter by double clicking on the executable icon. Set the working directory by clicking on *File* → *Set Directory* and selecting any file in the folder (Figure 3.4). Note that you should select a file (which can also be the executable file itself) and not another folder. Additionally, the working directory must contain three folders named **Inputs**, **Outputs** and **Output\_Maps** which can be generated simply using Windows ‘New folder’ command. All the input files must be placed in the first folder. **The last two folders are fundamental: if they are not there and/or they are not named correctly the outputs will not be saved.**

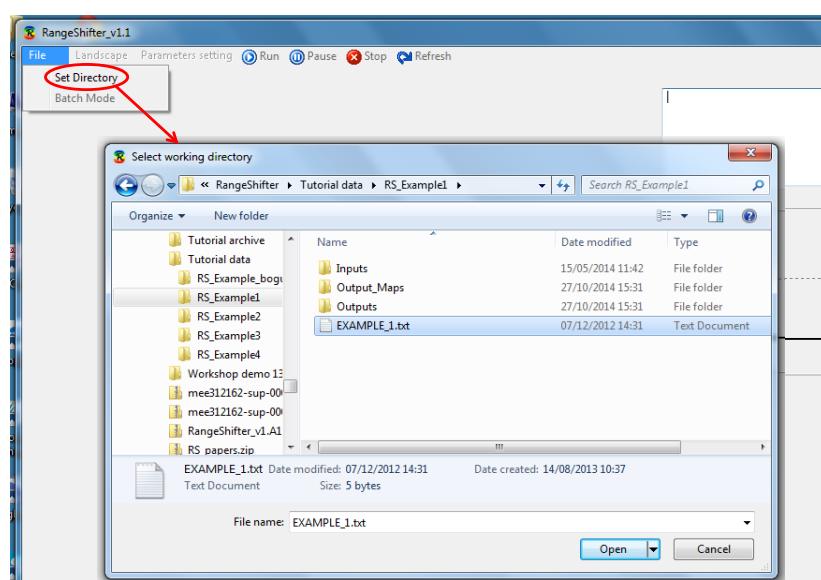


Figure 3.4. Setting the working directory.

There are two alternative options for running the model: from the GUI or in batch mode. In the first case, all the parameters are set from the user interface. To set up a simulation, you will need firstly to set the options and parameters relating to the landscape (see 3.2.3-5) and secondly set the species and simulation parameters (see 3.2.6-8). In the batch mode, all the parameters are imported from a set of text files, allowing multiple simulations to be run automatically. For running the model in batch mode, click *File → Batch Mode* ([see section 3.3](#)).

### 3.2.3 Setting the landscape

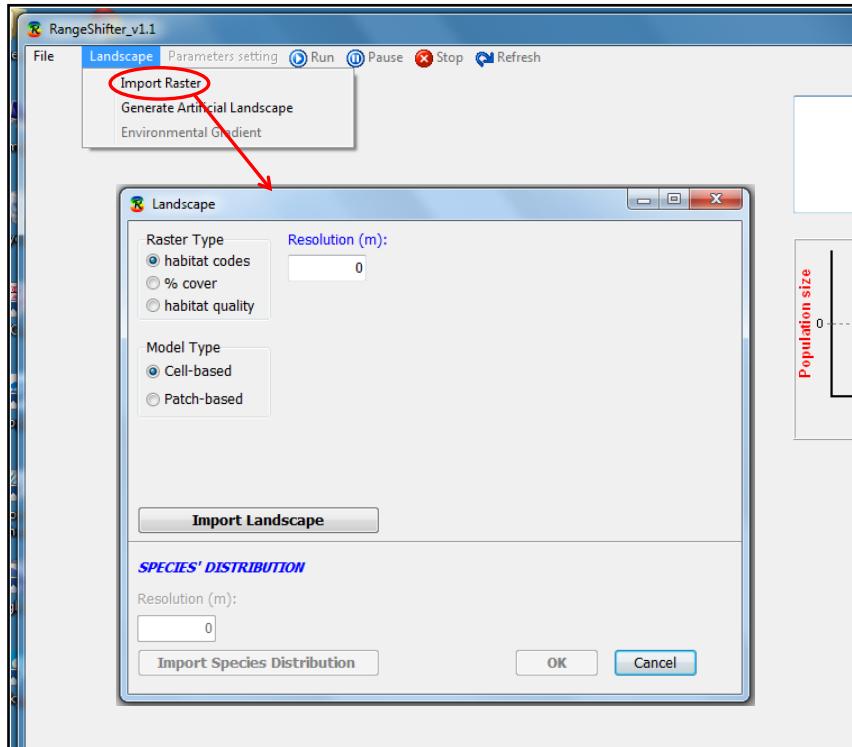
From the drop down *Landscape* sub-menu there are initially two options available:

1. *Import Raster*
2. *Generate Artificial Landscape*.

#### *Import raster*

In this case the model will run on imported maps. RangeShifter requires the maps to be text files with the standard six headers ([see section 3.1.1](#)). The maps can either be real landscapes or artificial landscapes that have been previously generated with any landscape generator (including the one available in RangeShifter).

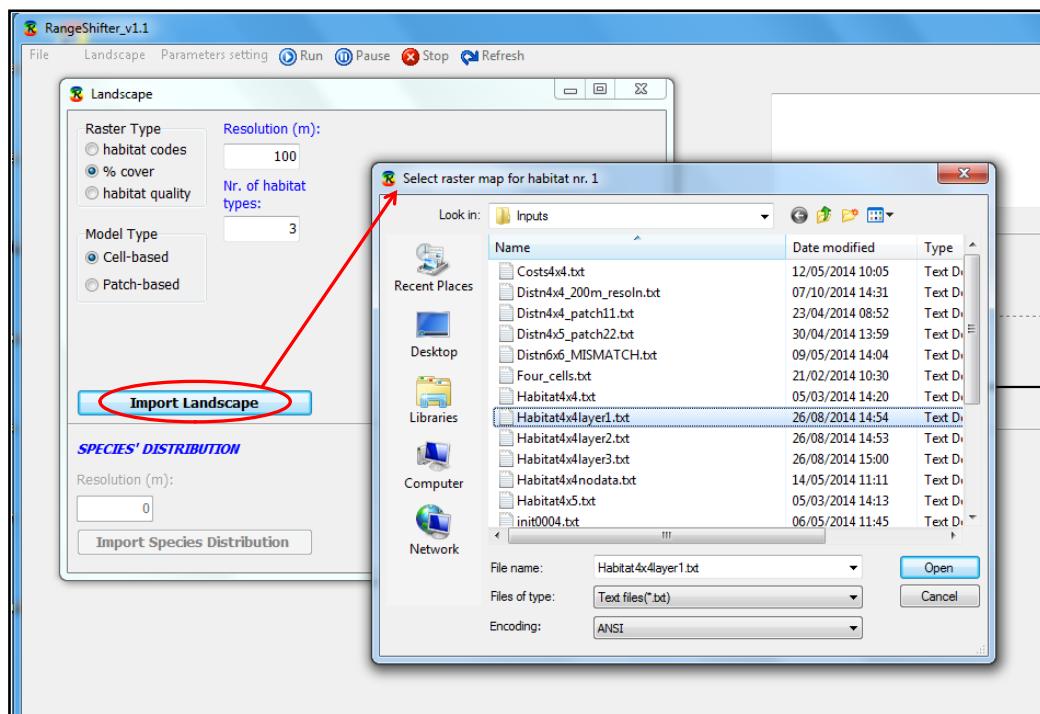
By clicking on *Landscape → Import Raster* the window *Landscape* will open (Figure 3.5).



**Figure 3.5.** The *Landscape* window.

The model can up-load three types of raster maps, differing according to the type of data they contain ([see section 3.1.1](#)): *habitat codes*, *percentage cover* and *habitat quality*. Choose the option corresponding to the landscape to be loaded.

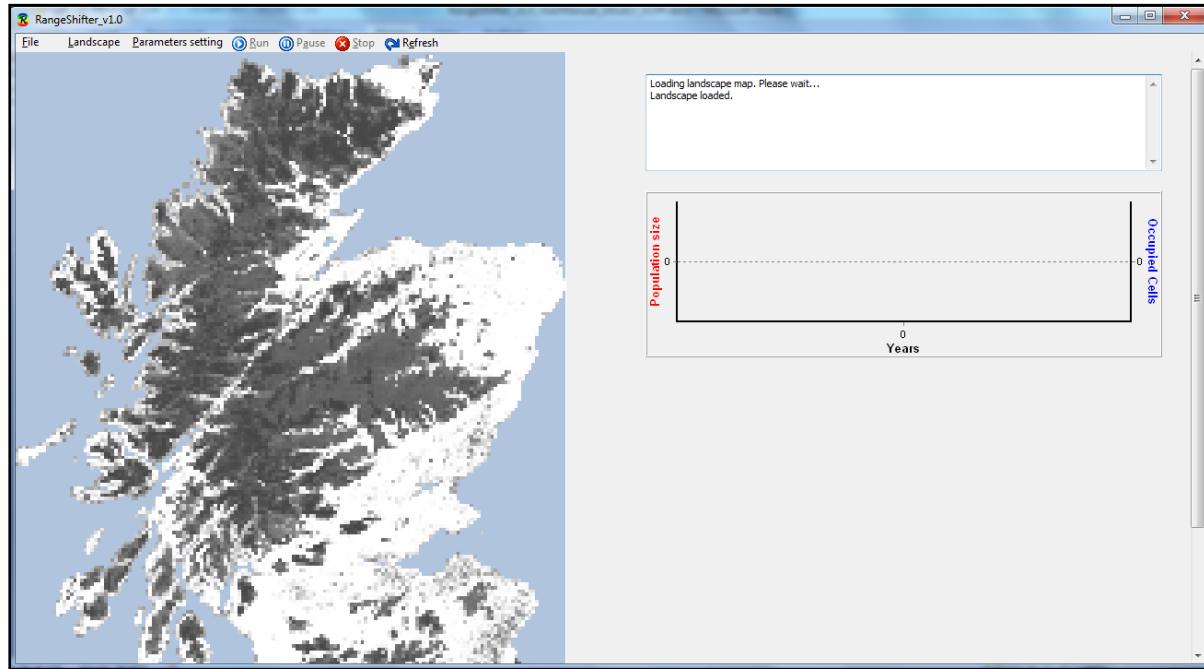
- 1. Raster with habitat codes.** Set the landscape *resolution* (meters), which has to match the one in the raster file, click on the button *Import Landscape* and from the dialog *Select raster map* select the desired map file. The *number of habitat types* and the habitat codes themselves will be determined from the file as it is read into the program.
- 2. Raster with habitat percentage cover.** Set the landscape *resolution* (meters), which has to match the one in the raster file, and the *number of habitat types*. By clicking on the button *Import Landscape* the dialog *Select raster map for habitat nr. 1* will appear. Select the habitat for the first habitat type (Figure 3.6). If the set number of habitats is greater than one, a corresponding number of dialogs will open sequentially allowing importing a map for each habitat type.



**Figure 3.6.** Importing a landscape given by the percentage cover of multiple habitats.  
A dialog for selecting a raster map for each habitat type will appear sequentially.

**Raster with habitat quality.** In this case there are no habitat types as such, but only a quality value from 0.0 to 100.0, which will be linked linearly to the carrying capacity of the cell ([see 3.1.1](#)). As in the other cases, set the landscape *resolution* (meters) and then click on the

button *Import Landscape* to load the landscape map. The map will be visualised with a grey scale, where black corresponds to quality = 0 and white to quality = 100 (Figure 3.7).



**Figure 3.7.** Habitat quality map for mink (*Neovison vison*) in Scotland. Habitat quality was derived from a model of the probability of occurrence of mink in Scotland, which in turn was predicted from presence-only data using a logistic regression model (Elaine Fraser, *pers. comm.*).

#### *Import raster: model type*

RangeShifter can be run either as cell-based or as patch-based model ([see section 2.4.1](#)). The default mode is cell-based, but this can be changed by selecting *Patch-based* in the box *Model Type*. Select this option before importing the landscape. When this option is selected, the box *Visualise patch landscape* appears. Ticking this will present an image of the landscape (in an additional window once the patches are loaded), in which each patch is identified by a unique colour.

For running in **patch-mode**, RangeShifter needs an additional file to the habitat map ([see 3.1.1](#)). This is a raster map having the same cell size and the same dimensions as the habitat map and containing the patch ID of each cell. After the habitat map has been imported, a confirmation message will appear, followed immediately by the dialog *Select patch raster map*, enabling loading of the patch IDs file, which may take some time, because patches' spatial characteristics are computed and stored during loading.

### Changing the default colours

In the case of habitat codes and habitat percentage cover landscapes, once all the files (including, if selected, the patch file) have been read successfully, a table listing the habitat codes (numbered 1...N for percentage cover). There are three additional columns for each habitat, named R, G and B. These refer to the standard RGB colour system where the colour of a screen pixel is defined by the combination of red, green and blue, each of which is an integer that can vary between 0 and 255. The RGB columns set a specific colour for each habitat type. There are 21 colours given by default (Table 1). These colours can be left as they are or changed at the user's discretion by editing them and clicking on the *Change Habitat Colours* button. After the 21<sup>st</sup> habitat, all colours are set to black (RGB = (0,0,0)) and therefore need to be set manually. Note that RangeShifter represents the population size in each cell or patch with a colour scale going from dark red to bright orange, hence choosing similar colours for the habitat types can create confusion in the visualisation. Note also that for habitat percentage cover landscapes, the colour in which a cell is displayed will be the one for the most abundant habitat, and cells where all layers are zero are drawn in black.

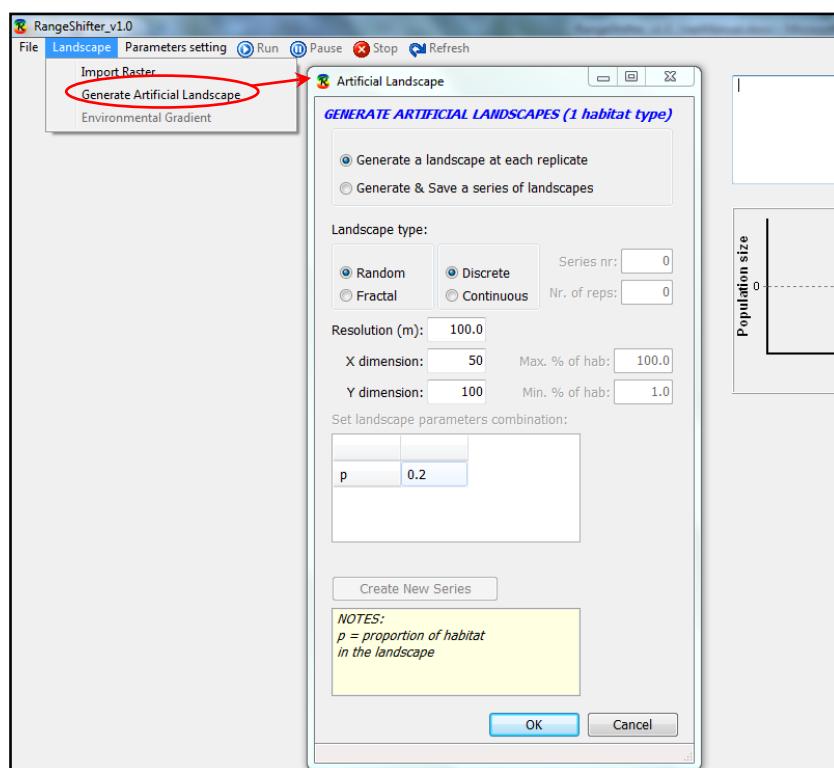
**Table 1.** Default colour codes for the first 21 habitat types.

Habitat	R	G	B
1	0	200	50
2	250	200	150
3	200	200	100
4	100	250	100
5	200	150	250
6	150	150	150
7	153	128	0
8	255	100	60
9	128	26	128
10	230	140	166
11	0	100	0
12	0	128	115
13	0	0	255
14	0	180	190
15	200	200	200
16	60	60	60
17	0	0	0
18	204	179	0
19	255	255	128
20	128	102	255
21	0	0	128

### Artificial landscapes

As an alternative to importing landscape maps, either real or artificial, RangeShifter can be set to generate a new neutral artificial landscape at each replicate by using the landscape generator embedded within it ([see 2.3.2](#)). From the *Landscape* sub-menu, click on *Generate Artificial Landscape* to open the window *Artificial Landscape* (Figure 3.8). This landscape generator allows creating single-habitat maps (habitat vs. matrix). From the first box at the top of the window choose how to use the landscape generator. There are two options:

1. Generate a landscape at each replicate
2. Generate & Save a series of landscapes



**Figure 3.8.** The *Artificial Landscape* window.

#### Artificial landscapes: generate a landscape at each replicate

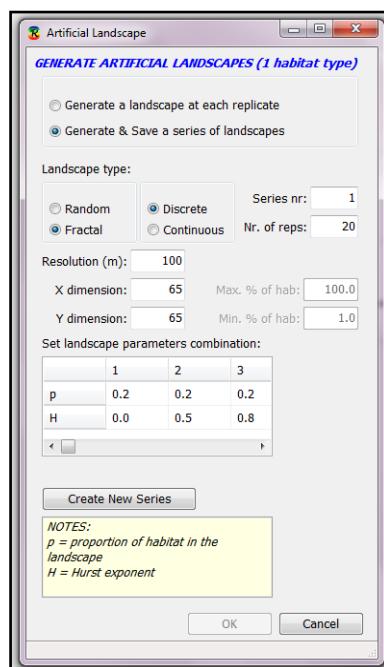
The next choice to be made defines the type of landscape: *Random* or *Fractal* and *Discrete* or *Continuous* ([see 2.3.2](#) for a description of the different types). Next, set the landscape resolution (metres) and its x and y dimensions. Note that for fractal landscapes, there are some constraints to the dimensions: (a) y must be equal to or greater than x, (b) x and y must be equal to  $2^n+1$  (where  $n$  is a positive integer, which may be larger for x than for y, e.g.

X dimension = 33, Y dimension = 65). If *Continuous* landscape is selected, set the minimum and maximum percentage of habitat for a single cell.

- *Random* landscape: set the proportion of habitat cells in the landscape ( $p$ ).
- *Fractal* landscape: set the proportion of habitat cells in the landscape ( $p$ ) and the Hurst exponent ( $H$ ).

#### *Artificial landscapes: generate & save a series of landscapes*

This option allows generation of a series of artificial landscapes, which can be subsequently used within RangeShifter (by importing them as raster maps) or elsewhere. In addition to setting all the option described above, set the series number and the number of landscape replicates. The series number is important, as it will determine the names of the landscapes. Each landscape is saved as a text file in the folder *Inputs*, and a file named *LandFileNNN.txt* (where  $NNN$  is the series number) contains a list of all the landscapes in the format required for running RangeShifter in batch mode. For example, if you create series 123 of 20 random discrete landscapes of 100 rows by 50 columns having  $p = 0.2$ , each map will be named as follows: *Series123discRandom\_X50Y100\_p0.2\_nrN.txt*, where  $N$  is the sequential replicate number from 0 to 19. A series can contain replicates of landscape with different  $p$  values or, in case of fractals, with different combinations of  $p$  and  $H$  (Figure 3.9).

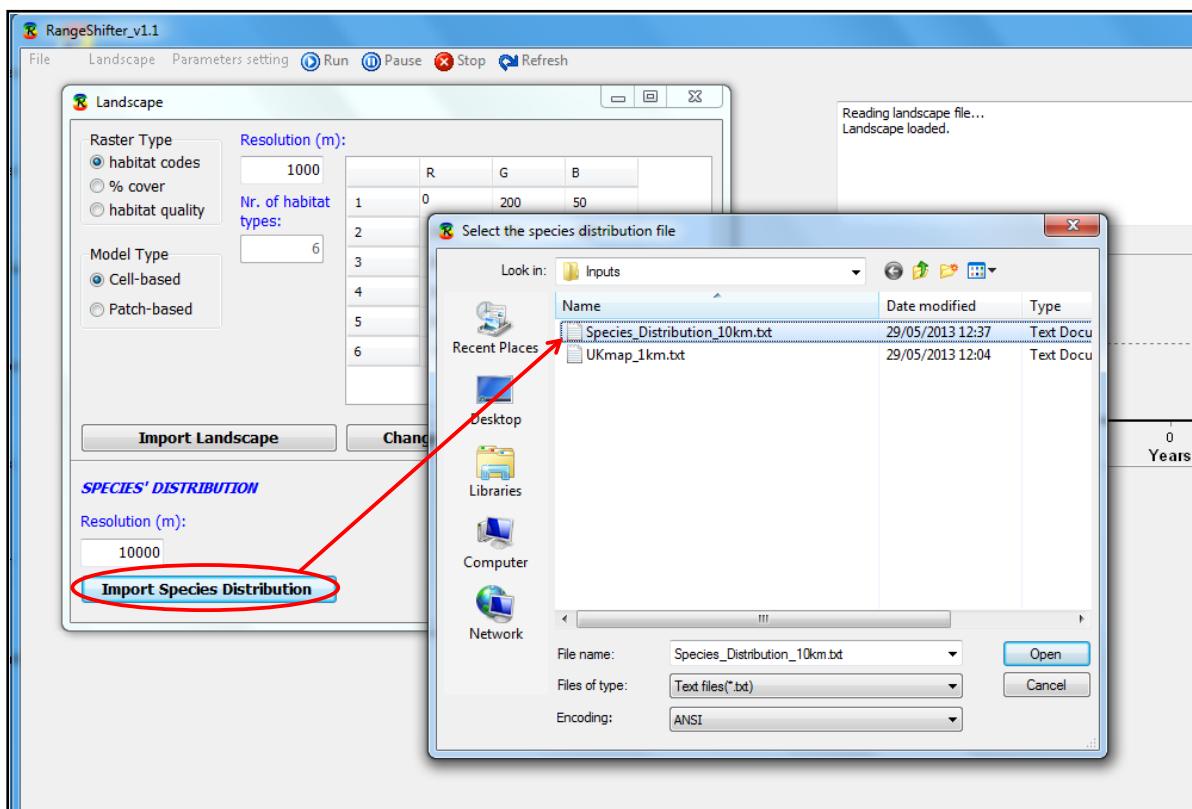


**Figure 3.9.** Example of parameter settings for generating and saving a series of fractals landscapes. Clicking on the button *Create New Series* will generate a series (Series1) of 20 maps with  $p = 0.2$  and  $H = 0.0$ , 20 maps with  $p = 0.2$  and  $H = 0.5$  and 20 maps with  $p = 0.2$  and  $H = 0.8$ , for a total of 60 maps. Each map will be a 65 x 65 raster with a cell resolution of 100m.

**Important note:** Although you are generating a series of *artificial* landscapes, if you subsequently set up a batch to run a set of simulations using that series, the landscapes are regarded and imported as *real* landscapes (because they are *not* generated during the batch run of the program). Moreover, as it is a condition of the batch mode that a landscape having habitat codes must have the codes numbered 1... $N$ , all *discrete* generated landscapes contain habitat codes 1 and 2 only, where 1 is the matrix and 2 is the suitable breeding habitat. Thus they differ from artificial landscapes generated within RangeShifter at run time, which represent the matrix by habitat code 0 and the suitable breeding habitat by habitat code 1.

### 3.2.4 Importing a species distribution map

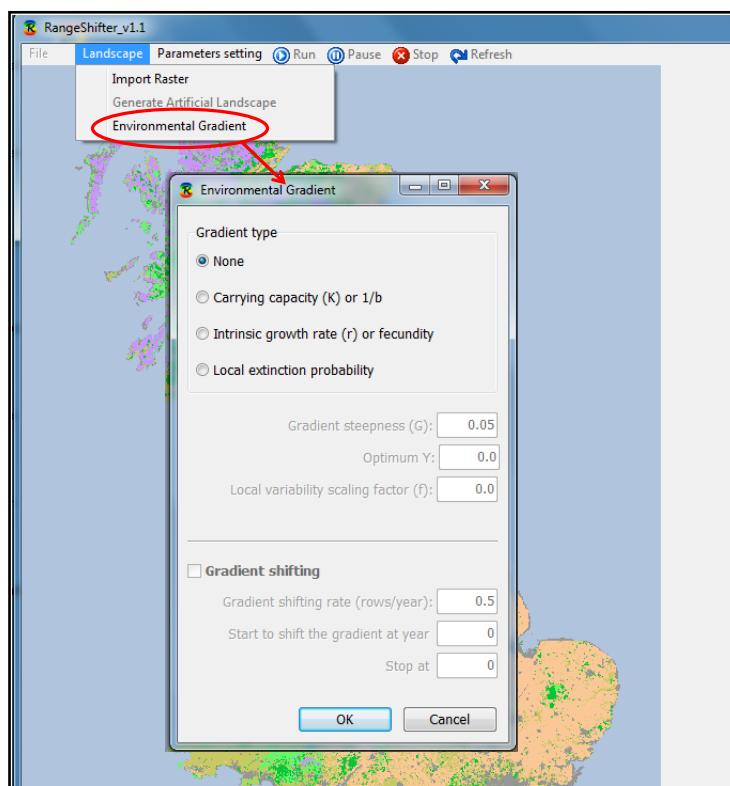
The lower section of the window *Landscape* allows importing of a species distribution map ([see 3.1.2](#)) to be overlaid on the landscape map (note that this option is not available when using the RangeShifter landscape generator to create an artificial landscape at each replicate). This section will become active only after the landscape has been imported. To import the map, first set the *Resolution* (which must be an integer multiple of the landscape resolution) and then click on the button *Import Species Distribution* and select the appropriate file (Figure 3.10).



**Figure 3.10.** Importing the species distribution map derived from Exercise 1, [section 4.1](#)).

### 3.2.5 Environmental gradient

Whether the landscape is imported or automatically generated, it is possible to produce an artificial environmental gradient to be overlaid on top of the habitat map. **This option is available only for cell-based models and not for patch-based models.** By clicking on *Landscape → Environmental Gradient* (which becomes available once the landscape is loaded), the window *Environmental Gradient* will open. Select the *Gradient type* to activate a gradient (Figure 3.11).



**Figure 3.11.** The *Environmental Gradient* window.

There are three types of environmental gradient that can be set ([see section 2.3.3](#) for a full description of the different types):

1. Carrying capacity ( $K$ ) or  $1/b$  in the case of stage-structured models
2. Intrinsic growth rate ( $R$ ) or fecundity ( $\phi$ ) in the case of stage-structured models
3. Local extinction probability

After having chosen the type of gradient set the following parameters:

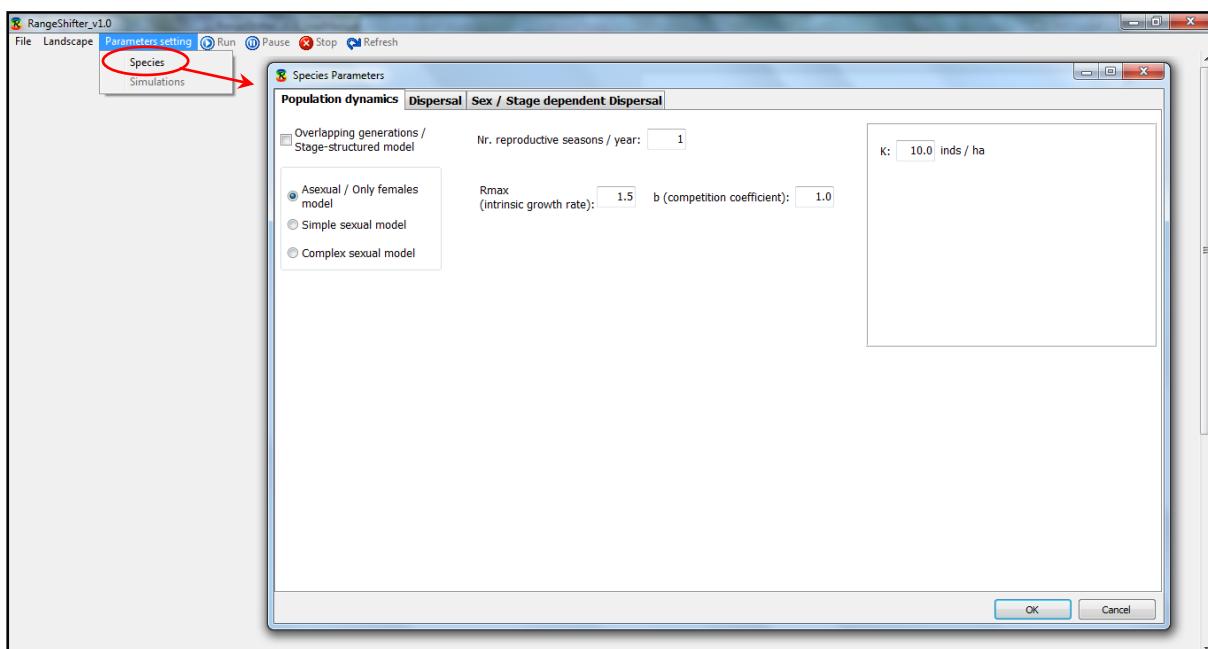
1. Gradient steepness ( $G$ )
2. Optimum Y (the gradient will be created along the y axis)

3. Local variability scaling factor ( $f$ )
4. Local extinction probability at optimum (to be set only if the gradient is in local extinction probability)

The gradient itself must be specified on a scale of 0 to 1, where a value of 1 occurs at the gradient optimum. When applied to carrying capacity or growth rate, the optimum values of  $K$  and  $R$  respectively will be the ones set in the *Species Parameters* window (see 3.2.6). In the case of stage-structured population models, the gradient in  $R$  will be effectively a gradient in fecundity  $\phi$ . If different stages have different fecundities, the same gradient will be applied to the respective fecundity values, assuming that the specified fecundities apply at the gradient optimum. The gradient is constructed in the same way for local extinction probability, but reversed on application, such that the lowest probability of extinction occurs at the gradient optimum.

It is possible to simulate shifting of the gradient by checking the box *Gradient shifting* and setting the shifting rate (rows/year), the year at which the shifting starts and the year at which it ends. The gradient will shift along the y axis towards increasing y (northwards). For an example see the third tutorial (section 4.3).

### 3.2.6 Setting the species parameters: population dynamics



**Figure 3.12.** The *Species parameters* window.

After having set the landscape, the sub-menu *Parameters setting → Species* should be selected to open the *Species Parameters* window (Figure 3.12). The window is composed of three pages: *Population dynamics*, *Dispersal* and *Sex / Stage dependent Dispersal* ([see 3.2.7](#)).

For the population dynamics, the first choice to make is between a model with or without stage structure and overlapping generations. This choice is made by checking / un-checking the box *Overlapping generations / Stage-structured model*.

#### *Non-overlapping generations & no stage structure*

Set the *Number of reproductive seasons / year*. This number must be an integer equal to or greater than 1. Choose between the following three options ([see 2.4.2](#) for the methods description):

1. *Asexual / Only female model*; set the intrinsic growth rate  $R_{max}$  and the competition coefficient  $b_c$
2. *Simple sexual model*; sexual model with no explicit mating system. Set  $R_{max}$ ,  $b_c$  and the *proportion of males*
3. *Complex sexual model*; sexual model with explicit mating system. Set  $R_{max}$ ,  $b_c$ , the *proportion of males* and the maximum harem size  $h$

#### *Overlapping generations & stage-structure*

Set the following three parameters (for details [see section 2.4.2](#)):

1. *Number of reproductive seasons / year*
2. *Probability of reproducing*
3. *Number of reproductive seasons between subsequent reproductions*

Choose between the following three options ([see 2.4.2](#) for the methods description):

1. *Asexual / Only female model* (Figure 3.13a)
2. *Sexual model - no explicit mating system* (Figure 3.13b); set the *proportion of males*
3. *Sexual model - explicit mating system* (Figure 3.13c); set the *proportion of males* and the average harem size  $h$

The parameters for the stage structure are set in the lower panel *Stage-structure population model*. Set the *Number of stages* and the *Max. age*. Note that the number of stages cannot be less than 2 because of the default juvenile stage required, nor greater than

10 (see [2.4.3](#)). The maximum age sets an upper age limit at which each individual that reaches it dies; if a very high maximum is set, all mortality is stochastic as determined by the specified transition matrix parameters (and very old individuals may occur by chance).

*Transition Matrix.* Parameters for reproduction, survival and development are entered in the form of a transition matrix ([see 2.4.3](#) and Figure 3.13).

*Minimum Ages.* Set the minimum age for each stage, i.e. the age which an individual in stage  $s-1$  must already have reached before it can develop into stage  $s$  (**note that the interpretation of minimum age is different in v1.1 than in v1.0**). This allows combining a stage-structured model with an IBM running on a yearly basis, and therefore explicitly accounting for the individuals' ages. The minimum age for juveniles (stage 0) is by definition zero, and the minimum age for stage 1 must also be zero (because individuals may not persist as juveniles beyond the breeding season in which they are born).

*Scheduling of Survival.* Select when survival and development should occur between the three following options ([see 2.4.3](#)):

1. *At reproduction*
2. *Between reproductive events*
3. *Annually*

**Figure 3.13 (next page).** Parameter windows for setting the models used in Box 1a and 4 ([section 2.4.3](#)). (a) Asexual / only-female, 4 stages model (juveniles + 3 stages). Fecundities  $\phi_2$  and  $\phi_3$  represent the mean number of female offspring produced per reproductive female. (b) Sexual model without complex mating system or sex-dependent demographic parameters. Fecundities  $\phi_2$  and  $\phi_3$  represent the mean number of offspring (males and females) produced per reproductive female. (c) Sexual model with complex mating system ( $h = 1$ ) and sex-dependent demographic parameters. The blue rectangles highlight what should be set in place of male fecundity: 1 for reproductive males or zero for non reproductive males. Note that in this case not all the matrix is visible in the figure. In all models the value of  $1/b$  (strength of density dependence in reproduction) is set in the top-right box. Note that the maximum age is set to an arbitrary high value which is the way, in RangeShifter, of not imposing any maximum age.

(a) Population dynamics | Dispersal | Sex / Stage dependent Dispersal

Overlapping generations / Stage-structured model      Nr. reproductive seasons / year: 1      1/b: 10000. Strength of density-dependence

Asexual / Only females model       Simple sexual model       Complex sexual model

Probability of reproducing: 1.0      Nr. of reproductive seasons between subsequent reproduction: 0

**Stage-structure population model**  
Nr. of stages: 4 Max. age: 1000

**Transition Matrix**

	juv	1	2	3
juv	0.0	0.0	1.5	2.5
1	1.0	0.0	0.0	0.0
2	0.0	0.5	0.0	0.0
3	0.0	0.0	0.7	0.8

$\sigma_0 \gamma_0$        $\sigma_1 \gamma_1$        $\sigma_2 \gamma_2$        $\phi_2 & \phi_3$

**Minimum Ages**

Stage	Age
1	0
2	0
3	0

**Scheduling of Survival**  
 At reproduction       Between reproductive events       Annually

**Density Dependence**  
 Fecundity       Development       Survival

**Stages' weights**  
 Fecundity       Development       Survival

**Set weights**

(b) Population dynamics | Dispersal | Sex / Stage dependent Dispersal

Overlapping generations / Stage-structured model      Nr. reproductive seasons / year: 1      1/b: 10000. Strength of density-dependence

Asexual / Only females model       Simple sexual model       Complex sexual model

Sex ratio (proportion of males): 0.5

Probability of reproducing: 1.0      Nr. of reproductive seasons between subsequent reproduction: 0

**Stage-structure population model**  
Nr. of stages: 4 Max. age: 1000

**Transition Matrix**

	juv	1	2	3
juv	0.0	0.0	3.0	5.0
1	1.0	0.0	0.0	0.0
2	0.0	0.5	0.0	0.0
3	0.0	0.0	0.7	0.8

**Minimum Ages**

Stage	Age
1	0
2	0
3	0

**Scheduling of Survival**  
 At reproduction       Between reproductive events       Annually

**Density Dependence**  
 Fecundity       Development       Survival

**Stages' weights**  
 Fecundity       Development       Survival

**Set weights**

(c) Population dynamics | Dispersal | Sex / Stage dependent Dispersal

Overlapping generations / Stage-structured model      Nr. reproductive seasons / year: 1      1/b: 10000. Strength of density-dependence

Asexual / Only females model       Simple sexual model       Complex sexual model

Sex ratio (proportion of males): 0.5      h (maximum harem size): 1

Probability of reproducing: 1.0      Nr. of reproductive seasons between subsequent reproduction: 0

**Stage-structure population model**  
Nr. of stages: 4 Max. age: 1000

**Transition Matrix**

	1 m	1 f	2 m	2 f	3 m	3 f
juv	0.0	0.0	1.0	3.0	1.0	5.0
1 m	0.0	0.0	0.0	0.0	0.0	0.0
1 f	0.0	0.0	0.0	0.0	0.0	0.0
2 m	0.5	0.0	0.0	0.0	0.0	0.0
2 f	0.0	0.5	0.0	0.0	0.0	0.0

$\phi_{2f} & \phi_{3f}$

**Minimum Ages**

Stage	Age
1 m	0
1 f	0
2 m	0
2 f	0
3 m	0
3 f	0

**Scheduling of Survival**  
 At reproduction       Between reproductive events       Annually

**Density Dependence**  
 Fecundity       Development       Survival

**Stages' weights**  
 Fecundity       Development       Survival

**Set weights**

*Density dependence.* On the right hand side of the *Stage structure population model* panel, select the level(s) at which density dependence acts: *Fecundity*, *Development* and/or *Survival*. In the case of density-dependence in development or survival, set the relative coefficients  $C_\gamma$  and  $C_\sigma$  (see eqns. 11 and 13 and Figure 3.14a). Density-dependence can be uniform across stages or stage-specific, i.e. each stage can have a different effect on the demographic processes of each other stage, and it is affected differently from each stage (see eqns. 10, 12 and 14). This can be set in the box *Stages' weights* by checking the processes for which density dependence should be stage specific (Figure 3.14b). Clicking on the button *Set weights*, the window *Stage-specific density dependence - Stages' weights* will show (Figure 3.14c). The matrices have to be filled in with the stages' weights  $\omega_{ij}$ , i.e. the effect of density of stage  $j$  on the demographic parameters of stage  $i$ . A value of zero means that stage  $i$  is not affected by stage  $j$ .

(a) **stage-structure population model**

Nr. of stages: 4 Max. age: 1000

**Transition Matrix**

	juv	1	2	3
juv	0.0	0.0	1.5	2.5
1	1.0	0.0	0.0	0.0
2	0.0	0.5	0.0	0.0
3	0.0	0.0	0.7	0.8

**Minimum Ages**

Stage	Age
1	0
2	0
3	0

**Scheduling of Survival**

- At reproduction
- Between reproductive events
- Annually

**Density Dependence**

- Fecundity
- Development
- Survival

$C_\gamma$  Development coeff.  
1.0 Development coeff.  
 $C_\sigma$  Survival coeff.  
1.0 Survival coeff.

Processes upon which density dependence is acting

(b) **stage-structure population model**

Nr. of stages: 4 Max. age: 1000

**Transition Matrix**

	juv	1	2	3
juv	0.0	0.0	1.5	2.5
1	1.0	0.0	0.0	0.0
2	0.0	0.5	0.0	0.0
3	0.0	0.0	0.7	0.8

**Minimum Ages**

Stage	Age
1	0
2	0
3	0

**Scheduling of Survival**

- At reproduction
- Between reproductive events
- Annually

**Density Dependence**

- Fecundity
- Development
- Survival

1.0 Survival coeff.

Stage specific density dependence

**Set weights**

(c) **Stage-specific density dependence - Stages' weights**

**Fecundity**

	juv	1	2	3
juv	0.0	0.0	0.0	0.0
1	0.0	0.0	0.0	0.0
2	0.0	0.0	0.7	0.7
3	0.0	0.0	1.0	1.0

$\omega_{32} = \text{Effect of } n_2 \text{ on } \phi_3$

$\omega_{23} = \text{Effect of } n_3 \text{ on } \phi_2$

**Development**

	juv	1	2	3
juv	0.0	0.0	0.0	0.0
1	0.0	0.2	0.2	0.2
2	0.0	0.5	0.5	0.5
3	0.0	1.0	1.0	1.0

$\omega_{11} = \text{Effect of } n_1 \text{ on } \sigma_1$

$\omega_{31} = \text{Effect of } n_1 \text{ on } \sigma_3$

**Survival**

	juv	1	2	3
juv	0.0	0.0	0.0	0.0
1	0.0	0.2	0.2	0.2
2	0.0	0.5	0.5	0.5
3	0.0	1.0	1.0	1.0

OK Cancel

**Figure 3.14.** Options and parameters for density dependence in stage-structured models. The settings in (b) and (c) reproduce , example (b) of Box 3 ([section 2.4.3](#)). Panel (c) provides an illustration of how to enter stage weights  $\omega_{ij}$  for density dependence in fecundity and survival.

### *Demographic density dependence*

At the top-right corner of the *Population dynamics* page there is a panel for setting the demographic density dependence. For a non stage-structured model that applies the Maynard-Smith and Slatkin function, two parameters determine the nature of density-dependence,  $b_c$  and  $K$  ([see 2.4.2](#)). For stage-structured models, the density dependence of each demographic process is determined by a single parameter,  $b$  ([see 2.4.3](#)).

Depending on the type of landscape, there will be either a single value (single habitat type) or the possibility of entering a value for each habitat type.  $K$  or  $1/b$  are expressed in individuals per hectare.

1. **Landscape with habitat codes.** Each cell will have a single value of either  $K$  or  $1/b$  that depends on the cell size and on its habitat type. In patch-based models, the total value for a patch will be calculated by RangeShifter to be the sum of the values of each cell in the patch.
2. **Landscape with habitat percentage cover.** The cell's  $K$  (or  $1/b$ ) is determined by the amount of each habitat in the cell. For example, let's consider a simple case of a Maynard-Smith and Slatkin model where there is one habitat type having  $K = 50/\text{ha}$  and the landscape resolution is 100m. A cell with 30% of habitat cover will have a carrying capacity of 15 individuals. Let's then consider an example where there are two habitat types, where  $K_1 = 50/\text{ha}$  and  $K_2 = 100/\text{ha}$ . A cell with 30% cover of habitat 1 and 50% cover of habitat 2 will have a carrying capacity of 65 individuals.
3. **Landscape with habitat quality.** When the landscape is based on habitat quality, a straight-line relationship between demographic density dependence and quality is assumed. It is up to the user to define quality in a way that leads to a linear relationship at the time of map pre-processing ([see 3.1.1](#)). Therefore, if for example the  $K$  is set to 50/ha, a cell with quality equal to 50.0 will have a carrying capacity of 25 individuals.

*What is  $K$  in a stage-structure model?* Whereas in Maynard-Smith & Slatkin's (1973) model (eqns. 5 and 6), the population equilibrium density is defined by the parameter  $K$ , equilibrium density is an emerging property of the potentially multiple density dependencies in standard matrix modelling. Thus, there is no single parameter to define a priori carrying capacity, and  $1/b$  should not be interpreted as such.

*Estimating the parameters for K or b:*

These parameters related to demographic density-dependence can have a major influence on the outcomes of a model. Thus it is important that care is taken in specifying their values. However, gaining robust estimates for these parameters can be challenging.

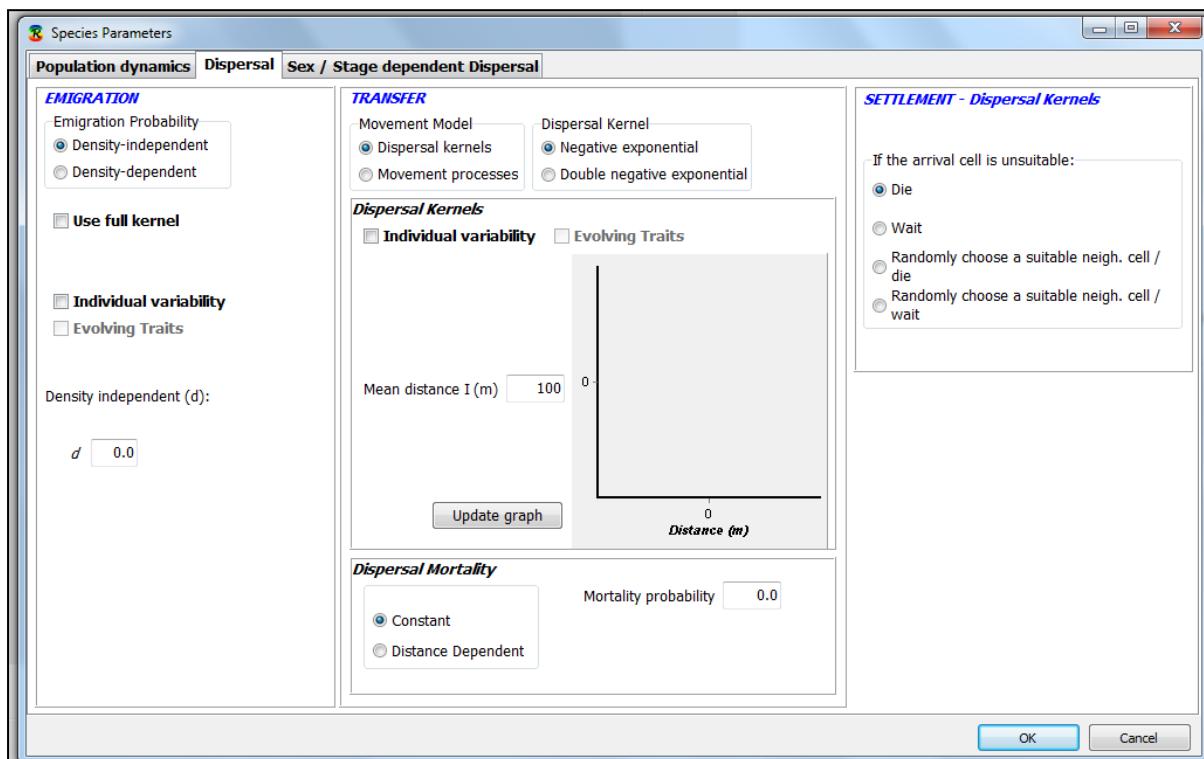
Perhaps ideally, long term data on population abundance will exist for the focal species in multiple locations. In the simplest case where there has been an absence of disturbances, some species will exhibit relatively constant population size and this value can sensibly be used as the carrying capacity ( $K$ ). However, in many cases a population's abundance will fluctuate through time due both to intrinsic (e.g. over-compensatory density-dependence) and extrinsic effects (natural and anthropogenic disturbances). Pragmatically, in such cases, potentially the best approach to gain parameter estimates is likely to involve fitting relatively simple models of population dynamics to the data (e.g. Balčiauskas & Kawata 2009). This can yield both  $K$  where a simple stage unstructured model is being used or  $b$  where a stage-structured model is desired. However, note that obtaining estimates of density-dependence in population dynamics is an important sub-discipline in its own right and one that continues to attract considerable attention (e.g. Lande et al. 2006; Coulson et al. 2008). There will be considerable scope for adopting some of the approaches to make the best possible use of the available time-series data.

Other methods can also be used to obtain estimates for  $K$ . For example, it may be possible to empirically estimate the total amount of food available in a habitat and then divide that value by how rapidly an individual consumes that resource (e.g. Hobbs & Swift 1985; Petit & Pors 1996).

In the absence of empirical data for a focal species, we suggest that judicious use is made of data from related species (where it exists) and expert knowledge. Meta-analyses on the nature of density-dependence in different vital rates and at different life-history stages (e.g. Bonenfant et al. 2009) may also provide useful information that can help guide model parameterisation. It will be important to always visualise the density-dependent relationship gained with different  $b$  values and ensure that they appear sensible. Of course, where there is less data available and thus greater uncertainty in these parameters, it will be even more important that the robustness of results to the particular values selected is ascertained.

### 3.2.7 Setting the species parameters: dispersal

Options and parameters relating to the dispersal process, other than those which are sex- or stage-dependent, are set in the *Dispersal* page of the *Species Parameters* window (Figure 3.15). This page is divided into three panels concerning the three phases of dispersal: *Emigration*, *Transfer* and *Settlement*.



**Figure 3.15.** Page for setting options and parameters relating to Dispersal.

#### Emigration

The first panel concerns the emigration probability, i.e. the probability that an individual will leave its natal patch. The first choice to be made is between density-independent or density-dependent emigration:

1. *Density-independent emigration*; set the emigration probability  $d$ . If this option is chosen and transfer is by dispersal kernel, then the option *Use full kernel* may be checked, which will prevent re-sampling from the kernel if the distance sampled does not move the individual out of its natal cell/patch. Such individuals are treated as philopatric recruits, and hence the kernel determines the probability of emigration. in this case, the emigration probability for all stages/sexes which potentially disperse should be set to 1.0.

2. *Density-dependent emigration*; set the three parameters defining the emigration reaction norm to density (see 2.5.1): maximum emigration probability  $D_0$ , slope  $\alpha$  and inflection point  $\beta$

*Sex / Stage dependent emigration.* Emigration probability or the dependence of emigration on density can be specific to sex, stage or both. Set these options by checking / un-checking the boxes *Sex dependent* and *Stage dependent*, and enter the relevant parameters in the corresponding tables in the *Sex / Stage dependent Dispersal* page (Figure 3.16).

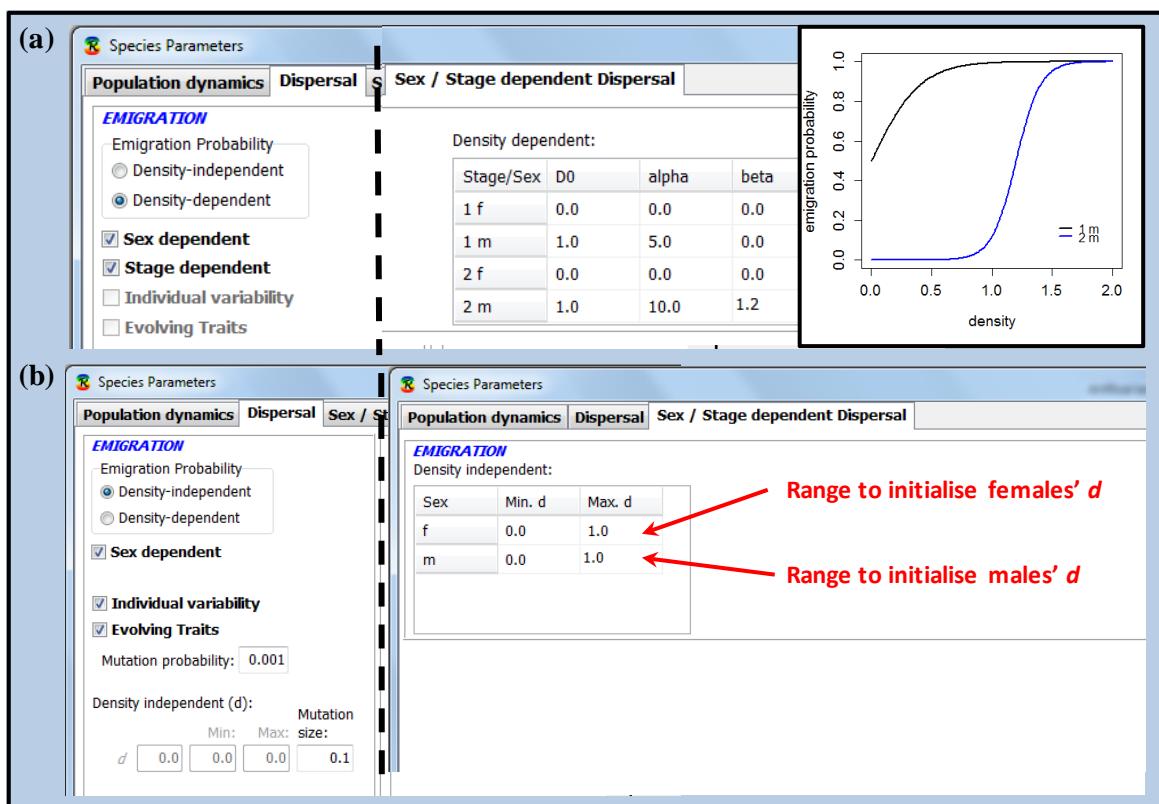
*Comments on parameterising density-dependent emigration (and settlement).* In an ideal case, empirical data would be available to establish the relationship between emigration probability and population density. It would then be possible to estimate the three parameters for the reaction norm directly. However, there will likely be many cases where such data are not available, yet it is still desirable to assume that emigration is density-dependent. A good starting point is to assume limited emigration until density approaches equilibrium density, and a rapid increase around this density until an asymptote is reached at some point above equilibrium density. Obtaining this function is straight-forward in the case of non stage-structured models, where we define the equilibrium density as  $K$ . For stage-structured models, it will first be necessary to establish the emergent equilibrium density. For example, in boxes 1, 2, 3 and 4 (section 2.4.3) this has been achieved both with RangeShifter and with Excel. Of course, the same could be achieved by solving the matrix analytically. Similar approaches can be taken for parameterising the function for density-dependent settlement decisions.

*Inter-individual variability.* Emigration parameters can be set to vary between individuals by checking the box *Individual variability*. The current version of RangeShifter does not allow for this option with stage-structured models. If the option for inter-individual variability is selected, at the initialisation time, each individual will be given traits randomly chosen from uniform distributions, for which the user has to specify the minimum and maximum values.

1. *Density-independent emigration.* Set the minimum and maximum emigration probability  $d$ . The initial individual trait will be sampled from  $U(\min_d, \max_d)$ .
2. *Density-dependent emigration.* Set the minimum and maximum values for the three parameters  $D_0$ , slope  $\alpha$  and inflection point  $\beta$ . The initial individual traits will be:  
$$D_0 = U(\min_D_0, \max_D_0), \alpha = U(\min_\alpha, \max_\alpha) \text{ and } \beta = U(\min_\beta, \max_\beta).$$

*Evolving traits.* If there is inter-individual variability in the emigration traits, these traits can be allowed to evolve (2.1.4) by checking the box *Evolving Traits*. In this case, the parameters to set are the *Mutation probability*, i.e. the probability that each trait will independently mutate, and the *Mutation size ( $\mu$ )* for each trait. For example, if the emigration is density-independent and has a mutation size of 0.1, a mutation event will change the individual  $d$  to  $d + U(-0.1, 0.1)$  (Figure 3.16b).

Inter-individual variability and evolution of traits are possible also in case of sex-dependent emigration (Figure 3.16b).

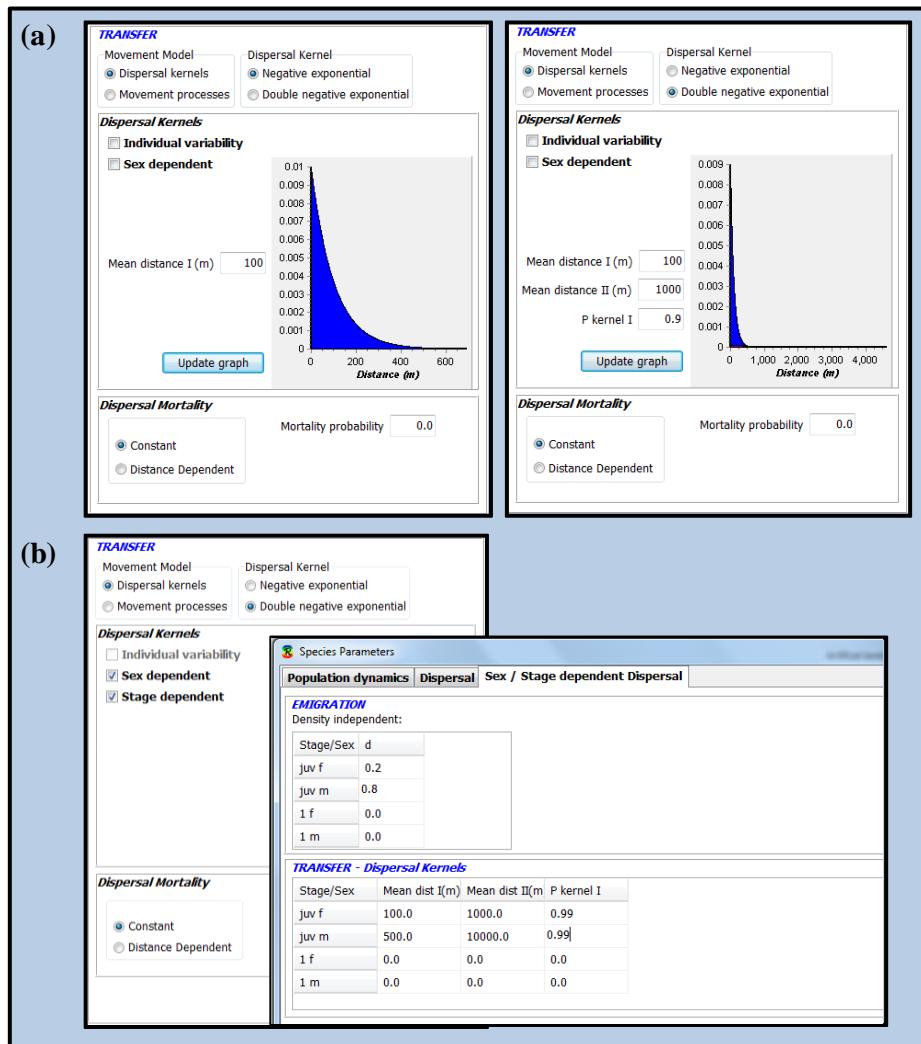


**Figure 3.16.** Options and parameters for the first phase of dispersal: emigration. (a) Example of sex- and stage-specific density-dependent emigration where only males emigrate and different stages respond differently to density. (b) Example of sex-specific density-independent emigration where the emigration probability  $d$  varies between individuals and is allowed to evolve with a mutation probability of 0.001 and a mutation size of 0.1. Each individual of the initial population, both males and females, will receive a value of  $d$  randomly drawn between 0.0 and 1.0.

#### Transfer: dispersal kernels

The transfer phase, i.e. the actual movement of an individual from the natal site to a breeding site, can be modelled either with dispersal kernels or through mechanistic movement models (SMS or CRW) (see 2.5.4). In the RangeShifter GUI, this choice is made in the panel

*Transfer* by selecting between *Dispersal kernels* and *Movement processes* in the *Movement Model* box (Figure 3.17). This section will focus on the first option.



**Figure 3.17.** Options and parameters for dispersal kernels. (a) Negative exponential and mixed kernel (double negative exponential). (b) Sex- and stage-specific mixed kernel.

There are two types of kernels available, which can be selected in the box *Dispersal Kernel*, while the parameters can be set in the corresponding panel (Figure 3.17a):

1. *Negative exponential*. Set the mean of the kernel, *Mean distance I (m)*.
2. *Double negative exponential*. Set the means for the two kernels, *Mean distance I (m)* and *Mean distance II (m)*, and the probability that an individual will disperse according to the first kernel, *P kernel I*.

To visualise the kernels, click on the button *Update graph*.

Note that mean dispersal distances must be equal or greater than the cell size. Or conversely, the landscape resolution should be chosen to be equal or smaller than the mean dispersal distance. In fact, distance and direction are re-sampled until the individual leaves the natal cell (2.5.3); therefore a mean dispersal distance that is too small relative to the cell size could potentially cause the program to re-sample indefinitely. To avoid these problems the program does not allow setting mean dispersal distances that are smaller than the landscape resolution. There is only one exception to re-sampling, if the *Use full kernel* option is specified. In this case the dispersal kernel encompasses both emigration and transience phases.

*Sex- / Stage-dependent dispersal kernels.* Both types of kernel can be sex- or stage-dependent or both. Set these options by checking / un-checking the boxes *Sex dependent* and *Stage dependent* and enter the relevant parameters in the tables in the *Sex / Stage dependent Dispersal* page (Figure 3.17b).

*Inter-individual variability.* As for emigration, dispersal kernel parameters can be set to vary between individuals by checking the box *Individual variability* (option not possible with stage-structured models). The traits will be initialised from uniform distributions with the set limits:

1. *Negative exponential*; set the minimum and maximum mean for the kernel, *Mean distance I* (m)
2. *Double negative exponential*; set the minimum and maximum values for the three parameters *Mean distance I* (m), *Mean distance II* (m) and *P kernel I*

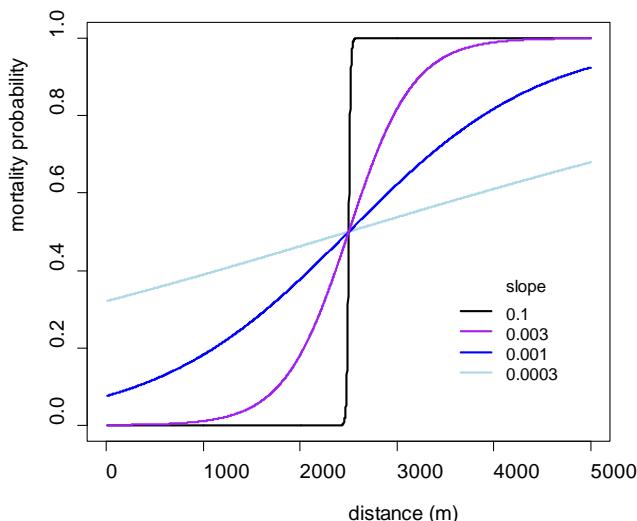
*Evolving Traits.* The dispersal kernel traits can be set to evolve by checking the box *Evolving Traits*. Set the *Mutation probability*, i.e. the probability that each allele will independently mutate, and the *Mutation size ( $\mu$ )* for each trait. As for emigration, inter-individual variability and evolution of dispersal kernels are possible also in the case of sex-dependent kernels.

It is important to stress again here the difference between kernels that apply only to individuals that emigrate and kernels that apply to the entire population. In the first case, mean dispersal distances are not allowed to evolve below the cell resolution; the proportion of individuals dispersing is determined by the emigration probability, which can be set to evolve as well. In the second case, the kernel is applied to all individuals and mean dispersal

distances are allowed to evolve down to zero. Therefore, evolving this type of kernel means evolving together (and not independently) emigration probability and dispersal distance.

*Dispersal Mortality.* In addition to the inherent dispersal mortality emerging from the interaction between the implementation of the kernel and the landscape structure ([see 2.5.3](#)), it is possible to set an explicit dispersal mortality probability which can be either *constant* or *distance-dependent*. Select one of these two options from the box located at the bottom of the *Transfer* panel.

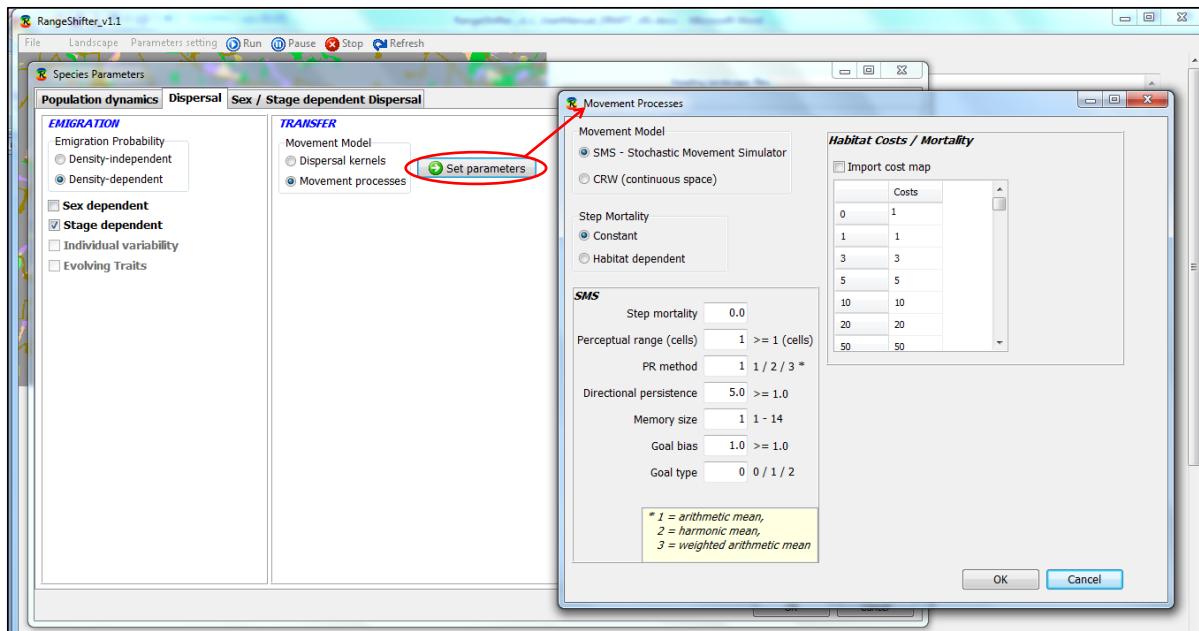
1. *Constant* dispersal mortality. Set the *Mortality probability*.
2. *Distance-dependent* dispersal mortality. Set the *slope* and the *inflection point* for the distance-dependence function (Figure 3.18).



**Figure 3.18.** Distance-dependent dispersal mortality. Examples of how the mortality probability increases with distance are shown for four different slopes. The inflection point is 2000m in all cases.

#### *Transfer: movement processes*

There are two movement models available within RangeShifter: the Stochastic Movement Simulator, SMS (Palmer et al. 2011) and correlated random walk, CRW ([see 2.5.4](#)). By selecting *Movement processes*, the button *Set parameters* appears. Clicking on it will open the window *Movement Processes* where the movement parameters can be set (Figure 3.19).



**Figure 3.19.** Opening the *Movement Processes* window.

### Stochastic Movement Simulator, SMS

Two panels allow setting the parameters for SMS (Figure 3.19). This version of RangeShifter does not incorporate sex- or stage-dependent parameters for SMS nor individual variability or traits evolution.

1. *Habitat Costs / Mortality* panel. There are two ways of setting the habitat costs. Costs must be integer numbers equal to or greater than 1 ([see 2.5.4](#)).
  - a. *Import cost map*. By checking this box, the costs will be imported as a map ([see 3.1](#) for details on the map format). When the rest of the SMS parameters have been set, clicking on the OK button will allow selecting of the cost map. It is possible to visualise the cost map by checking the box *Visualise costs landscape*. When the habitat map is a raster with habitat percentage cover or habitat quality, importing a cost map is the only possible option.
  - b. *Manually insert cost for each habitat type*. Habitat costs can be entered manually in the dedicated table.
2. *SMS* panel. Set the SMS parameters:
  - a. *Step mortality*. Use this box to set the per-step mortality if *Step Mortality* has been set to *Constant*. In the case of habitat-dependent per-step mortality, select that option in the box *Step Mortality* and enter a per-step mortality probability for each habitat type in the dedicated table.

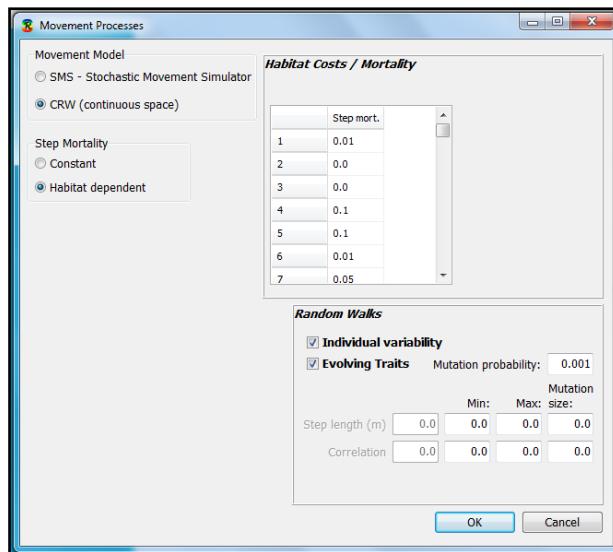
- b. *Perceptual range (cells)* must be equal to or greater than 1.
- c. *PR method*. Method for calculating the effective costs based on what the individual perceived within its perceptual range. This parameter can assume one of three values: 1 (arithmetic mean), 2 (harmonic mean) and 3 (weighted arithmetic mean).
- d. *Directional persistence* must be equal to or greater than 1.
- e. *Memory size* must be an integer in the range 1 to 14.
- f. *Goal bias* must be equal to or greater than 1.
- g. *Goal type* may currently only take the values 0 (none) or 2; the latter case applies a bias away from the natal location (i.e. dispersal bias), the strength of which is determined by the *Goal bias* parameter.

#### *Correlated random walk, CRW*

The CRW parameters are set in the panel *Random Walks* (Figure 3.20). These are *Step length (m)*, step *Correlation* and *Step mortality*. The per-step mortality probability is set through the relevant box if constant or through the habitat-dependent step mortality table, where a probability must be entered for each habitat type. As for SMS, it is not possible to have sex- / stage- dependent parameters for CRW.

*Inter-individual variability.* Step length and correlation can vary between individuals. Check the box *Individual variability* and set the minimum and maximum values. The traits will be initialised from uniform distributions with the set limits.

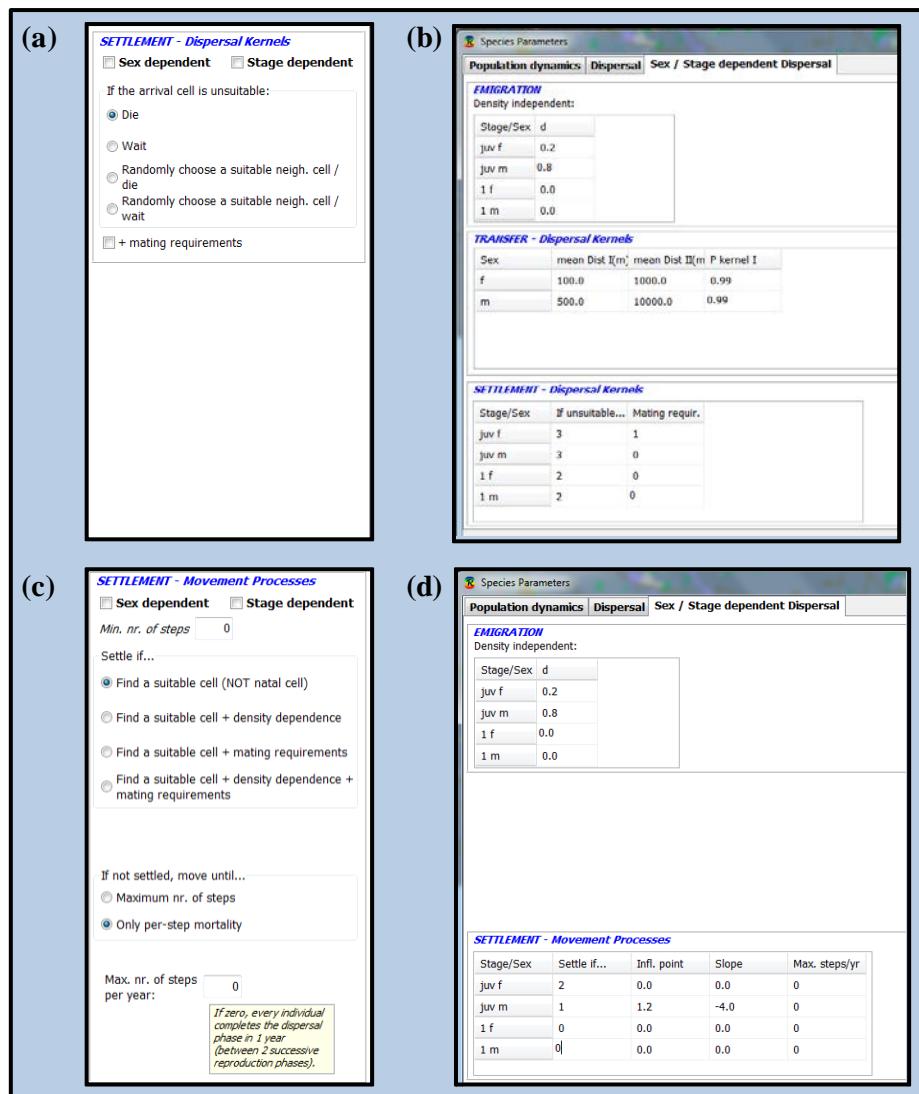
*Evolving traits.* The CRW traits can also be allowed to evolve. Check the box *Evolving traits* and set the *Mutation probability* and the *Mutation size* for both traits. If you would like only one of the two traits to evolve, just set the mutation size for the other one equal to zero. Per-step mortality is not allowed to vary between individuals or to evolve. Note that step length may not evolve below one fifth of the landscape resolution, and correlation may not evolve above 0.999.



**Figure 3.20.** Setting the parameters for CRW.

### Settlement

The last panel in the *Dispersal* page is dedicated to the settlement rules, i.e. the rules that determine whether a dispersing individual will stop in a particular cell or patch and settle there to breed. RangeShifter provides different settlement rules depending on whether the transfer involves dispersal kernels or movement processes ([see 2.5.5](#)). When selecting between these two options, the panel *Settlement* will automatically change (Figure 3.21). The current version of RangeShifter does not implement individual variability or evolution of settlement strategies.



**Figure 3.21.** Options and parameters for the settlement phase. (a) Settlement in the case of transfer modelled with dispersal kernels. (b) Sex- and stage-specific settlement rules in the case of transfer modelled with dispersal kernels. (c) Settlement rules in the case of transfer modelled with movement processes. (d) Sex- and stage-specific settlement rules in the case of movement processes.

#### Settlement with dispersal kernels

When individuals are dispersing according to dispersal kernels, they are displaced from the natal cell/patch to another cell/patch at a distance and direction randomly chosen according to the kernel. Once an individual has been placed in the new cell/patch, if the new location is suitable it settles there; otherwise, there are four options ([see 2.5.5](#)):

0. *Die*.
1. *Wait*. Possible only in the case of stage-structured models. The individual stays in dispersal mode, and waits there until the next dispersal event when it will be displaced again from its current location to a new location according to the set kernel.

2. *Randomly choose a suitable neighbouring cell / die.* The model checks the eight nearest neighbouring cells, and if one or more cells are suitable, the individual is randomly placed in one of them. If none of the neighbouring cells is suitable, the individual dies. In the case of patch-based models, if there is a suitable patch adjacent to the current cell, the individual will be placed in that patch.
3. *Randomly choose a suitable neighbouring cell / wait.* As in option 2. If none of the neighbouring cells is suitable, the individual waits until the next dispersal event as in option 1.

A cell/patch is considered suitable if it contains some suitable habitat. In case of sexual models, an additional condition can determine the suitability of the arrival location: the presence of a mate. This option is activated by checking the box *+ mating requirements*. In the current version, this option is not specific to any particular mating system, but simply requires that at least one individual of the opposite sex is present in the arrival cell/patch for settlement to take place.

*Sex / Stage dependent settlement rules.* The four settlement options described above, plus the mating requirements, can be set as sex- or stage-specific or both. Check the boxes *Sex dependent* and *Stage dependent* and set the parameters in the *Sex / Stage dependent Dispersal* page. An example is illustrated in Figure 3.21b, where in the table *SETTLEMENT - Dispersal Kernels*, the four rows represent females (f) and males (m) at the two stages, while the two columns represent the settlement rule in case of arriving in an unsuitable cell/patch and whether the individual requires finding a mate to settle. Numbers between 0 and 3 (corresponding to the four rules described above) should be entered in the first column. The second column requires either 0 (no mating requirements) or 1. In this example only the juveniles, both males and females, will emigrate, and dispersal is male biased, males dispersing more and further. As juveniles, both sexes, if arriving in an unsuitable cell/patch, will look for a suitable neighbouring location and if unsuccessful will wait to move again the next season. A female will consider a cell/patch suitable for settling if there is suitable habitat present; a male will require both the presence of suitable habitat and of at least one female. However, if either sex has waited, and developed into an adult, no second wait is allowed, nor is there any requirement to find a mate.

*Settlement with movement processes*

Individuals dispersing by movement processes take a variable number of steps and stop according to rules that must be set (Figure 3.21c).

*Minimum number of steps.* Number of steps that an individual has to take before it is allowed to settle. The default value for this parameter is zero, i.e. the individual will settle as soon as it finds suitable conditions which satisfy the settlement rules.

*Settlement rules:*

0. *Find a suitable cell/patch.* Dispersers settle if they find a cell/patch of suitable habitat.
1. *Find a suitable cell/patch + density dependence.* Individuals settle in suitable cells/patches with a probability dependent on the density of the resident population (see eqn. 16).
2. *Find a suitable cell/patch + mating requirements.* Individuals settle in suitable cells/patches if there is at least one individual of the opposite sex present.
3. *Find a suitable cell/patch + density dependence + mating requirements.* Individuals settle in suitable cells/patches with a density-dependent probability and if there is at least one individual of the opposite sex.

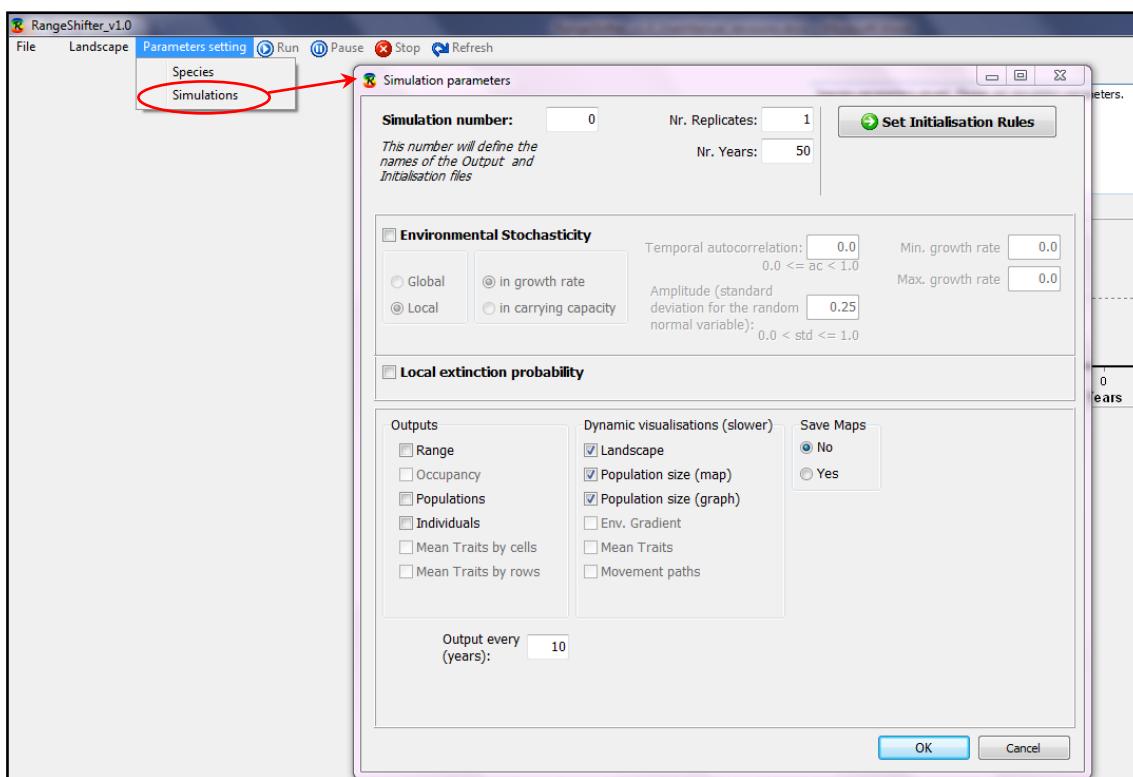
For options 1 and 3, two extra parameters have to be set to define the shape of the density-dependent settlement probability. These are the slope and inflection point for eqn. 16. An additional rule must be also set to prevent an individual moving continually if it does not find the conditions for settling. This rule is set in the box *If not settled, move until...* The default option is *Only per-step mortality*, which means that if an individual does not settle it will eventually stop because of stochastic mortality. The other option is setting, additionally or alternatively to the per-step mortality, a *Maximum number of steps*. In this case, when the maximum number of steps is reached, the individual will stop where it is, regardless of the location conditions. If the model is set for overlapping generations and individuals can disperse during multiple seasons a *Maximum number of steps per year* must be set.

*Sex / Stage dependent settlement rules.* Checking the boxes *Sex dependent* and/or *Stage dependent* allows defining sex- and/or stage-specific settlement rules. The parameters can be set in the dedicated table in the *Sex / Stage dependent Dispersal* page. An example is illustrated in Figure 3.21d, where in the table *SETTLEMENT - Movement Processes*, the rows represent females (f) and males (m) in the two stages. The first column concerns the four

settlement rules described above and should be filled with integer numbers between 0 and 3. The second and third columns are for setting the inflection point and slope in case of density-dependent settlement, i.e. if the corresponding cell of the first column set either to 1 or 3. The last column concerns the maximum number of steps per year.

### 3.2.8 Setting the simulation parameters

Clicking on the sub-menu *Parameters setting* → *Simulations* accesses the window *Simulation parameters* (Figure 3.22). This window is for setting options and parameters regarding: simulation scheduling, initialisation rules, environmental stochasticity and local extinction probability, simulation outputs and dynamic visualisations.



**Figure 3.22.** The *Simulation parameter* window.

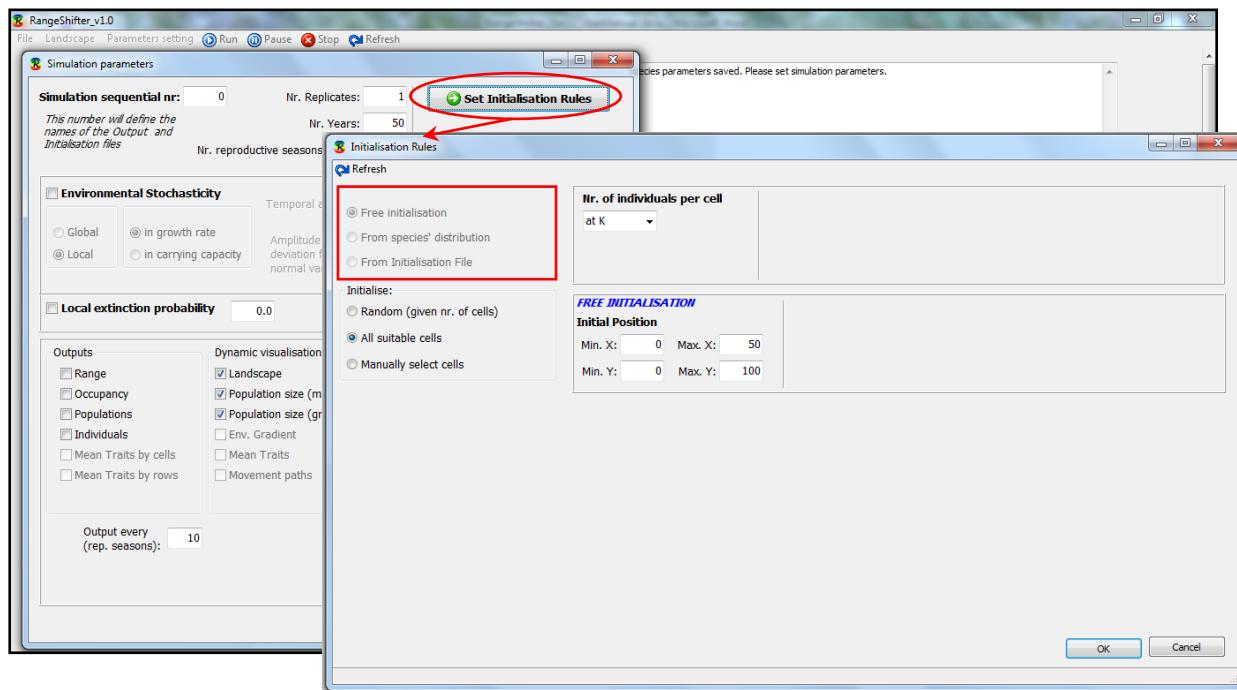
In the upper part of the window there are three parameters to be set:

1. *Simulation number*. This number defines the identity of the simulation and it is particularly important because it will be incorporated into the name of each output file produced. Changing this number prevents overwriting of outputs between different simulations.
2. *Number of replicates*. Number of times the model is repeated for a single set of parameter values (single simulation).

### 3. Number of years.

#### Initialisation rules

To set the initialisation rules, i.e. the rules by which initial individuals are placed in the landscape at the start of the simulation, click on the button *Set Initialisation Rules*. The window *Initialisation Rules* will appear (Figure 3.23).



**Figure 3.23.** *Initialisation Rules* window. The box highlighted in red is active in the case of an imported raster landscape, but inactive when using artificial landscapes generated by the program.

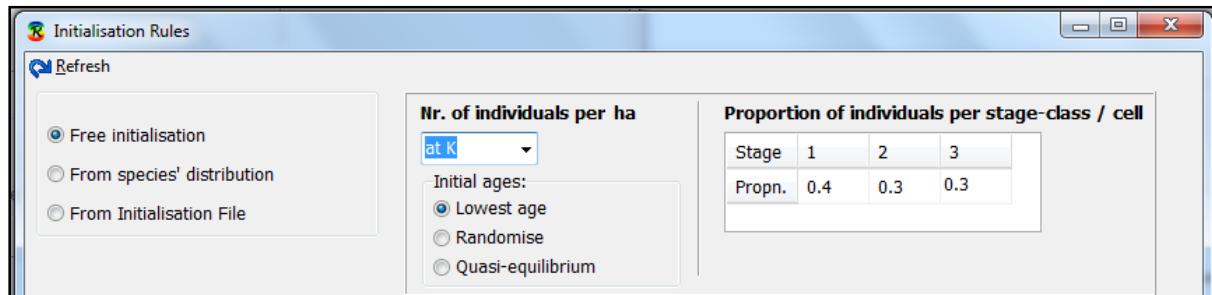
If the program is using imported landscape raster maps, there are three initialisation options which can be selected in the box in the top-left corner of the window:

1. *Free initialisation*. The cells / patches to be initialised are chosen without any reference to species distribution data. When the program is generating artificial landscapes internally, this will be the only option available, and this box will be inactive.
2. *From species' distribution*. The initialisation rules can be set making use of species distribution data previously loaded ([section 3.2.4](#)). The availability of this option is conditional on previously having loaded species distribution data.
3. *From Initialisation File*. The simulation can be initialised with an initialisation file previously saved. This option is possible only when working with imported landscape maps.

In any case, set the number of individuals that should be seeded in each cell / patch. From the drop-down box *Nr. of individuals per cell/patch*, chose between three options:

1. *At K*. The cell/patch will be saturated at its carrying capacity.
2. *At half K*. The cell/patch will be saturated at half its carrying capacity.
3. *Set value*. Set the number of individuals to be seeded in each cell or the density in each patch in the box appearing on the right.

In the case of stage-structured models, the user must specify the proportion of individuals that should be initialised at each stage class, as illustrated in the example below. Below, each patch will be initialised at its carrying capacity; 40% of the individuals will be at stage 1 age 1, 30% at stage 1 and minimum age for stage 1 and 30% at stage 2 and minimum age for stage 2. Note that these proportions must sum up to 1. Alternative initial age distributions comprise (i) *Randomise*, when individuals initialised in each stage will get an age randomly sampled between the minimum and the maximum age for the stage (note that this option is irrational without setting an absolute maximum age) and (ii) *Quasi-equilibrium*, for which initial age distributions are set approximately in accordance with the number of years taken to pass through the stage and the (female) survival rate of the stage.

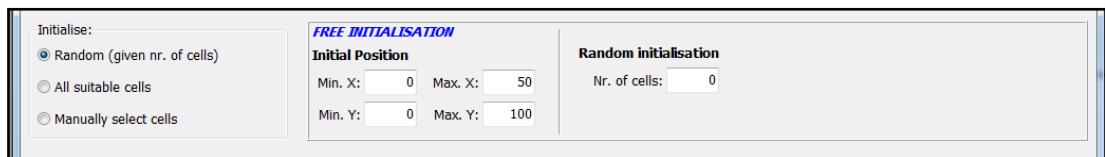


**Important Note:** every time you want to change initialisation rules from previously set ones, make sure you refresh the *Initialisation Rules* window using the dedicated button in the top-left corner. Trying to directly modifying the rules without having refreshed can cause unexpected errors.

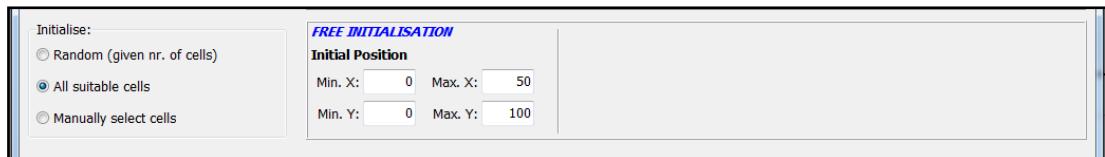
### *Free initialisation*

There are three options for the free initialisation which can be set in the box *Initialise* (Figure 3.23).

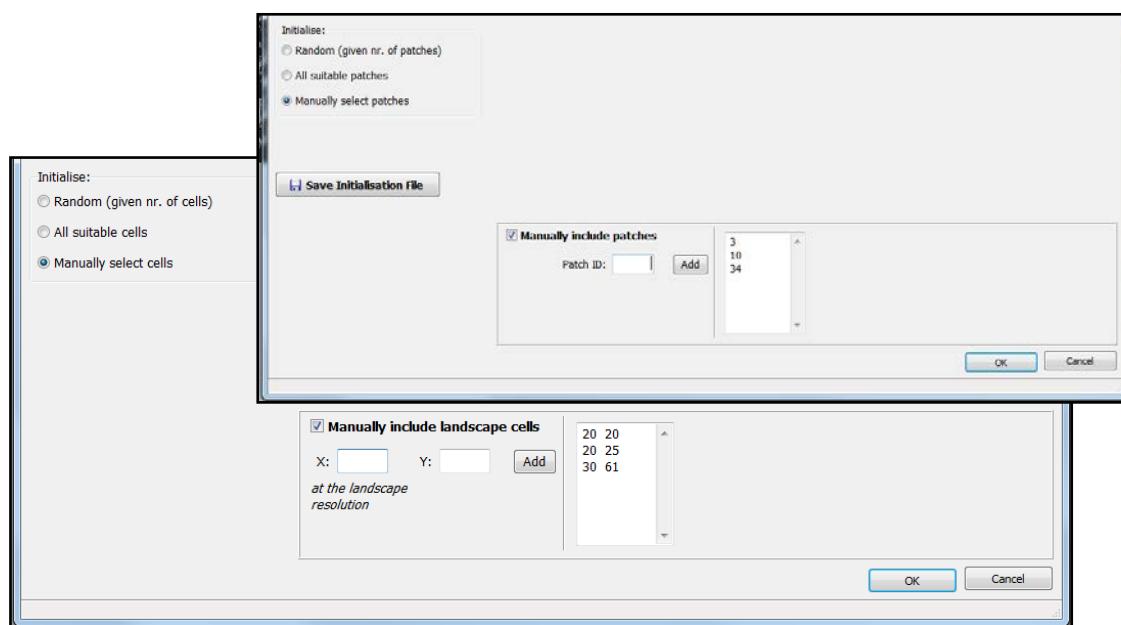
1. *Random (given nr. of cells / patches)*. A set number of cells/patches will be randomly chosen and initialised. The cells/patches can be selected from the entire landscape or from a specified area. Set the minimum and maximum x and y for the area to initialise (the whole landscape is set as default) and the *Nr. of cells/patches* to initialise.



2. *All suitable cells / patches*. All the suitable cells/patches in the defined area will be initialised.



3. *Manually selected cells / patches.* The coordinates of the cells to initialise (or the patch IDs in case of patch models) can be entered manually. Check the box *Manually include landscape cells* or *Manually include patches*; enter the x and y coordinate for the first cell (the patch ID for the first patch) and click on the button *Add*. The entered cell/patch will be added to the list on the right. Repeat the same operation for all the desired cells/patches. In the case of patch models, remember that 0 is the ID of everything that is not a patch, hence it cannot be initialised. Note that it is not possible to delete a cell/patch already entered. If you make a mistake or change your mind, you have to click on the *Refresh* button placed at the top-left corner of the *Initialisation Rules* window and re-start the initialisation.

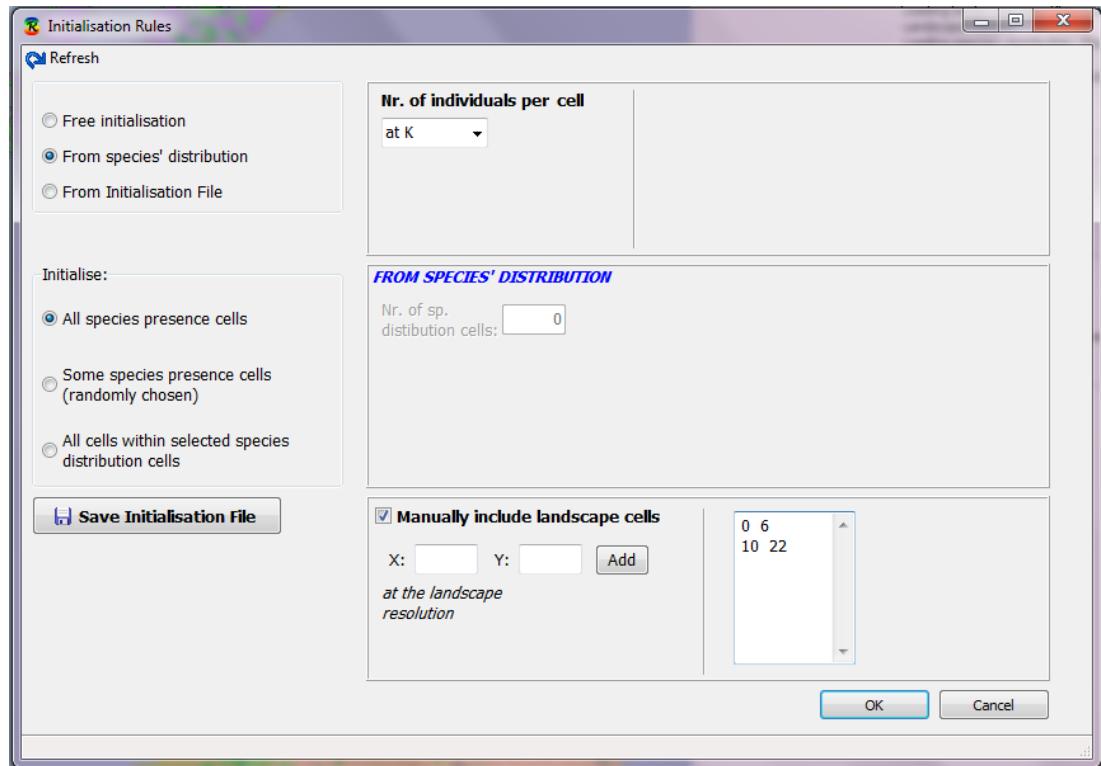


#### *From species distribution*

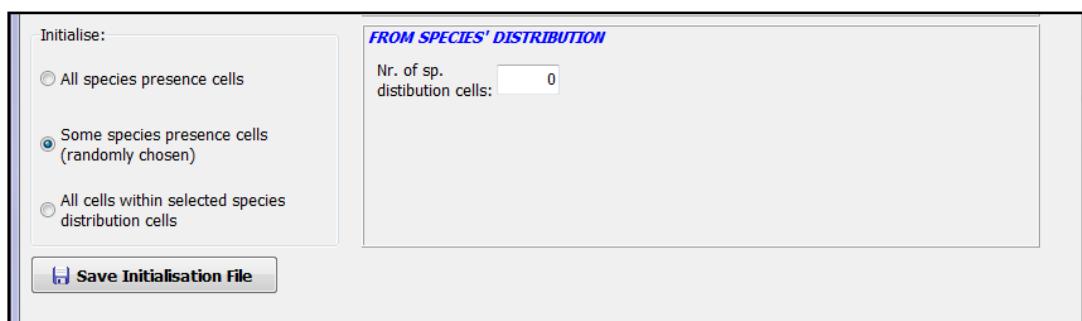
When basing the initialisation on the loaded species distribution, there are three options, which can be selected in the box *Initialise*.

*Cell-based models.*

1. *All species presence cells.* All the suitable landscape cells within each species presence cell will be initialised. Within this option (and for option 3) it is also possible to include additional landscape cells by checking the box *Manually include landscape cells* (see **Free initialisation** paragraph, point 3).

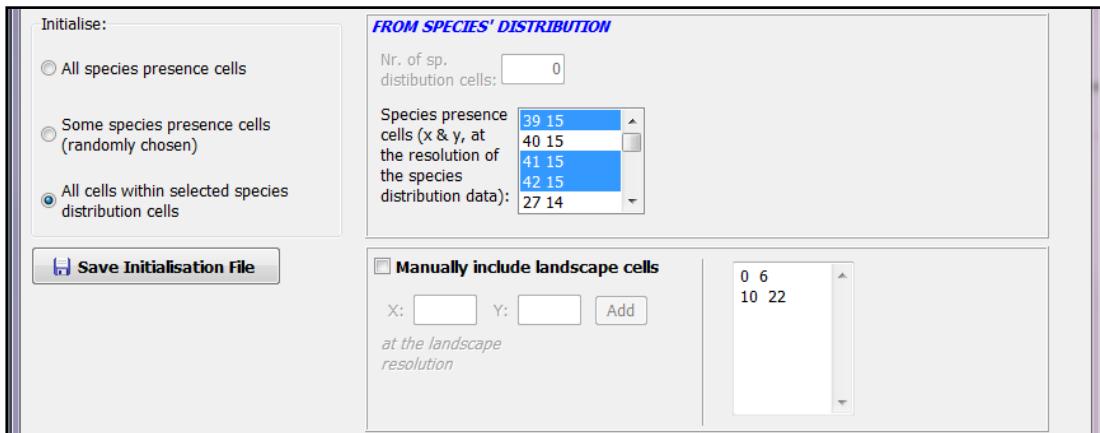


2. *All cells within some species presence cells (randomly chosen).* A set number of species presence cells will be randomly selected, and all the suitable landscape cells within them will be initialised. Set the number of species presence cells to initialise in the box *Nr. of sp. distribution cells*.



3. *All cells within selected species distribution cells.* This option allows specific selection of the species presence cells to initialise. All the suitable landscape cells

within each selected cell will be initialised. All the species presence cells are listed in the box *Species presence cells* (note that the x and y coordinates are at the species' distribution resolution). The selected cells will be highlighted in blue. To de-select a cell, click again on it.



#### *Patch-based models.*

In the case of patch based models, the three options will appear as follows:

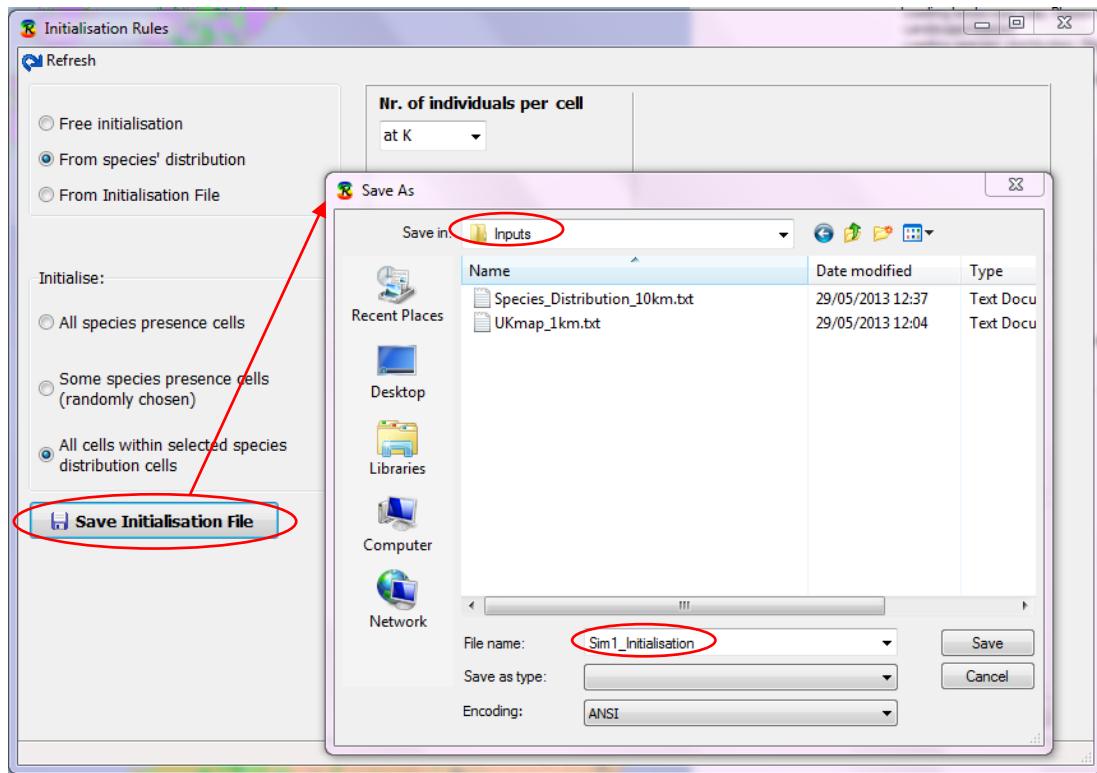
1. *All patches within all species presence cells.*
2. *All patches within some species presence cells (randomly chosen).*
3. *All patches within selected species distribution cells.*

#### *From initialisation file*

When working with an imported landscape, it is possible to save the set initialisation rules and use the generated file subsequently to initialise a new simulation on the same landscape map. This is particularly useful in the case of complex initialisation rules, which will be re-used several times.

1. Set the initialisation rules as described above.

2. Click on the button *Save Initialisation File*, select the folder *Inputs* from your main directory and save the file with the desired name:



3. Up to three initialisation files will be produced, depending on the options chosen. These may be used to set up an identical initial distribution for another simulation run from the GUI.

- a. *Sim1\_Initialisation.txt* (this name is the one chosen by the user). This is the main initialisation file which will be always generated. In the case of the example above it will look as follows:

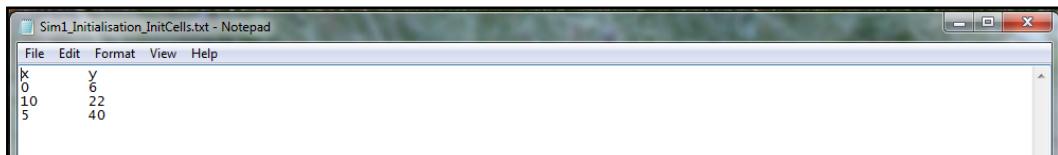
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
1	SeedType	FreeType	SpType	InitDens	IndXCell	IndXStage	InitAge	minX	maxX	minY	maxY	NCells	InitCells_File	NSpCells	InitSpDistCells_File
2	1	-9	2	1	-9	-9	-9	-9	-9	-9	-9	-9	Sim1_Initialisation_InitCells.txt	0	Sim1_Initialisation_InitSpDistCells.txt
3															
4															

- *SeedType*: type of initialisation (0 = free initialisation; 1 = from species' distribution)
- *FreeType*: type of free initialisation in the case of *SeedType* = 0 (0 = random; 1 = all suitable cells/patches; 2 = manually selected cells/patches; -9 if *SeedType* = 1)
- *SpType*: initialisation type when *SeedType* = 1 (0 = all species' presence cells / all patches within all species' presence cells; 1 = some randomly chosen

- species' presence cells (or all patches within them); 2 = All cells/patches within selected species' distribution cells; -9 if *SeedType* = 0)
- *InitDens*: how to initialise each cell/patch. 0 = saturate the cell/patch at its carrying capacity; 1 = saturate the cell/patch at half its carrying capacity; 2 = set the number of individuals
  - *IndXCell / Ind\_per\_ha*: number of individuals to seed in each cell/patch in case of *InitDens* = 2; equal to -9 otherwise
  - *IndXStage*: proportion of individuals to initialise in each stage class in the case of stage structured models; equal to -9 for non stage structured models
  - *InitAge*: in the case of stage structured models, 0 = initialise individuals at each stage with the minimum age for the stage; 1 = initialise individuals at each stage at an age randomly sampled between the minimum and the maximum age for the stage; 2 = initialise individuals at each stage according to a quasi-equilibrium distribution; -9 for non stage structured models
  - *minX, maxX, minY* and *maxY*: minimum and maximum *x* and *y* coordinates of the area to initialise in the case of free initialisation (*SeedType* = 0); if *SeedType* = 1, these are set to -9
  - *NCells*: number of cells / patches to initialise in the case of free random initialisation (*SeedType* = 0 and *FreeType* = 0); in any other case this is equal to -9
  - *InitCells\_File*: name of the file containing the list of cells coordinates (*x* & *y* at the landscape resolution) or patch IDs of the selected additional cells/patches; this second file will be generated when:
    - *SeedType* = 0 and *FreeType* = 2
    - *SeedType* = 1 and additional landscape cells are manually selected
 The file name will be composed of the name chosen for the initialisation file plus '\_*InitCells.txt*'. In the above example: *Sim1\_Initialisation\_InitCells.txt*. In the case this file is not produced, the file name will appear as -9 in the main initialisation file.
  - *NSpCells*: number of species' presence cells to initialise randomly when *SpType* = 1.
  - *InitSpDistCells\_File*: name of the file containing the list of species' distribution cells to initialise. This is the third file that is created if

*SeedType* = 1. Its name will be composed of the name chosen for the initialisation file plus ‘\_InitSpDistCells.txt’. In the above example: *Sim1\_Initialisation\_InitCells.txt*. If *SeedType* = 0 this file will not be produced and the file name will appear as -9 in the main initialisation file.

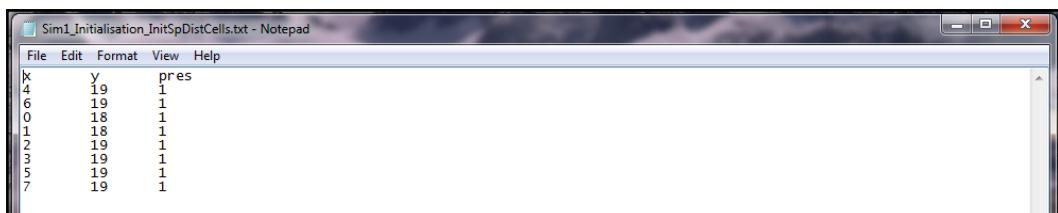
b. *Sim1\_Initialisation\_InitCells.txt*.



x	y
0	6
10	22
5	40

where x and y are the landscape cell coordinates.

c. *Sim1\_Initialisation\_InitSpDistCells.txt*.



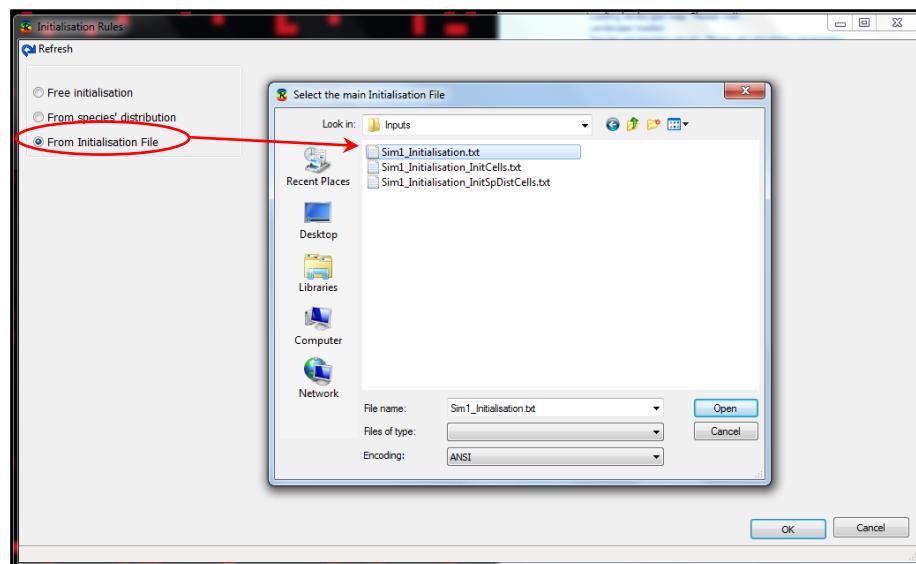
x	y	pres
4	19	1
6	19	1
0	18	1
1	18	1
2	19	1
3	19	1
5	19	1
7	19	1

where x and y are the cell coordinates referring to the species distribution map while the last column indicates that the species is present (1) in the cell.

Note that **the initialisation files produced in this way will be specific for the landscape map and species' distribution map for which they have been saved. The program has no means to check if these files are used with the right maps. Therefore attempting to use them with other maps will cause errors or wrong outputs.**

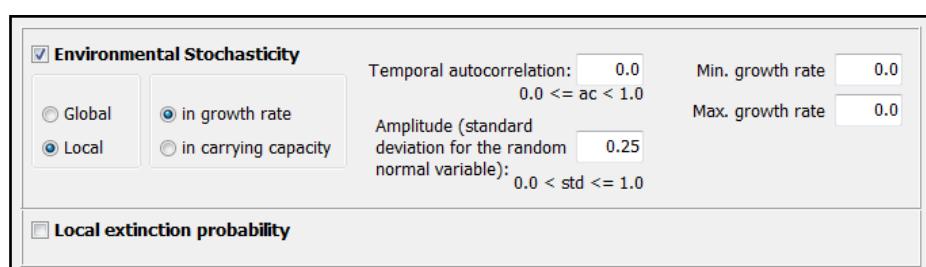
*Initialise the simulation with a previously saved initialisation file.*

To use a previously saved initialisation file to initialise the simulation, in the *Initialisation Rules* window select the option *From Initialisation File* and click on the OK button. In the dialog that will open, select the main initialisation file:



### *Environmental stochasticity*

Within RangeShifter, it is possible to model environmental stochasticity in carrying capacity or growth rate (or fecundity) acting at a global or local scale ([see section 2.3.4](#)). The relevant options and parameters can be set in the window *Simulation parameters* by checking the box *Environmental Stochasticity* (Figure 3.24).



**Figure 3.24.** Panel of the *Simulation parameters* window for setting the environmental stochasticity options and parameters.

1. Select between *Global* and *Local* (referring to the spatial scale of the stochasticity). In the case of patch-based models only the first option is allowed.
2. Select between *in growth rate* (or *in fecundities* for stage-structured models) and *in carrying capacity* (or *in dens. dependence* for stage-structured models).

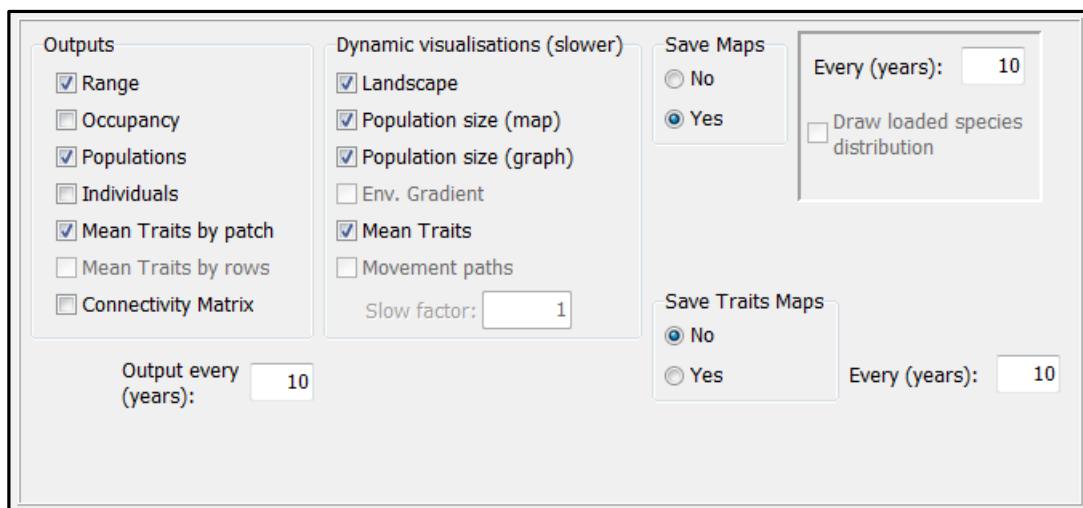
3. Set the autocorrelation coefficient ( $\kappa$  in eqn. 2, but note ‘ac’ on the form) in the box *Temporal autocorrelation*. It must be  $0.0 \leq ac < 1.0$ .
4. Set the amplitude of the fluctuations ( $\sigma$ , but note ‘std’ on the form) in the box *Amplitude*. It must be  $0.0 < std \leq 1.0$ .
5. Finally, set the minimum and maximum growth rate (or fecundity for stage-structured models) or carrying capacity (or  $1/b$  for stage-structured models) in the relevant boxes. These values will set a limit to the fluctuations.

#### *Local extinction probability*

In the window *Simulation parameters*, check the box *Local extinction probability* and set a value between zero and one. This represents the probability that each population (independently) goes extinct at each year. This option is only possible for cell-based models.

#### *Outputs*

The lower part of the window *Simulation parameters* concerns options for outputs and dynamic visualisations (Figure 3.25). RangeShifter can generate seven different outputs (described in detail in [section 3.4](#)), or eight in the case of patch-based models. To produce any of these outputs, the relevant box needs to be checked. In *Output every (years)* you can set how frequently output data are produced. The frequency is normally annual, but if there is more than one reproductive season in a year, data will be written for each season. A separate frequency can be set for the connectivity matrix.



**Figure 3.25.** The lower panel of the *Simulation parameters* window for setting options regarding outputs and dynamic visualisations.

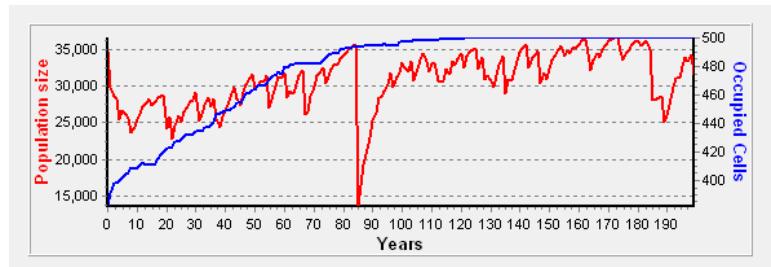
### Dynamic visualisations

Maps and summary information can be visualised on screen as the simulation progresses. Visualising the simulation can be very useful to understand how the model works, to check the simulation has been set up correctly and identify potential errors, for demonstrating or teaching purposes or to produce illustrative maps. However, you must be aware that the more visualisations are activated, the slower the simulation. Therefore, for running multiple simulations and/or large numbers of replicates, using the batch mode option is advisable.

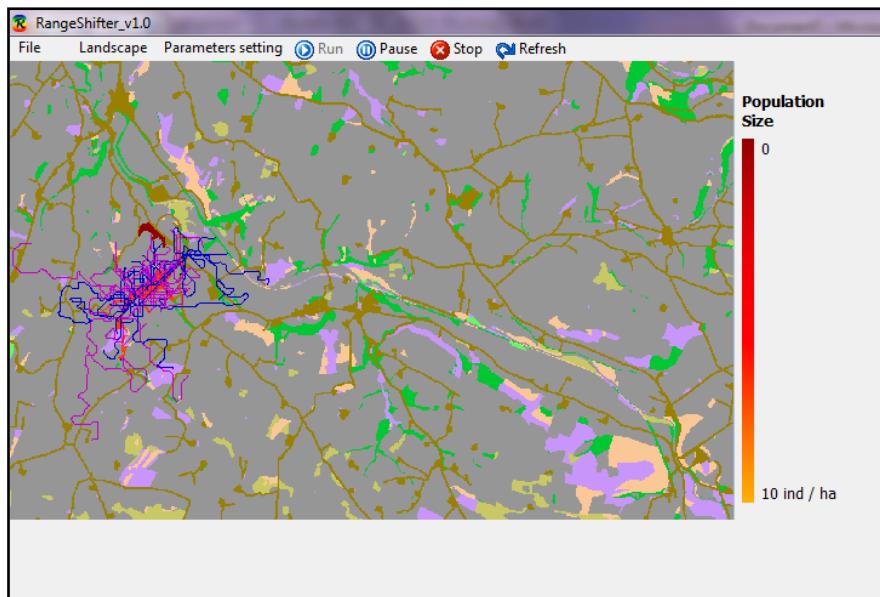
#### Possible dynamic visualisations

1. *Landscape*. This option allows visualising the landscape map in the main GUI window. The colour scheme will depend on the type of landscape (see [section 3.2.3](#)):
  - raster with habitat codes: each habitat will have a distinctive colour (either by default or set by the user);
  - raster with habitats percentage cover: each cell will be painted with the colour (either by default or set by the user) of its dominant habitat;
  - raster with habitat quality: cells will be coloured on a grey scale where black correspond to quality zero and white to quality 100;
  - artificial landscape (internally generated): in discrete landscapes cells will be either black (unsuitable) or white (suitable); in continuous landscapes cells will be coloured on a grey scale where black corresponds to absence of habitat cover and white to 100% habitat cover.Activating this option means also that in the case where a species distribution map is imported, it will be drawn on the top of the landscape with species presence cells drawn as yellow frames.
2. *Population size (map)*. For visualising the population densities. Densities will be shown on the landscape map; therefore this option is conditional on the latter being active. Each occupied cell will be coloured with a colour on a scale from dark red to bright orange. In the case of cell-based models, the colours indicate the number of individuals in a cell. For patch-based models, colours indicate the density of individuals (individuals/ha) in the patch. A legend bar will appear at the right hand-side of the landscape map. Unoccupied cells or patches will be coloured as landscape cells or patches as in 1 (Figure 3.26).

3. *Population size (graph)*. By choosing this option a graph on the right hand-side of the main window will show the changes in total population size (red line) and in total number of occupied cells / patches (blue line) through time:



4. *Env. Gradient*. This option will be available only if working with an environmental gradient. A map showing the gradient will be drawn in a separate window (for an example see the third tutorial in [section 4.3](#)).
5. *Mean Traits*. If the model has been set for inter-individual variability in one of the dispersal traits, it is possible, by checking this box, to visualise the mean trait values in each cell. Maps showing emigration traits will be drawn in the window *Mean emigration traits*, while maps for the transfer traits will be drawn in the window *Mean transfer traits* (for an example see the second tutorial in [section 4.3](#)).
6. *Movement paths*. In the case of mechanistic movement models (SMS or CRW), this option allows visualising the movement paths on the top of the habitat map. If males and females are modelled explicitly, the two sexes' paths will be drawn in blue (males) and pink (females) (Figure 3.26). Note that, depending on the simulation settings, the visualisation of the movement paths might be very fast and hence difficult to observe. The path speed may therefore be reduced by specifying a *Slow factor* (any integer > 1). Its effect in relation to its magnitude will depend on the number of dispersers, and must therefore be set by trial-and-error for each simulation (but it will typically need to be large, e.g. many thousands).



**Figure 3.26.** Example of the dynamic visualisation of movement paths. Individuals' movements are simulated with [SMS](#). Blue lines represent males, while female paths are drawn in pink.

The screen-shot is from the example in the second tutorial ([section 4.2](#)).

#### *Saving maps as bitmap files.*

RangeShifter offers the possibility of saving maps as outputs in bitmap (\*.bmp) format. All the maps produced will be saved in the folder *Output\_Maps*, which must be present in the working directory. Two types of map can be saved:

1. *Landscape map.* This will be a map of the landscape with the possibility of showing population size and initial species distribution. Choose the option *Save Maps* → *Yes* (Figure 3.25). This will be available only if the dynamic visualisation of the landscape is selected. For the map to show population size, the visualisation *Population size (map)* must be selected. For the map to show the initial (imported) species distribution, check the box *Draw loaded species distribution*. Finally, insert the time interval (years) at which the maps should be produced. The bitmap files will be named with a standard name comprising the simulation number, the number of the landscape to which the output refers (0 if not running in batch mode), the replicate number, the spatial resolution (meters) and the year and reproductive seasons to which they refer, for example *Sim1\_rep0\_land0\_yr20\_rs0.bmp*.
2. *Dispersal traits maps.* In the case of inter-individual variability (and evolution) of dispersal traits, maps of the mean trait values in each cell/patch can be saved. Select the option *Save Traits Maps* → *Yes* and set the time interval (years) at which the maps should be produced (Figure 3.25). For this option to be available, the dynamic

visualisation of traits must be selected. The map files will be named following the same rules as for the landscape maps. In this case, instead of the resolution, the type of trait represented will be indicated. For example, for emigration probability it will be *Sim0\_rep0\_EP\_year0\_rs0.bmp*.

### 3.3 Batch mode

The batch option for RangeShifter may be activated by selecting the *Batch Mode* option from the *File* menu, and it enables a number of simulations to be run without needing to set up all the required parameters separately for each simulation using the GUI. A batch comprises one or more sets of parameters (representing distinct simulations) run on one or more landscapes, although there are constraints on which types of simulations and which types of landscapes may be combined within a single batch.

A batch may also be processed using the batch-only version of RangeShifter, which is a command-line version of the program, i.e. it has no GUI. There are three possible ways to invoke the batch-only version:

1. Copy the batch executable file to the working directory you wish to use, and run the program from there. As with the GUI version, the working directory is required to have three sub-folders named *Inputs*, *Outputs* and *Output\_Maps*. The *Control File* (in the *Inputs* folder) must take the name *CONTROL.txt*.
2. Run the batch executable file from a script (or command line), passing it as a single argument the full path name (including final back-slash character) of the working directory you wish to use, which must not contain any embedded spaces. As above, the *Control File* must take the name *CONTROL.txt*. For example:

```
c:\Programs\RangeShifter_v1.1.1 c:\Projects\Connectivity\
```

3. Run the batch executable file from a script (or command line), passing it two arguments, the first being the full path name of the working directory (as above) and the second being the name of the *Control File* within its *Inputs* folder. In this case, the *Control File* may have any name, as long as it contains no embedded spaces. For example:

```
c:\Programs\RangeShifter_v1.1.1 c:\Projects\Connectivity\ Expt1_control.txt
```

A batch is specified in a set of tab-delimited text files, which may be prepared using any text editor. However, as all but the *Control File* comprise a number of formatted fields (columns), they are best edited using Microsoft Excel or similar spreadsheet-editing software. All the batch files must be located in the *Inputs* sub-folder of the folder specified through the *Set Directory* option of the *File* menu.

The *BatchLog.txt* output file documents the process of checking the batch input. Any detected errors are reported in this file, and must be corrected before any simulations will be run.

### **3.3.1    *Control file***

This is the principal file in which details of the batch simulation are provided by the user, and is the only file selected directly by the user. All other input files names are specified in the *Control File* (or hierarchically within other input files). The format of the *Control File* is strictly stipulated; case-sensitive parameter names must be provided exactly as specified.

### *Model parameters*

The first twelve lines of the *Control File* are parameters which are fixed for the entire batch run, and upon which the requirement for and format of other input options depend:

<b>Parameter</b>	<b>Values</b>	<b>Description</b>
BatchNum	$\geq 0$	Batch number, appears in all output file names
PatchModel	0 / 1	0 = cell-based model, 1 = patch-based model
Resolution	$> 0$	Landscape resolution (m)
LandType	0 / 2 / 9	0 = imported raster map with unique habitat codes 2 = imported raster map with habitat quality 9 = create an artificial landscape for each replicate
MaxHabitats	$> 0$	Maximum number of habitats in the landscapes to be used; must be $> 1$ for <i>LandType</i> = 0 must be 1 for <i>LandType</i> = 2 or 9
SpeciesDist	0 / 1	Load initial species distribution? 0 = no, 1 = yes
DistResolution	$> 0$	Resolution of the species distribution map (m) must not be less than the <i>Resolution</i> parameter
Reproduction	0 / 1 / 2	0 = asexual / only female model, 1 = sexual model (simple); 2 = sexual model (explicit mating system)
RepSeasons	$\geq 1$	No. of reproductive seasons per year
StageStruct	0 / 1	0 = no stage structure, 1 = stage-structured model
Stages	$> 1$	No. of stages (incl. juveniles) if stage-structured
Transfer	0 / 1 / 2	Transfer method: 0 = dispersal kernels, 1 = SMS (stochastic movement simulator), 2 = CRW (correlated random walk)

Thus, it is not possible, for example, to mix simulations for a stage-structured population with those for a non-structured population within a single batch run, or to model a single population on both a cell-based and a patch-based landscape. For such applications, separate batch runs are required. However, there is no limit to the number of parameter combinations nor to the number of landscapes used. Note that the total number of simulations is the product of the number of parameter sets and the number of landscapes, and, as each simulation may comprise many replicates, the volume of output produced by a single batch run may be substantial.

### *File name parameters*

The remaining seven lines of the *Control File* are the names of parameter files, of which six are compulsory. If not required (i.e. for a non-structured population), the *StageStructFile* filename must be set to NULL; otherwise, the name of a text file (including the .txt extension,

and without any embedded spaces) must be specified. Thereafter, lines in the *Control File* are not read by RangeShifter, and may be used for as much metadata/comment as is required.

Parameter	Required	Description
ParameterFile	yes	Principal file for model parameters, 1 line per simulation, simulations must be numbered sequentially includes habitat-dependent values for K
LandFile	yes	Identifies the landscape(s) to be used for each simulation in the <i>ParametersFile</i> ; format depends on <i>LandType</i> setting
StageStructFile	optional	Required for stage-structured model (StageStruct= 1), must have matching simulation nos. to those in <i>ParametersFile</i> 1 line per simulation
EmigrationFile	yes	
TransferFile	yes	Must have matching simulation nos. to those in <i>ParametersFile</i> no. lines per simulation depends on model stage and sex structure
SettlementFile	yes	
InitialisationFile	yes	Must have matching simulation nos. to those in <i>ParametersFile</i> 1 line per simulation

### 3.3.2 Parameter files

The required formats of the parameter files are described and illustrated in detail in a set of complementary spreadsheets, one for each file type, and only a brief summary of the general requirements is presented here. The specified format of a file (including column headers) must be strictly followed, and there must be no additional columns or rows within the file; thus, unlike in the *Control File*, there is no scope for including metadata within parameter files. Critically, the number of required columns in some of the parameter files depends on the value of certain parameters specified in the *Control File* (e.g. *LandType*, *MaxHabitats*, *Transfer*), and care must be taken to ensure that the correct file format is applied. If the wrong file type is specified, the *BatchLog* will report errors in the column headers.

It is very important to note that the batch checking procedure assumes that each column holds data in the correct format, i.e. integer number, decimal number (floating point) or text. If a column holds data in the wrong format, then reading of the file may terminate, usually resulting in an error message ‘Failed to read to EOF’ (i.e. to end of file). Text applies to file names only, and must not contain any embedded spaces; if no file is required for a particular simulation, the entry in the column must be set to NULL.

If a parameter is not required for a particular simulation, an entry in the correct format must still be placed in the relevant column. Do not leave an empty ‘cell’ where the parameter

should be; to do so will result in an error. In many cases, the value of such a parameter will not be checked, as the batch checking routine will already have determined that it is not required from the value of some other parameter, although there are some exceptions, particularly when checking for consistency between various combinations of parameters (especially 0/1 (no/yes) parameters). In the illustrative spreadsheets, such non-required parameters have mostly been shown as ‘-9’ (although it is not necessary to adopt this particular convention) and shaded in grey, whereas compulsory parameter entries have been highlighted in yellow.

#### *ParameterFile*

This is the first file (other than the *Control File*) read during checking of the batch input, and it determines the number of simulations to be run. The *Simulation* column must hold sequential positive integers, but they can start from any value. The *Simulation* number is included within the file name of all output files created by RangeShifter in the *Outputs* and *Output\_Maps* sub-folders.

#### *LandFile*

For *LandType* options 0 and 2 (imported raster landscapes – either real, or previously-generated artificial), the *LandFile* specifies one or more landscapes to be read by RangeShifter for each simulation specified in the *ParameterFile*. A landscape comprises the compulsory *LandscapeFile*, which holds either habitat codes (*LandType* = 0, integers, sequentially numbered from 1) or a landscape quality index (*LandType* = 2, decimal, from 0.0 to 100.0), and optionally a *PatchFile* identifying patches for a patched-based model and/or the *SpDistFile*, identifying the initial species distribution. These files must be in ArcGIS raster export format; their header records are checked, but no checks are conducted on the data values themselves.

For *LandType* option 9 (artificial landscapes), the *LandFile* specifies the parameter settings which will determine the layout of the generated landscapes (a new one for each replicate). Artificial landscapes have only two components: breeding habitat and matrix. The carrying capacity of matrix is always zero, and is therefore not specified in the *ParameterFile*.

For all *LandType* options, landscapes must be uniquely numbered in the *LandNum* column, which also is included in output file names.

### *StageStructFile*

This file specifies additional parameters required for a stage-structured model. These include the compulsory *TransMatrixFile*, and optional stage weights matrix files if there is stage-structured density-dependence in fecundity, development or survival. The structure of the transition matrix file depends on the number of stages and on whether the model is explicitly sexual or not, and it also includes the minimum age of each stage as an additional column.

### *Dispersal files*

The *EmigrationFile*, *TransferFile* and *SettlementFile* are all similar in they may have multiple lines for any one simulation of a stage-structured and/or sexual population (but there may be only one line per simulation for a non-structured asexual population). However, the number of lines required depends not on the population structure itself, but on the stage-dependency and/or sex-dependency of the dispersal phase in question. For example, a population may be stage-structured and explicitly sexual for the purposes of representing its demographics, but emigration may be of juveniles only and its probability not differ between the sexes; in that case, emigration would be stage-dependent (*StageDep* = 1), but not sex-dependent (*SexDep* = 0), and the number of required lines in the *EmigrationFile* would equal the number of stages in the population. For the same population, the mean of the dispersal kernel may differ between the sexes, and the *TransferFile* would therefore have *SexDep* = 1 and the number of required lines would be twice the number of stages.

When there is more than one line for a simulation, the *StageDep* and *SexDep* columns must be the same for all lines, but the *Stage* and *Sex* columns differ, indicating which line applies to each stage and/or sex. The lines for a simulation must be in ascending order of *Stage* and within *Stage* in ascending order of *Sex*. Note that *Sex* = 0 represents females and *Sex* = 1 represents males. Also note that there are certain parameters which are independent of stage or sex when there is stage- or sex-dependency (e.g. mutation probability), and these are read from the first line for the simulation only.

Examples of the possible combinations for each type of stage- and sex-dependency are presented in the complementary spreadsheets. Note that transfer by movement process (SMS or CRW) may not be stage- or sex-dependent, but the file format in this case depends on the type of landscape in the model.

### *InitialisationFile*

This file specifies how the initial population will be established, which may be from a species distribution map if one has been loaded. For a stage-structured population, the file includes columns specifying the proportion of individuals in each stage class, excluding juveniles (stage 0).

## 3.4 Outputs

RangeShifter can produce seven different types of outputs, or eight for patch-based models. All the output files will be named with a standard name reporting the simulation number and the type of output. In batch mode, the file name will start with the batch number, and also indicate the number of the landscape to which the output refers.

### 3.4.1 Parameters

For each simulation specified through the GUI or as part of a batch, all the set parameters will be automatically written to a text file (*Sim0\_Parameters.txt*, in the case of simulation number = 0).

### 3.4.2 Species range

This output is produced by checking the box *Range*. The file will be called *Sim0\_Range.txt*. Data are written before reproduction at each reproductive season at the specified yearly interval. An extra line is written at the end of the simulation. The file contains the following general information regarding the species' range:

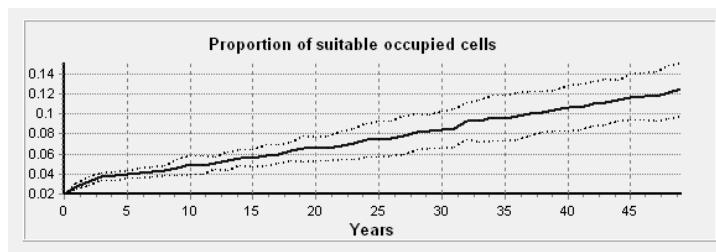
1. Replicate number (*Rep*)
2. Year (*Year*)
3. Reproductive season within the year (*RepSeason*)
4. Total number of individuals (*NInds*)
5. Total number of individuals in each stage (*NInd\_stageX*); these columns will be present only in case of stage-structured models
6. Total number of juveniles born (*NJuvs*); only in case of stage-structured models
7. Total number of occupied cells (*NOccupCells*) or total number of occupied patches (*NOccupPatches*)
8. Ratio between occupied and suitable cells or patches (*OccupSuit*)

9. Species' range, in term of maximum and minimum coordinates (*min\_X*, *max\_X*, *min\_Y*, *max\_Y*)

### 3.4.3 Occupancy

This output reports the cell/patch probability of occupancy, and it is produced by checking the box *Occupancy*. This is only possible if the number of replicates is greater than 1. Data will be recorded at the beginning of the year before any other process (and only once a year no matter the number of reproductive seasons per year). Two files will be produced:

1. *Sim0\_Occupancy.txt*. This file contains a list of all the cells in the landscape (*x* and *y* coordinates) or of all the patches (*PatchID*). The remaining columns give the occupancy probability of the cell/patch at defined time steps. The occupancy probability is obtained by dividing the number of times (replicates) that the cell/patch has been occupied in a given year, by the total number of replicates.
2. *Sim0\_Occupancy\_Stats.txt*. Summary occupancy statistics, i.e. the mean ratio between occupied and suitable cells (*Mean\_OccupSuit*) and its standard error (*Std\_error*) at the set time interval. These data are also displayed at the end of the simulation in the graph *Proportion of suitable occupied cells / patches*, where the solid line represents the mean proportion and the dashed lines  $\pm$  the standard error:



### 3.4.4 Populations

The population output, *Sim0\_Pop.txt*, is produced by checking the box *Populations*. It contains statistics regarding each population present in the landscape at a given time interval. As for the species' range output, data are collected before reproduction at each reproductive season at the specified yearly interval and at the end of the simulation. This output file contains the following information:

1. Replicate number (*Rep*)
2. Year (*Year*)

3. Reproductive season within the year (*RepSeason*)
4. Cell location (*x* and *y* coordinates ) or patch ID (*PatchID*)
5. Species number (*Species*); not yet used, always zero
6. Number of individuals in the population (*NInd*)
7. In the case of a stage-structured population, the number of individuals in each stage (*NInd\_stageX*). If the reproduction is sexual, these columns will be replaced by the number of females (*Nfemales\_stageX*) and of males (*Nmales\_stageX*) in each stage. In the case of sexual model without stage structure, two columns will indicate the number of females (*Nfemales*) and of males (*Nmales*) in the population.
8. In the case of a stage-structured population, the number of juveniles born (*NJuvs*). If the reproduction is sexual, these columns will be replaced by the number of females juveniles (*NJuvFemales*) and males (*NJuvMales*).

### **3.4.5 Individuals**

This output, *Sim0\_Rep0\_Inds.txt*, contains information regarding each individual at a given time step. It is produced by checking the box *Individuals*. To avoid the production of huge files, a separate file is saved for each replicate. Data are recorded after settlement and before aging (in the case of overlapping generations). For each individual the following data are collected:

1. Replicate number (*Rep*)
2. *Year*
3. Reproductive season within the year (*RepSeason*)
4. Individual ID (*IndID*), a unique integer number that identifies the individual
5. The individual's *Status* (see Table 2)
6. Natal cell (*Natal\_X* and *Natal\_Y*) and current cell (*x* and *y*) coordinates or natal and current patch IDs (*Natal\_patch* and *PatchID*)
7. *Sex*, in case of sexual model (0 = female, 1 = male)
8. *Age* in years, in case of overlapping generations
9. *Stage*, in case of stage structure
10. Emigration traits when there is inter-individual variability. These can be:
  - a. Density-independent emigration probability in an asexual model (*EP*)

- b. Sex-independent density-independent emigration probability in a sexual model; each individual carries two alleles (*EP\_A*, *EP\_B*), which are expressed identically for both sexes
  - c. Sex-specific density-independent emigration probability; each individual carries two alleles for female emigration probability (*F\_EP\_A*, *F\_EP\_B*) and two for male emigration probability (*M\_EP\_A*, *M\_EP\_B*) ([see 2.5.1](#)).
  - d. For density-dependent emigration probability, each occurrence of *EP* above is replaced by three loci (*D0*, *alpha* and *beta*); thus for the most complex option of sex-dependent density-dependent emigration probability, the alleles are *F\_D0\_A*, *F\_D0\_B*, *M\_D0\_A*, *M\_D0\_B*, *F\_alpha\_A*, *F\_alpha\_B*, *M\_alpha\_A*, *M\_alpha\_B*, *F\_beta\_A*, *F\_beta\_B*, *M\_beta\_A*, *M\_beta\_B*
11. Dispersal kernel traits, if the transfer is modelled with dispersal kernels that vary between individuals. These traits can be:
- a. Mean of a negative exponential kernel in an asexual model (*mean\_distI*)
  - b. Sex-independent mean of a negative exponential kernel in a sexual model; each individual carries two alleles (*mean\_distI\_A*, *mean\_distI\_B*), which are expressed identically for both sexes
  - c. Sex specific mean of a negative exponential kernel; each individual carries two alleles for female (*F\_mean\_distI\_A*, *F\_mean\_distI\_B*) and two for male mean dispersal distance (*M\_mean\_distI\_A*, *M\_mean\_distI\_B*) ([see 2.5.3](#))
  - d. For a mixed kernel composed by two negative exponential distributions, each option above has additional loci for the mean of the second kernel (*mean\_distII*) and the probability that the individual will disperse according to the first kernel (*PfirstKernel*); thus for the most complex option of a sex-dependent mixed kernel, the alleles are *F\_mean\_distI\_A*, *F\_mean\_distI\_B*, *M\_mean\_distI\_A*, *M\_mean\_distI\_B*, *F\_mean\_distII\_A*, *F\_mean\_distII\_B*, *M\_mean\_distII\_A*, *M\_mean\_distII\_B*, *F\_PfirstKernel\_A*, *F\_PfirstKernel\_B*, *M\_PfirstKernel\_A*, *M\_PfirstKernel\_B*
12. If the transfer is modelled with inter-individually variable CRW, columns in point 11 are replaced by the individual step length (*StepLength*) and walk correlation (*Rho*)
13. Distance moved in meters (linear distance from the centre of the starting cell to the centre of the arrival cell - *DistMoved*)
14. Number of steps taken (*Nsteps*) for movement models

**Table 2.** Status codes reported in the Individuals output file

Status code	Description
0	Initial status in natal patch / philopatric recruit
1	Disperser
2	Disperser awaiting settlement in possible suitable patch
3	Waiting between dispersal events
4	Completed settlement
5	Completed settlement in a suitable neighbouring cell/patch
6	Died during transfer by failing to find a suitable patch (includes exceeding maximum number of steps)
7	Died during transfer by constant, step-dependent, habitat-dependent or distance-dependent mortality
8	Failed to survive annual (demographic) mortality
9	Exceeded maximum age
+10	The addition of 10 to any of the above codes indicates that the individual is about to develop to the next stage

### 3.4.6 Traits

In the case of inter-individual variability and evolution of the dispersal traits, it is possible to output the mean traits of the population. There are two types of traits output:

1. *Mean traits by cell/patch* (*Sim0\_TraitsXcell.txt* or *Sim0\_TraitsXpatch.txt*). This file reports mean and standard deviation of the varying/evolving traits for each cell/patch, for each replicate and reproductive season at the set year interval.
2. *Mean traits by row* (*Sim0\_TraitsXrow.txt*). The mean and standard deviation of the varying/evolving traits are computed at the row (y) level, pulling together all the populations occupying cells in y. Values are reported for each replicate and reproductive season at the specified yearly interval. This is particularly useful for analyzing the structuring of traits along latitudinal gradients. It is possible to compute this output only for cell-based models.

Data for these outputs are collected at the same time as for the range and population outputs, i.e. before reproduction at each reproductive season at the set year interval and at the end of the simulation. For sexual models, the standard deviation relates to the variation between all

alleles in the local population (which is greater than the variation in phenotypic expression; if the phenotypic s.d. is required, it must be calculated from individual-level output data).

### 3.4.7 Connectivity matrix

The connectivity matrix output, *Sim0\_Connect.txt*, is available for a patch-based model only, and is obtained by checking the box *Connectivity Matrix*. It presents counts of the number of individuals successfully dispersing from each patch to each other patch for each year specified by the *Connectivity Matrix every (years)* box. If there is more than one reproductive season during the year, cumulative year-end totals are reported. Although the file contains the data required for true  $N \times N$  matrices, the data are presented in list format (which can readily be converted to matrices by most analytical software):

1. Replicate number (*Rep*)
2. Year (*Year*)
3. ID number of natal patch (*StartPatch*)
4. ID number of settlement patch (*EndPatch*)
5. Number of individuals dispersing from *StartPatch* to *EndPatch* (*NInds*)

## 4 Examples & Tutorials

---

In this section we will go step by step through the examples presented in the companion paper. These will cover some of the main features of RangeShifter, and help in becoming familiar with the software. We will use the same parameters we used in the paper; however, experimenting by trying different parameters and combinations of options is recommended good practice for getting to know the program. An additional exercise (not presented in the paper) illustrates how to prepare input files to run one of the examples in batch mode. Data layer files and parameters are provided in the corresponding folders provided with this manual.

### 4.1 Exercise 1

#### 4.1.1 *Species range expansion, long-distance dispersal and environmental stochasticity*

This is an example of how RangeShifter can be used at national scale for modelling species range dynamics. Here we model a hypothetical grassland species distributed initially in the South-West of England, and assume that from the start of the simulation the species is free to expand its range. This could be the case for alien species that naturally start to expand after having gone through an establishment phase, alien or native species that have been released from natural enemies or competitors, or species for which a previously prohibiting climate has become suitable. We assume that we have data about the current species distribution and use it as a starting point. The objective is to investigate how different assumptions about the dispersal ability of the species and about temporal environmental stochasticity can affect the modelled range expansion. We start with the basic setting of a single dispersal kernel and no environmental stochasticity (Figure 2a in the paper).

##### 1. *Starting the program*

Double-click on the RangeShifter executable file to start the program. Click on *File → Set Directory*. Select the provided folder named **RS\_Example1** as the working directory. In the dialog *Select working directory*, open the folder, select any file in it (not a sub-folder) and click *Open*. Note that the folder contains 3 sub-folders named **Inputs**, **Outputs** and **Output\_Maps**; these folders are required by the program and always have to be present in the working directory.

## 2. Landscape and species distribution

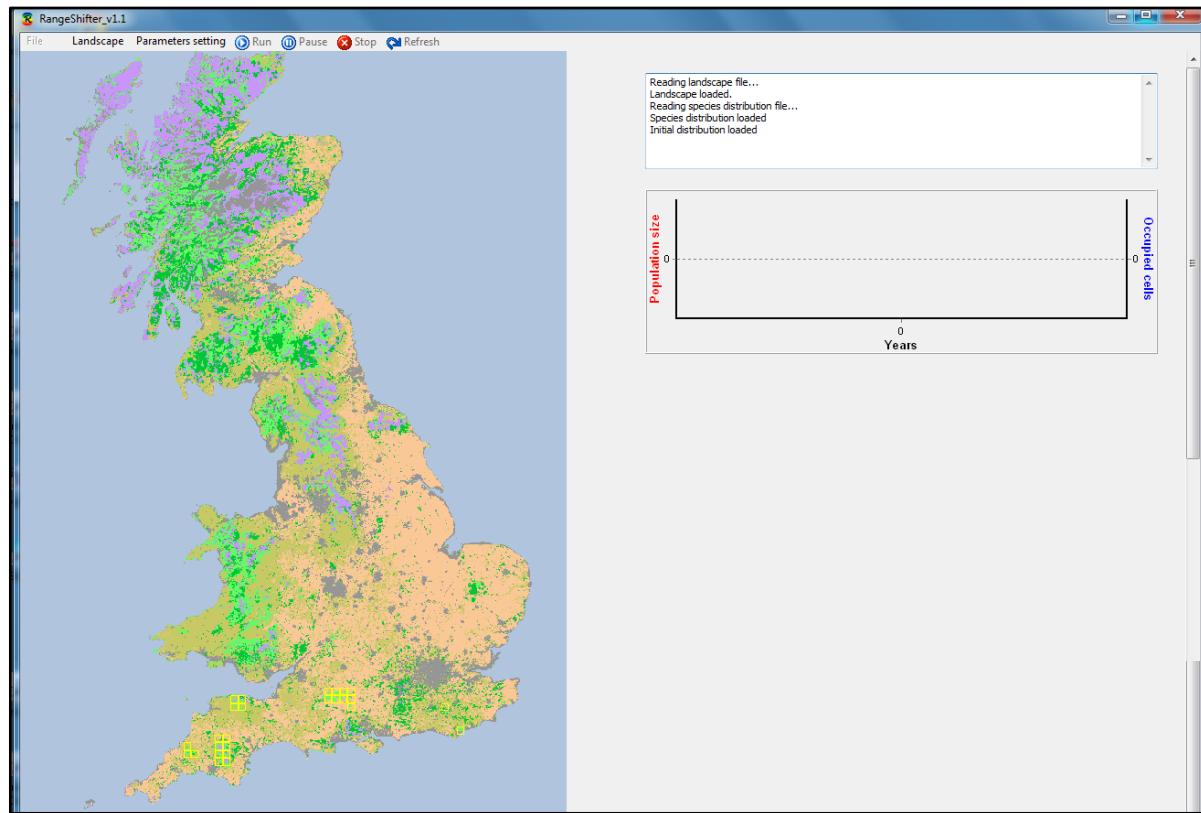
We use a land-cover map of Great Britain at 1km resolution. Six dominant aggregated habitat types were derived from Land Cover Map 2007<sup>©</sup> (database rights NERC (CEH) 2011). The map, *UKmap\_1km.txt*, is a raster in the standard text format, where each cell holds the code of its dominant habitat type. For simplicity, the codes were set as sequential numbers from 1 to 6:

- 1 = woodland (broadleaved and conifer)
- 2 = arable
- 3 = improved grassland
- 4 = semi-natural grassland (acid, neutral and calcareous grassland)
- 5 = heath and bog
- 6 = other (urban, water & coastal habitats)

To load the map click on *Landscape* → *Import Raster*. Select *Raster Types* → *habitat codes* and *Model Type* → *Cell-based*. Set the *Resolution* at 1,000m Click on the button *Import Landscape*. In the dialog that will open select the landscape file (*Inputs* → *UKmap\_1km.txt*) and click *Open*. A table on the right, displaying six rows for the six habitat types. The habitat codes appear automatically as sequential integer numbers, which have been read from the data file. The three columns on the right are for setting the RGB code for the colours to be used for each habitat. Default values are provided but they can be changed by editing them and clicking on the *Change Habitat Colours* button. Note that population densities will be displayed with a scale going from dark red to orange and the species distribution with yellow frames; it is therefore advisable to avoid using these colours for the landscape.

After the landscape is loaded, we next specify the *Species' Distribution* in the lower panel of the *Landscape* window. Set the resolution at 10,000m and click on the button *Import Species' Distribution*. In the dialog select the species data file required to run this example (*Inputs* → *Species\_Distribution\_10km.txt*) and click *Open*.

Finally, click on *OK* to display the landscape on the screen. The cells having presence records will be shown with yellow frames (it may be necessary to scroll down to see them, as they are all in the south of the country):



### 3. Species parameters

To set the species parameters, click on *Parameters setting* → *Species*. The window *Species Parameters* will open at the *Population dynamics* page. For this exercise, we assume very simple population dynamics, i.e. an only-female model with non-overlapping generations. Leave the default settings for all the options. The only parameter that needs to be set is the carrying capacity. On the right there is a table that allows setting K for each habitat. We assume that the species can reproduce only in semi-natural grassland, which has the code 4 (light green by default). Set the K for this habitat equal to 5 individual/ha.

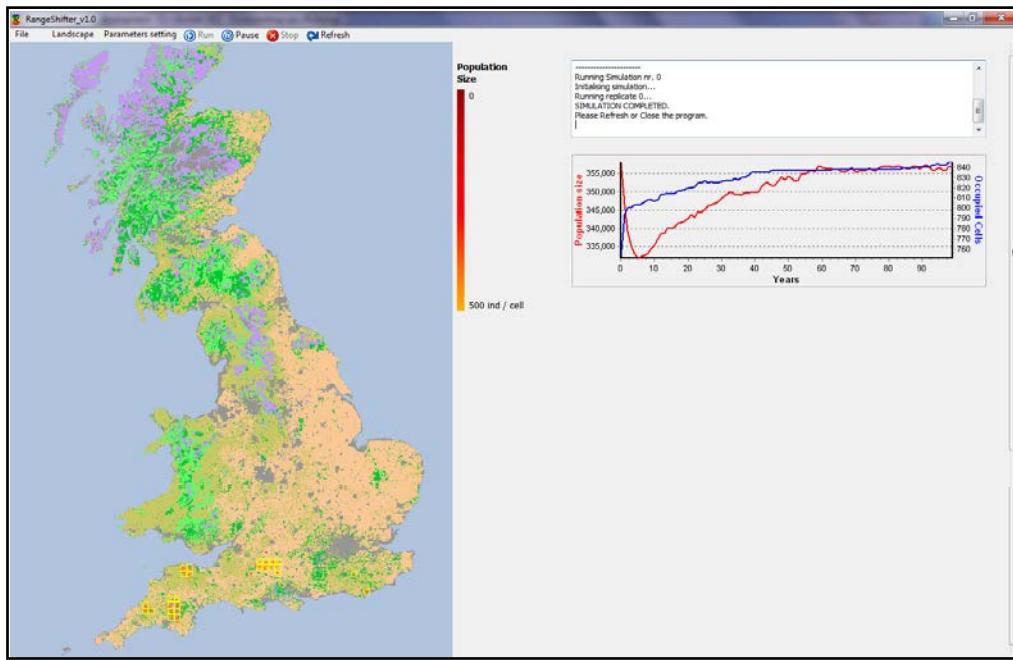
After setting the carrying capacity, click on the *Dispersal* page. We assume density-independent emigration probability (which is the default option). Set the emigration probability  $d = 0.1$ . The transfer phase is modelled with dispersal kernels (again the default option). To start, leave the type of kernels on *Negative Exponential* and set the *Mean distance I* to 2,000m. If you wish, you can click on *Update graph* to see the shape

of the kernel. Leave the dispersal mortality at zero, as there is already considerable mortality deriving from how the kernel is implemented (see 2.5.3). For the settlement, leave the default option *Die*, i.e. if an individual arrives into an unsuitable cell it dies. Click on the *OK* button to close the *Species Parameters* window and save the parameters.

#### 4. *Simulation parameters*

Click on *Parameters setting* → *Simulations*. Set the following parameters: *Simulation number* = 0; *Nr. Replicates* = 20; *Nr. Years* = 100. Click on the button *Set Initialisation Rules* to set how the simulation will be initialised. We want to initialise all the habitat cells that are present inside the 10km x 10km cells of the species distribution, and we want each of those cells to be initialised at its carrying capacity. Select *From species' distribution* and *Initialise* → *All cells within all species presence cells*. Change the setting of *Nr. of individuals per cell* to *at K* and click *OK* to return to the simulation parameters window. For this first run we do not want any environmental stochasticity. Select *Outputs* → *Range* and set *Output every (years)* to 5. Finally, select *Save Maps* → *Yes*, set *Every (years)* to 5 and select *Draw loaded species' distribution*. Click *OK* to save the parameters and close the window. Note that this will produce a total of 420 maps (20 replicates x 21 years), and you might decide to produce maps only for a smaller number of replicates or to set a longer interval.

5. The simulation is now ready to be started by clicking on *Run* in the main menu. It will run for 20 replicates (which may take more than 10 minutes to complete) and produce outputs in the **Outputs** and **Output\_Maps** folders. At the end of the simulation the screen should look something like this:



The range output, *Sim0\_Range.txt*, should look like following:

	A	B	C	D	E	F	G	H	I	J	K
1	Rep	Year	RepSeason	Ninds	NOccupCells	OccupSuit	min_x	max_x	min_y	max_y	
2	0	0	0	75100	751	0.0316011	211000	568000	60000	155000	
3	0	5	0	157168	800	0.0336629	211000	568000	58000	161000	
4	0	10	0	204394	807	0.0339575	211000	568000	58000	169000	
5	0	15	0	219673	817	0.0343783	211000	568000	58000	169000	
6	0	20	0	226768	829	0.0348832	211000	568000	46000	169000	
7	0	25	0	230272	833	0.0350515	211000	568000	46000	169000	
8	0	30	0	232806	834	0.0350936	211000	568000	46000	169000	
9	0	35	0	233769	838	0.0352619	211000	568000	46000	169000	
10	0	40	0	234766	838	0.0352619	211000	568000	46000	169000	
11	0	45	0	234638	838	0.0352619	211000	568000	46000	169000	
12	0	50	0	234876	838	0.0352619	211000	568000	46000	169000	
13	0	55	0	234761	842	0.0354303	211000	568000	46000	169000	
14	0	60	0	235270	843	0.0354723	211000	568000	46000	169000	
15	0	65	0	234980	846	0.0355986	211000	568000	46000	169000	
16	0	70	0	235966	847	0.0356406	211000	568000	46000	169000	
17	0	75	0	237408	848	0.0356827	211000	568000	46000	169000	
18	0	80	0	236571	849	0.0357248	211000	568000	46000	169000	
19	0	85	0	237465	851	0.035809	211000	568000	45000	169000	
20	0	90	0	238248	851	0.035809	211000	568000	45000	169000	
21	0	95	0	237265	851	0.035809	211000	568000	46000	169000	
22	0	100	0	238284	851	0.035809	211000	568000	46000	169000	
23	1	0	0	75100	751	0.0316011	211000	568000	60000	155000	
24	1	5	0	156273	804	0.0338313	211000	568000	58000	169000	
25	1	10	0	206032	809	0.0340417	211000	568000	58000	169000	
26	1	15	0	220091	817	0.0343783	211000	568000	58000	169000	
27	1	20	0	226710	818	0.0344204	211000	568000	58000	169000	
28	1	25	0	228134	823	0.0346308	211000	568000	58000	169000	
29	1	30	0	230083	826	0.034757	211000	568000	58000	169000	
30	1	35	0	230129	830	0.0349753	211000	568000	58000	169000	

The meanings of the different columns are described in [section 3.4](#). In order to produce Figure 2a in the paper, we plotted the number of occupied cells (column E) against years (column B), considering each replicate as a single line. The values reported in the paper for the mean rate of range expansion were calculated by taking the arithmetic mean and

standard deviation across replicates of the rate of increase in number of occupied cells, i.e.  $(N\text{OccupCells\_Year}100 - N\text{occupCells\_Year}0) / 100$ .

In the next step of this exercise we explored how the results are affected if we include the possibility of rare long-distance dispersal events (Figure 2b in the paper). If you have not closed the program from the previous exercise, click on *Refresh* in the main menu. This allows changing only the desired parameters without having to re-load the landscape and reset all the parameters. If you have closed the program, re-open it and repeat steps 1 to 4 above. We need to change the parameters for the transfer phase. Go to *Parameters setting* → *Species* → *Dispersal* and in the *Transfer* section select *Double negative exponential*. Set *Mean distance I* = 2,000m, *Mean distance II* = 10,000m and *P kernel I* = 0.99 (i.e. each individual has 0.01 probability of dispersing according to the second kernel). In the *Simulation parameters* window, change the *Simulation number* to 1 to avoid overwriting the previous output. *Run* the simulation as before. You will see, both from the visualisations and from the output, how having just 1% of individuals dispersing long distance can substantially increase the modelled range expansion. Moreover, the expansion rate is no longer steady through the suitable habitat, but is a combination of slow local expansion and occasional jumps which create colonisation foci from which the expansion proceeds further. This increases the variance between the runs, thereby increasing the uncertainty around the projection.

Finally, we incorporated temporal environmental stochasticity (Figs. 2c,d in the paper) which is recognized to be fundamental for both ecological and evolutionary processes (Ruokolainen et al. 2009) and it is expected to increase in frequency and become more auto-correlated with climate change (Easterling 2000; Coumou & Rahmstorf 2012; Hansen et al. 2012). The options for the environmental stochasticity are set in the *Simulation parameters* form. Check the box *Environmental Stochasticity*. For this example we used the options *Global* (referring to the spatial extent) and *in growth rate* (for methods see [section 2.3.4](#)). We explore two types of stochasticity: temporally uncorrelated (white noise) and positively correlated (red noise). For the first case (Figure 2c in the paper) set the *Temporal autocorrelation* to 0.0 and the *Amplitude* to 0.25 (default options). Also, you need to set the range within which the growth rate is allowed to vary; set *Min. growth rate* = 0.5 and *Max. growth rate* = 2.5. Before running the simulation, remember to change the simulation number to 2. For the second case (Figure 2d in the paper), set the *Temporal autocorrelation* to 0.7 and leave the rest as before.

Change the simulation number to 3 and run it. As we show in the paper, you will be able to see how temporal stochasticity hampers range expansion, as well as increasing the variance between simulations.

## 4.2 Exercise 2

### 4.2.1 *Landscape-scale connectivity, matrix permeability and dispersal behaviour*

In our second example, RangeShifter is used at the landscape scale to model functional connectivity of a woodland network for a hypothetical woodland species (Figure 3 in the paper). The aims are: to illustrate how the program can be used to investigate connectivity issues as well as species spatial dynamics at local and landscape scales; to show how the program can be run as patch-based; to show how additional complexity in the population dynamics and dispersal behaviour can be incorporated; and to show how the connectivity analyses can be dependent upon the type of model and on the modelled dispersal behaviour.

We will simulate a sexual species with simple, two-stage, [stage-structured population dynamics](#). Parameters are chosen to be representative of species having moderately high fecundity, high juvenile mortality and low adult mortality. After reproduction, only juveniles can disperse according to a [density-dependent emigration](#) probability. To account for functional connectivity, we use a mechanistic movement model which enables individuals to interact with the landscape and determine their path according to what they can perceive in the landscape. Therefore we will simulate movements with [SMS](#) (Palmer et al. 2011), where individuals move stepwise (each step being one cell - 10m) and the direction chosen at each step is determined by the land cover costs, the species' perceptual range and directional persistence. Once arrived in a new patch, an individual can decide to settle or not based on certain settlement rules.

To reproduce what is presented in the paper, we need to run four different experiments:

- a) Explicit sexual model. Constant per-step mortality probability of 0.01. Individuals settle only if at least one individual of the opposite sex is present in the patch (Figure 3b in the paper).
- b) As in (a), but with different settlement rules. Females settle in suitable patches, while males will settle only if at least one female is present in the patch (Figure 3c in the paper).

- c) Only-female model. Constant per-step mortality probability of 0.01. Females settle in suitable patches (Figure 3d in the paper).
- d) As in (a), but with habitat-specific per-step mortality.

Let us start with experiment (a).

## 1. Starting the program

Double-click on the RangeShifter executable file to start the program. Click on *File → Set Directory* and select the working directory, **RS\_Example2**. In the dialog *Select working directory*, open the folder, select any file in it (not a sub-folder) and click *Open*. Note that the folder contains three sub-folders named **Inputs**, **Outputs** and **Output Maps**; these folders are required by the program and always have to be present in the working directory.

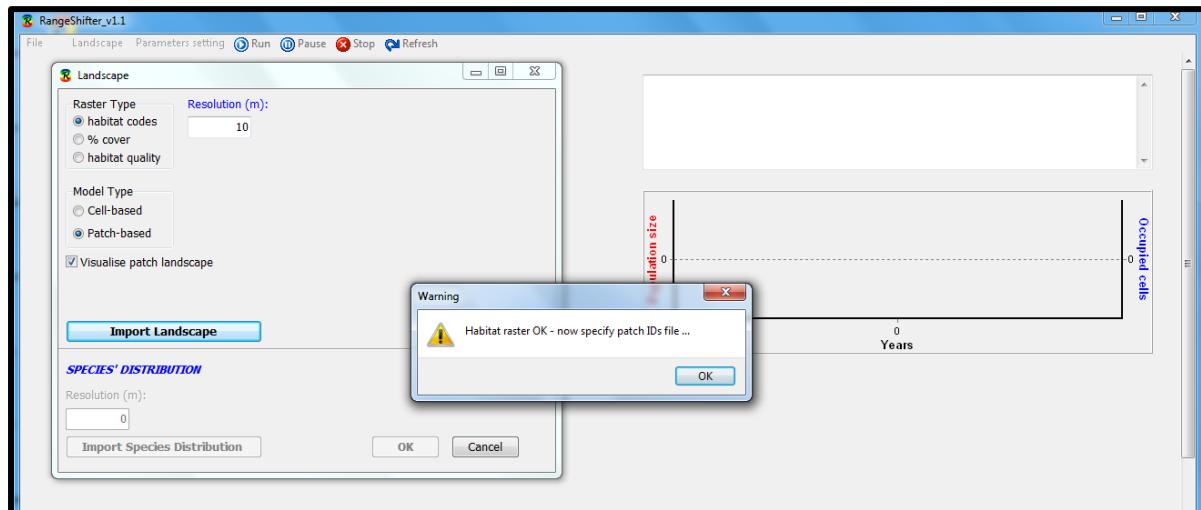
## 2. Landscape

We use a typical British lowland, agricultural landscape having small fragments of woodland, as used by Forest Research, UK, in Watts et al. (2010). The landscape map has an extent of 10km by 6km and a resolution of 10m. Land-covers were aggregated into seven categories (Figure 3a in the paper). As in the first exercise, the map, *landscape\_10m.txt*, is a raster map having codes for different land-cover types. The codes are as follows:

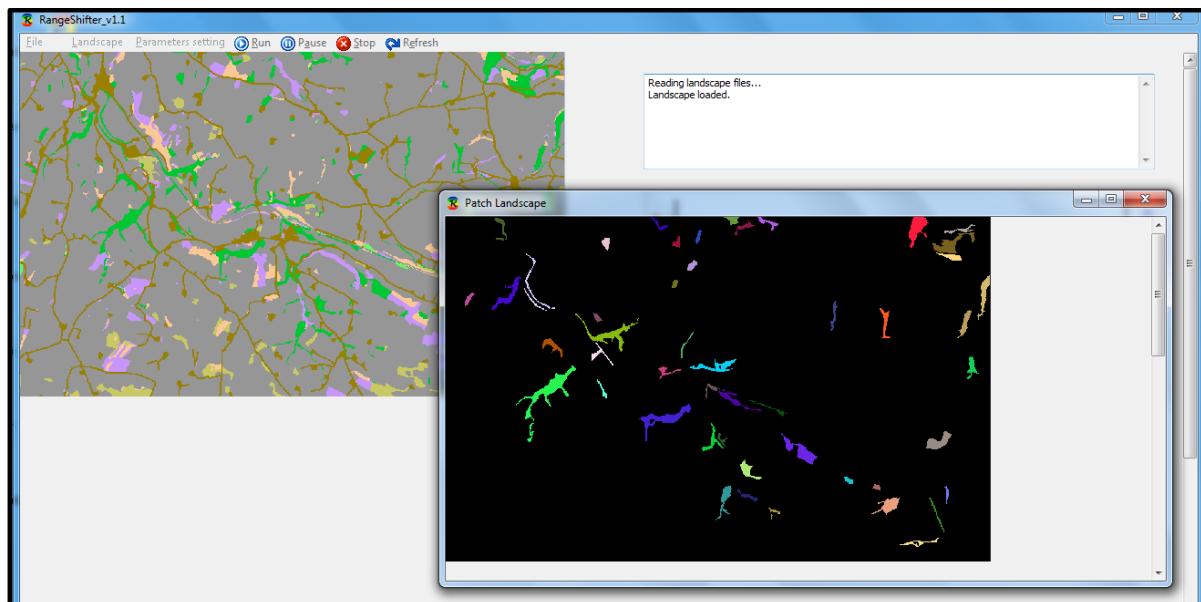
- 0 = semi-natural broad-leaved woodland
- 1 = planted/felled broad-leaved and mixed woodland, shrubs and bracken
- 3 = heathland, marshy grassland
- 5 = unimproved grassland, mire
- 10 = planted/felled coniferous woodland, semi-improved grassland, swamp
- 20 = improved grasslands, arable, water
- 50 = roads, buildings.

To load the map, click on *Landscape → Import Raster*. Select *Raster Types → habitat codes* and *Model Type → Patch-based*. Check the box *Visualise patch landscape*. Set the *Resolution* at 10mThen click on the button *Import Landscape* and select the landscape file (*Inputs → landscape\_10m.txt*). A message box should now be displayed, reporting ‘*Habitat raster OK – now specify patch IDs file...*’ (Figure 4.1). Click on *OK*, and in the dialog that will then open, select the file *woodland\_1ha\_patchIDs.txt*. In this file, each cell holds the unique ID number of the

patch to which it belongs. At this point, you may change the default habitat colours if you wish (see Exercise 1). Note that the habitat codes need not be sequential in the GUI version (but they must be when running in batch mode). Clicking on *OK* will draw the landscape and the window *Patch Landscape* will open showing each patch in a random colour on a black background (Figure 4.2).



**Figure 4.1.** Exercise 2: Importing the landscape map.



**Figure 4.2.** Exercise 2: the window *Patch Landscape* shows each individual patch in a random colour.

### 3. Species parameters

Click on *Parameters setting* → *Species* to open the *Species Parameters* window. Check the box *Overlapping generations / Stage-structured model* and select the option *Simple sexual model*. In the bottom frame, *Stage-structure population model*, set the

number of stages to 3 and leave the *Max. age* as the default, which is equivalent to not applying a maximum age. The transition matrix employed in the paper is:

$$A = \begin{pmatrix} 0.1 & 5.0 \\ 0.4 & 0.8 \end{pmatrix}$$

To implement the corresponding matrix in RangeShifter whilst allowing for juvenile dispersal before any mortality happens, we need explicitly to add a juvenile stage which will develop to the first stage at the end of the first year with probability of 1.0 (see [section 2.4.3](#)). Fill in the *Transition Matrix* as follows:

Stage-structure population model			
Nr. of stages:	3	Max. age: 1000	
<b>Transition Matrix</b>			
	juv	1	2
juv	0.0	0.0	5.0
1	1.0	0.1	0.0
2	0.0	0.4	0.8

Minimum Ages	
Stage	Age
1	0
2	0

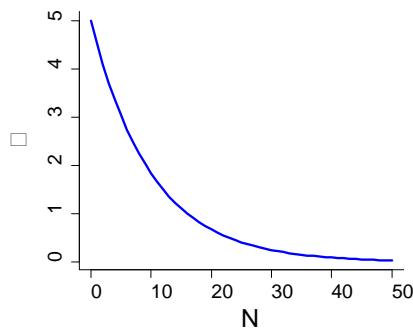
Scheduling of Survival		
<input type="radio"/> At reproduction	<input type="radio"/> Between reproductive events	<input checked="" type="radio"/> Annually

Density Dependence		
<input checked="" type="checkbox"/> Fecundity	<input type="checkbox"/> Development	<input type="checkbox"/> Survival

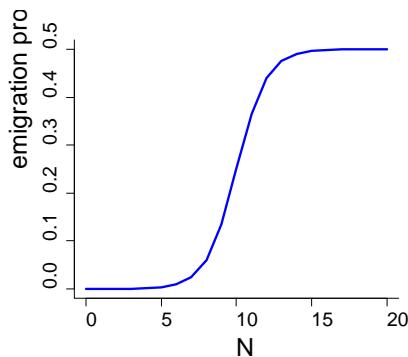
Stages' weights		
<input type="checkbox"/> Fecundity	<input type="checkbox"/> Development	<input type="checkbox"/> Survival

Set weights

Leave all the other default parameters values. You also need to set the parameter  $1/b$  for [density-dependence](#) in fecundity. This can be set in the table at the top, *Habitat-specific strength of density-dependence*. Set it to 10 in the row corresponding to habitat 0 (woodland) and leave all the other columns at zero. This means that in a 1ha patch, the relationship between the number of individuals  $N$  and fecundity  $\phi$  will look as follows:

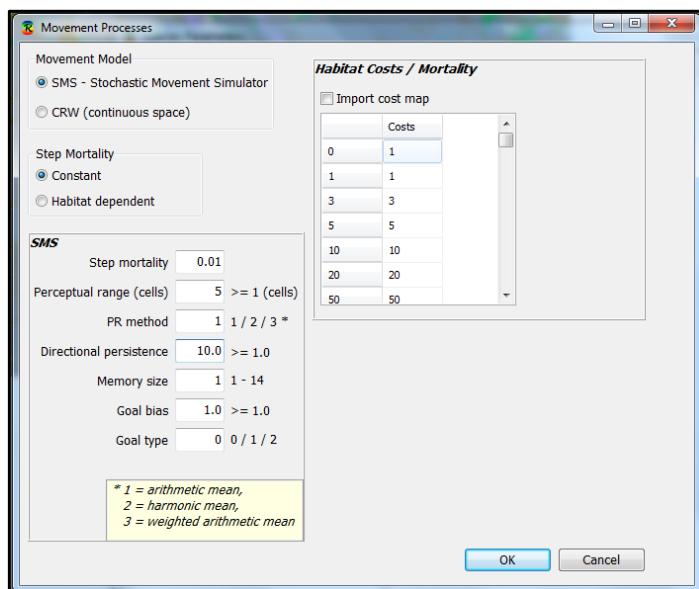


Proceed then to the *Dispersal* page. For the emigration phase, select *Density-dependent* and *Stage-dependent* and go to the page *Sex/Stage dependent Dispersal* to set the parameters. We want to model only juvenile dispersal, and hence you need to fill in only the row relating to the juveniles. The parameters required are  $D_0 = 0.5$ ,  $\alpha = 10.0$  and  $\beta = 1.0$ . As the parameter  $b$  is also used for the density-dependence in dispersal, having  $1/b = 10$  will lead to the following reaction response in a patch of 1ha size:



where  $N$  is the number of individuals.

After having set the emigration parameters, return to the *Dispersal* page for setting the transfer phase options. Choose the option *Movement Model → Movement processes* and click on the button *Set parameters* that will appear. This will open the *Movement Processes* window. The default options are [SMS](#) and constant per-step mortality: leave these settings. Set the other parameters as shown:



This means that individuals have a perceptual range of 50m, use the arithmetic mean method for calculating effective cost (which tends to emphasize the avoidance of high-

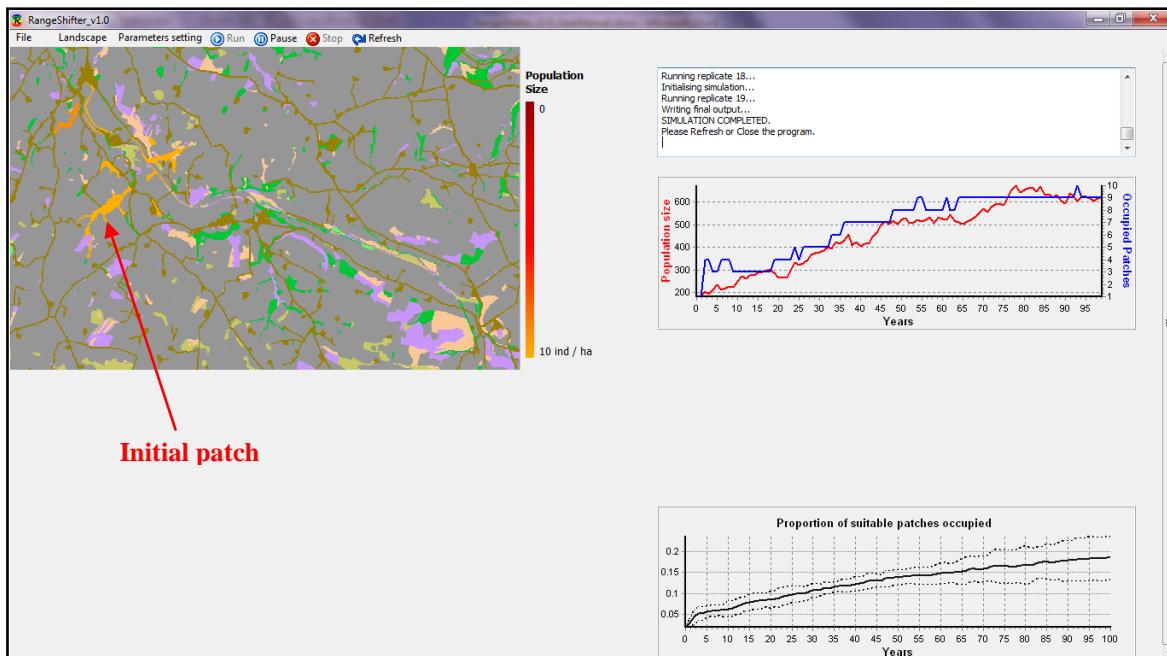
cost landscape features) and tend to follow highly correlated paths within the landscape. To save the parameters and close the window, click on the *OK* button. Finally, set the settlement parameters. Choose *Find a suitable patch + mating requirements*. Leave the rest as it is and click *OK*.

#### 4. *Simulation parameters*

Click on *Parameters setting* → *Simulations*, and set the following parameters: *Simulation number* = 0; *Nr. Replicates* = 20; *Nr. Years* = 100. Click on the button *Set Initialisation Rules* to set how the simulation will be initialised. In this example, we started by initialising one patch (Figure 4.3) which has ID = 30. Select *Free initialisation* and *Initialise* → *Manually select patches*. The box *Manually include patches* will become active; check it, insert 30 in the box *Patch ID* and click on the button *Add*. In the upper panel, set the *Nr. of individuals per ha* at a *set value* of 10, set *Initial ages* to *Lowest age* and set the *Proportion of individuals per stage-class / patch* to 0.5 for stage 1 and 0.5 for stage 2.

Finally, click the *OK* button for saving the initialisation rules and going back to the simulation parameters window. Here, select the outputs *Range*, *Occupancy* and *Populations* and set the output interval at 1 year. If you wish to see the movement paths on the screen check the box *Dynamic visualisation* → *Movement paths*. For this example, movements will be very quick; the paths may be made to display more clearly by increasing the *Slow factor* – try 2 initially. Close the simulation parameters window by clicking *OK*.

#### 5. Run the simulation by clicking on *Run*. At the end of the simulation the screen should appear as in Figure 4.3.



**Figure 4.3.** Exercise 2: Screen-shot of the RangeShifter GUI at the end of the simulation.  
The output files will be:

a. *Sim0\_Range.txt*

	A	B	C	D	E	F	G	H	I	J	K	L	M
1	Rep	Year	RepSeason	Nlnds	Nlnd_stage1	Nlnd_stage2	NJuv	NOccupPatches	OccupSuit	min_X	max_X	min_Y	max_Y
2	0	0	0	191	96	95	96	1	0.02	258902	259982	274403	275813
3	0	1	0	178	62	116	123	1	0.02	258902	259982	274403	275813
4	0	2	0	181	66	115	126	1	0.02	258902	259982	274403	275813
5	0	3	0	174	62	112	126	1	0.02	258902	259982	274403	275813
6	0	4	0	177	66	111	115	2	0.04	258902	260652	274403	276203
7	0	5	0	177	60	117	135	2	0.04	258902	260652	274403	276203
8	0	6	0	200	82	118	141	3	0.06	258902	260652	274403	276273
9	0	7	0	197	84	113	119	3	0.06	258902	260652	274403	276273
10	0	8	0	197	78	119	104	3	0.06	258902	260652	274403	276273
11	0	9	0	186	62	124	119	3	0.06	258902	260652	274403	276273
12	0	10	0	191	75	116	88	3	0.06	258902	260652	274403	276273
13	0	11	0	186	63	123	119	3	0.06	258902	260652	274403	276273
14	0	12	0	208	82	126	124	3	0.06	258902	260652	274403	276273
15	0	13	0	201	67	134	164	3	0.06	258902	260652	274403	276273
16	0	14	0	229	95	134	141	3	0.06	258902	260652	274403	276273
17	0	15	0	230	82	148	154	3	0.06	258902	260652	274403	276273
18	0	16	0	233	87	146	117	3	0.06	258902	260652	274403	276273
19	0	17	0	232	77	155	156	3	0.06	258902	260652	274403	276273
20	0	18	0	248	103	145	178	4	0.08	258902	261112	274403	276713
21	0	19	0	282	123	159	139	4	0.08	258902	261112	274403	276713
22	0	20	0	288	104	184	182	4	0.08	258902	261112	274403	276713

b. *Sim0\_Occupancy.txt*

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
1	PatchID	Year_0	Year_1	Year_2	Year_3	Year_4	Year_5	Year_6	Year_7	Year_8	Year_9	Year_10	Year_11	Year_12	Year_13	Year_14	Year_15
2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	24	0	0.05	0.05	0.05	0.1	0.15	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.3	0.3	0.3
26	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	26	0	0.25	0.5	0.6	0.65	0.7	0.85	0.95	0.95	0.95	0.95	0.95	0.95	0.95	1	1
28	27	0	0	0.05	0	0.1	0.1	0.1	0.15	0.15	0.15	0.25	0.35	0.35	0.4	0.4	0.45

c. *Sim0\_Occupancy\_Stats.txt*

	A	B	C
1	Year	Mean_OccupSuit	Std_error
2	0	0.02	0
3	1	0.026	0.00210263
4	2	0.034	0.00327671
5	3	0.035	0.00320362
6	4	0.038	0.00321182
7	5	0.04	0.00324443
8	6	0.045	0.00320362
9	7	0.047	0.00262578
10	8	0.048	0.00267542
11	9	0.048	0.00267542
12	10	0.05	0.00271448
13	11	0.053	0.003
14	12	0.056	0.004
15	13	0.058	0.00381134
16	14	0.059	0.0036921
17	15	0.06	0.00383886
18	16	0.061	0.00396697
19	17	0.066	0.00412948
20	18	0.069	0.00446625
21	19	0.071	0.00446625
22	20	0.074	0.0046112

d. *Sim0\_Pop.txt*

	A	B	C	D	E	F	G	H	I	J	K	L	M
1	Rep	Year	RepSeason	PatchID	Ncells	Species	NInd	Nfemales_stage1	Nmales_stage1	Nfemales_stage2	Nmales_stage2	NJuvFemales	NJuvMales
2	0	0	0	0	584137	0	0	0	0	0	0	0	0
3	0	0	0	30	1919	0	191	48	48	52	43	44	52
4	0	1	0	0	584137	0	0	0	0	0	0	0	0
5	0	1	0	30	1919	0	178	30	32	62	54	63	60
6	0	2	0	0	584137	0	0	0	0	0	0	0	0
7	0	2	0	30	1919	0	181	33	33	61	54	68	58
8	0	3	0	0	584137	0	0	0	0	0	0	0	0
9	0	3	0	30	1919	0	174	36	26	58	54	57	69
10	0	4	0	0	584137	0	0	0	0	0	0	0	0
11	0	4	0	27	280	0	4	1	3	0	0	0	0
12	0	4	0	30	1919	0	173	29	33	57	54	59	56
13	0	5	0	0	584137	0	0	0	0	0	0	0	0
14	0	5	0	27	280	0	3	1	0	1	1	3	1
15	0	5	0	30	1919	0	174	32	27	60	55	55	76
16	0	6	0	0	584137	0	0	0	0	0	0	0	0
17	0	6	0	26	401	0	4	2	2	0	0	0	0
18	0	6	0	27	280	0	5	3	1	0	1	0	0
19	0	6	0	30	1919	0	191	29	45	66	51	79	62
20	0	7	0	0	584137	0	0	0	0	0	0	0	0
21	0	7	0	26	401	0	3	1	2	0	0	0	0
22	0	7	0	27	280	0	7	4	1	0	2	0	0
23	0	7	0	30	1919	0	187	41	35	60	51	58	61
24	0	8	0	0	584137	0	0	0	0	0	0	0	0
25	0	8	0	26	401	0	7	3	4	0	0	0	0
26	0	8	0	27	280	0	5	1	1	2	1	7	5
27	0	8	0	30	1919	0	185	40	29	57	59	37	55

The left-hand panels of Figure 3b-e in the paper represent the occupancy probability for each patch after 100 years calculated over 20 replicates. These maps were produced in ArcGis10® by plotting the probabilities given in the file *Sim0\_Occupancy.txt*, row *Year\_100*. The right-hand panels show the mean waiting time to first colonization for those patches having occupancy probability greater than zero at year 100. The year of first colonization for each patch in each replicate was extracted from the outputs *Sim0\_Pop.txt* and then averaged across the 20 replicates. The results given in the text regarding the mean number of suitable patches colonized after 100 years were taken directly from the output *Sim0\_Occupancy\_Stats.txt*.

*Experiment b)*

This experiment was designed to provide an example of how the dispersal behaviour of the species and how we model settlement rules can change the estimated connectivity of a habitat network.

If you have not closed the program from the previous simulation, click Refresh and then *Parameters setting* → *Species* to open the *Species Parameters* window. If you have closed the program, repeat the steps above. On the *Dispersal* page of the *Species Parameters* window, change the settlement rules by checking the box *Sex dependent*. Go to the *Sex / Stage dependent Dispersal* page and set the parameters as follows:

SETTLEMENT - Movement Processes				
Sex	Settle if...	infl. point	slope	Max. step/year
f	0	0.0	0.0	0
m	2	0.0	0.0	0

Close the *Species Parameters* window by clicking *OK* and open the simulation parameters window (*Parameters setting* → *Simulations*). Set the *Simulation number* = 1, and if you are restarting from the beginning follow the instructions in step 4 above. From both the visualisation and the results, you will be able to see how this change in the settlement rules substantially increases the number of patches which in at least some simulations become occupied, their probability of occupancy and the mean time to colonization, changing the overall modelled functional connectivity of the woodland network over 100 years.

#### *Experiment c)*

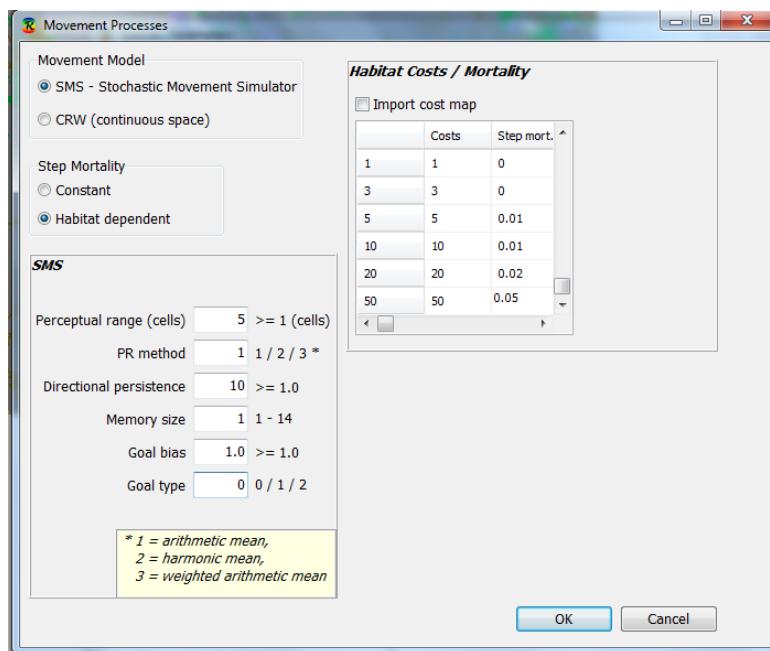
Here we change the way we model the population dynamics such that we use an only-female model. This change also has important consequences for the dispersal process and potential implications for patterns of colonization across a landscape. The stage-structured model remains the same apart from being an only-female model. This assumes that males are not limiting, and that the population dynamics are driven only by females. It also means that sexes are not modelled explicitly and it is not possible to account for behaviours like mate-finding in the settlement decisions; females will settle in suitable habitat patches and then will automatically be able to attempt reproduction.

In the *Species Parameters* window, select the option *Asexual / Only females model*. Because now only females are considered, some parameters need to be changed. Set the fecundity of stage 2 at 2.5 instead of 5.0 and  $1/b$  to 5 instead of 10. In the *Dispersal* page, set the parameters for emigration and transfer as before, and choose *Settle if... → Find a suitable patch* as the settlement option. Set the simulation parameters as before (but remember to change the *Simulation number*) and run the model. As we show in the

companion paper, not accounting explicitly for sexes and settlement behaviours leads to a drastic increase in the overall occupancy of the habitat network after 100 years.

#### *Experiment d)*

In this last experiment, we will demonstrate how RangeShifter can incorporate more complexity in the way that movement is modelled. In this case, we relaxed the unrealistic assumption that the per-step mortality is constant across all the land-cover types, and assigned different mortality values to each habitat. To set up this simulation, repeat for the methods of Experiment (a), except for changes in the *Movement Processes* window. Here, set *Step Mortality → Habitat dependent* and the other parameters as follows:



Change the *Simulation number* and run the simulation. You will see that such small changes in the per-step mortality, in interaction with the landscape structure, make a big difference in the results, in this case decreasing the functional connectivity of the network.

### 4.3 Exercise 3

#### 4.3.1 Evolution of dispersal during range shifting

With this example, we show how RangeShifter can be used for theoretical application regarding eco-evolutionary species spatial dynamics. We will model the evolution of dispersal strategies (emigration probability, dispersal distance or both) across the range of a hypothetical species. The species' range is assumed to be structured along a linear

environmental gradient, which is shifted northwards for a period of time at a constant rate. This illustrates phenomena such as evolution of dispersal along stationary gradients (Dytham 2009), evolutionary rescue of the species' range during environmental changes through evolution of dispersal (Henry et al. 2013), correlation between the evolution of two dispersal traits, and how the latter can influence the extent and pattern of the rescue process. We will run three experiments: a) only emigration probability evolves; b) only dispersal distance evolves and c) both traits evolve.

#### *Experiment a)*

##### *1. Starting the program*

Double-click on the RangeShifter executable file to start the program. Click on *File* → *Set Directory* and select the provided folder named **RS\_Example3** as the working directory. In the dialog *Select working directory*, open the folder, select any file in it (not a sub-folder) and click *Open*. Note that the folder must contain three sub-folders named **Inputs**, **Outputs** and **Output\_Maps**; these folders are required by the program and have to be present in the working directory.

##### *2. Landscape*

We used artificial random discrete landscapes of 50 columns (*x*) and 800 rows (*y*), 30% of the cells being suitable habitat and the rest being unsuitable for the species. A new random landscape was produced at each replicate by the [landscape generator](#) embedded in RangeShifter. Click on *Landscape* → *Generate Artificial Landscape* to open the window *Artificial Landscape*. Leave the default options *Generate a landscape at each replicate*, *Landscape type* → *Random* and *Discrete* and the resolution at 100m. Set the *X dimension* to 50, the *Y dimension* to 800 and *p* (proportion of suitable cells) to 0.3. Click *OK* to save the parameters and close the window. You will be able to see the generated landscapes once the simulation has started.

##### *3. Environmental gradient*

Click again on *Landscape* in the main menu, but this time select *Environmental Gradient*. In the *Environmental Gradient* window, select the option *Gradient type* → *Carrying capacity (K) or 1/b*. Set the *Gradient steepness (G)* to 0.02 and *Optimum Y* to 100. Check the box *Gradient shifting* and set the following parameters: *Gradient shifting rate* = 1 row/year, *Start to shift the gradient at year* 500 and *Stop at year* 800. Click *OK* to save the parameters and close the window.

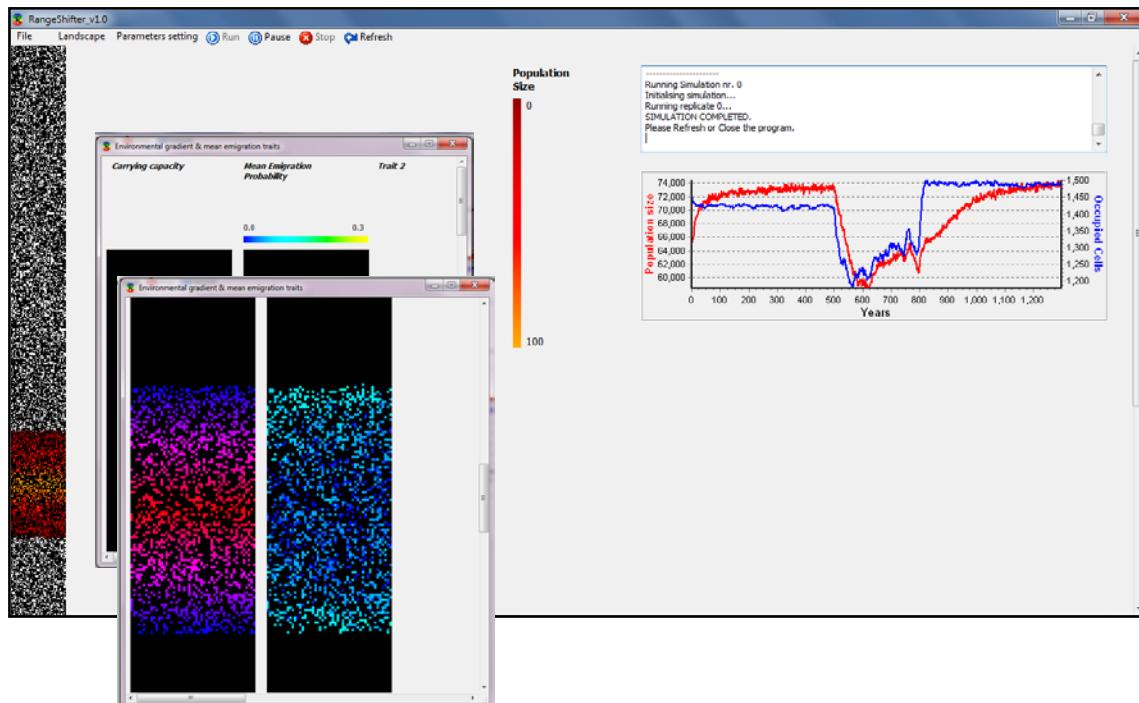
#### 4. Species parameters

Click on *Parameters setting* → *Species* to open the *Species Parameters* window. In this case, we assume a simple asexual model. Set *Rmax* to 4.0 and *K* to 100 individuals/ha (which will be the value for cells at the optimum row) and leave all the other parameters as default. In the *Dispersal* page, select *Density-independent* emigration probability and check the boxes *Individual variability* and *Evolving Traits*. Leave the *Mutation probability* at 0.001. Set the *Min* and *Max* values for *Density independent (d)* to 0.0 and 0.3 respectively and the *Mutation size* to 0.1. Leave the default options for transfer, other than setting *Mean distance I* to 200m, and settlement, and click the *OK* button.

#### 5. Simulation parameters

Click on *Parameters setting* → *Simulation*. Set the *Nr. Replicates* to 20 and the *Nr. Years* to 1300. Click on the button *Set Initialisation Rules* to open the initialisation window. Leave the option *Initialise* → *All suitable cells*, set the *Nr. of individuals per cell* to be *at K*, and set the *Max. Y* to 200 for initialising all the suitable cells in the initial range. Click *OK* to return to the *Simulation parameters* window. Select the outputs *Range*, *Individuals* and *Mean Traits by rows* to be output every 50 years. Select the options *Dynamic visualisation* → *Env. Gradient* and *Mean Traits*. The visualisation options slow down the simulation considerably, and you might prefer to run just example simulations with those on, but switch them off when running 20 replicates. To produce the same type of figures as Figure 4 in the paper, you need the visualisations switched on and to select the option *Save Traits Maps* → *Yes*, every 25 years. Maps will be saved as bitmap files in the folder *Output\_Maps*. You might not want to produce all the maps for 20 replicates.

6. Run the simulation by clicking *Run* in the main menu. When finished, the screen should look like this, where the additional window shows the gradient (from red at  $K = 100$  individuals/ha to blue at  $K = 1$  individual/ha) and the mean trait value per cell:



The output files will be:

a. *Sim0\_Range.txt*

	A	B	C	D	E	F	G	H	I	J	K
1	Rep	Year	RepSeason	NInds	NOccupCells	OccupSuit	min_x	max_x	min_y	max_y	
2	0	0	0	71518	1415	1	0	4900	5100	14900	
3	0	50	0	67880	1372	0.969611	0	4900	5100	14900	
4	0	100	0	69060	1379	0.974558	0	4900	5200	14900	
5	0	150	0	69317	1373	0.970318	0	4900	4700	14900	
6	0	200	0	68859	1384	0.978092	0	4900	4700	14900	
7	0	250	0	69402	1368	0.966784	0	4900	5100	15300	
8	0	300	0	69679	1366	0.965371	0	4900	5100	14900	
9	0	350	0	69661	1370	0.968198	0	4900	4800	15000	
10	0	400	0	69942	1375	0.971731	0	4900	5100	15000	
11	0	450	0	69641	1364	0.963958	0	4900	5100	14900	
12	0	500	0	69852	1373	0.970318	0	4900	4700	14900	
13	0	550	0	60545	1176	0.830508	0	4900	10000	19600	
14	0	600	0	59829	1212	0.830137	0	4900	14900	24100	
15	0	650	0	63269	1357	0.886928	0	4900	19900	29900	
16	0	700	0	61764	1400	0.908501	0	4900	24800	34200	
17	0	750	0	58269	1414	0.912258	0	4900	29500	39600	
18	0	800	0	58752	1385	0.914795	0	4900	34700	45100	
19	0	850	0	61251	1489	0.983487	0	4900	35000	44900	
20	0	900	0	64293	1487	0.982166	0	4900	34900	45100	
21	0	950	0	67879	1490	0.984148	0	4900	35000	45300	
22	0	1000	0	69445	1482	0.978864	0	4900	34900	45000	
23	0	1050	0	71480	1485	0.980845	0	4900	34700	45000	
24	0	1100	0	73028	1482	0.978864	0	4900	34400	45000	
25	0	1150	0	72591	1472	0.972259	0	4900	34800	44900	
26	0	1200	0	73616	1476	0.974901	0	4900	35000	45000	

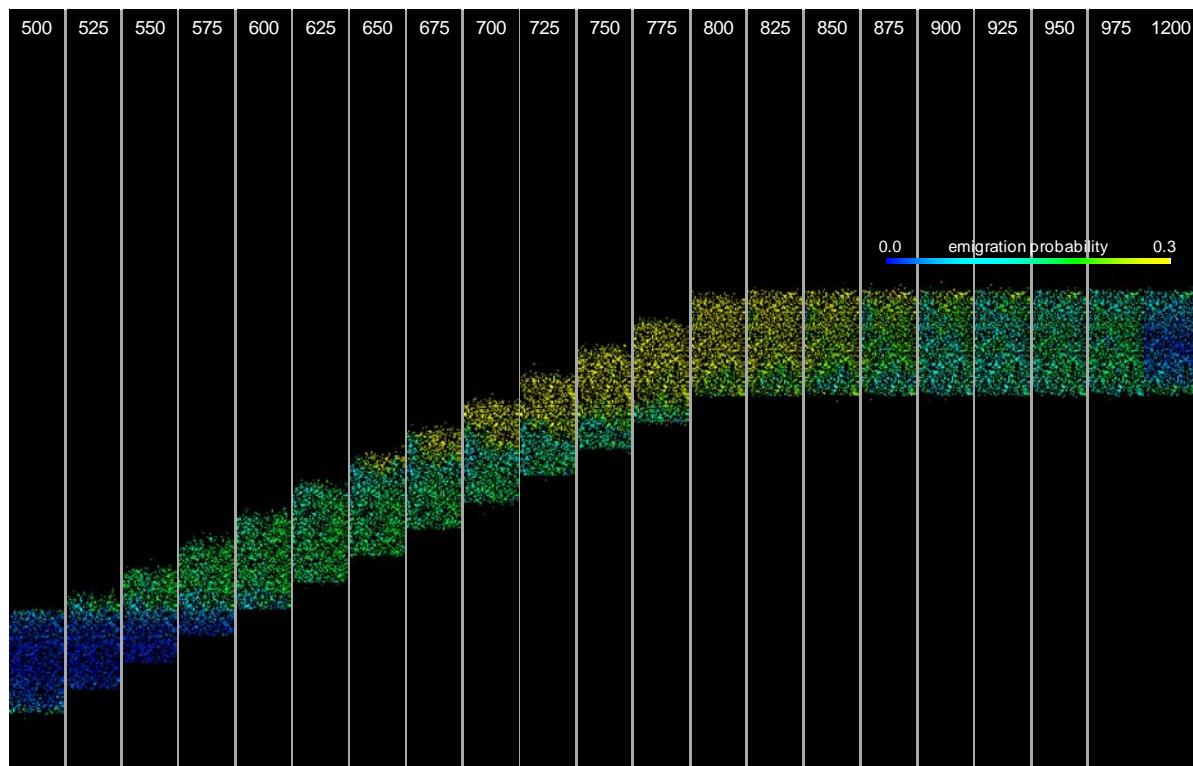
- b. *Sim0\_Rep0\_Inds.txt*: note that to avoid producing huge files, for the individual output a new file is produced at each replicate. EP (column K) is the emigration probability value applied to each individual:

	A	B	C	D	E	F	G	H	I	J	K	L
1	Rep	Year	RepSeason	Species	IndID	Status	NatalX	NatalY	X	Y	EP	DistMoved
2	0	0	0	0	76068	0	49	83	49	83	0.0677697	0
3	0	0	0	0	76069	0	49	83	49	83	0.175	0
4	0	0	0	0	76070	0	49	83	49	83	0.0412511	0
5	0	0	0	0	76071	0	49	83	49	83	0.0412511	0
6	0	0	0	0	76072	0	49	83	49	83	0.00132274	0
7	0	0	0	0	76073	0	49	83	49	83	0.173039	0
8	0	0	0	0	76074	0	49	83	49	83	0.173039	0
9	0	0	0	0	76075	0	49	83	49	83	0.194021	0
10	0	0	0	0	76076	4	49	83	49	84	0.194021	100
11	0	0	0	0	76077	0	49	83	49	83	0.273816	0
12	0	0	0	0	76078	6	49	83	48	83	0.171164	100
13	0	0	0	0	76079	0	49	83	49	83	0.296836	0
14	0	0	0	0	76080	6	49	83	49	82	0.216357	100
15	0	0	0	0	76081	6	49	83	47	79	0.17475	447.214
16	0	0	0	0	76082	0	49	83	49	83	0.118101	0
17	0	0	0	0	76083	6	49	83	49	82	0.118101	100
18	0	0	0	0	76084	0	49	83	49	83	0.162882	0
19	0	0	0	0	76085	0	49	83	49	83	0.0301794	0
20	0	0	0	0	76086	0	49	83	49	83	0.27385	0
21	0	0	0	0	76087	0	49	83	49	83	0.110127	0
22	0	0	0	0	76088	0	49	83	49	83	0.110127	0
23	0	0	0	0	76089	0	49	83	49	83	0.110127	0
24	0	0	0	0	76090	6	49	83	49	87	0.298904	400
25	0	0	0	0	76091	0	49	83	49	83	0.238844	0

- c. *Sim0\_TraitsXrow.txt*: this file reports the mean and standard deviation for the emigration probability in each row, y (column F and G).

	A	B	C	D	E	F	G	
1	Rep	Year	RepSeason	y	N	meanEP	stdEP	
2	0	0	0	0	51	18	0.192521	0.0725359
3	0	0	0	0	52	44	0.168354	0.0821132
4	0	0	0	0	53	90	0.140585	0.0894511
5	0	0	0	0	54	120	0.146466	0.0902496
6	0	0	0	0	55	130	0.138862	0.0880306
7	0	0	0	0	56	240	0.150233	0.0881298
8	0	0	0	0	57	182	0.14633	0.0837013
9	0	0	0	0	58	160	0.142852	0.0885307
10	0	0	0	0	59	216	0.144136	0.0887835
11	0	0	0	0	60	260	0.152294	0.0909456
12	0	0	0	0	61	242	0.152051	0.0834435
13	0	0	0	0	62	432	0.145731	0.0819386
14	0	0	0	0	63	390	0.156716	0.0868763
15	0	0	0	0	64	532	0.14755	0.0868055
16	0	0	0	0	65	630	0.149763	0.0876945
17	0	0	0	0	66	352	0.139182	0.0863734
18	0	0	0	0	67	510	0.145496	0.0862919
19	0	0	0	0	68	504	0.148502	0.0883357
20	0	0	0	0	69	646	0.148326	0.0892678
21	0	0	0	0	70	440	0.150183	0.0867941
22	0	0	0	0	71	504	0.159148	0.0847465
23	0	0	0	0	72	704	0.145516	0.0867413
24	0	0	0	0	73	552	0.147987	0.0881355
25	0	0	0	0	74	576	0.147025	0.0849748

If you have saved the trait maps, a typical temporal sequence for emigration probability will look like the following (the numbers at the top represent years and the colour of pixels represent the mean emigration probability for the cell):



Typically, under stationary range, selection against dispersal prevails across the range apart from near the margin, where the emigration probability evolves to be higher. When the environmental gradient starts to shift, because of the very low emigration probability in most of the range, the species lags behind its suitable environmental space. At the same time, selection for increased dispersal occurs, especially at the leading edge. Emigration probability evolves upwards, and the trait surfs back towards the centre and rear of the range. This ‘rescue’ effect enables the species to keep up with the shifting environment. After the shifting stops, high emigration is not advantageous anymore, and the trait gradually evolves back to values observed prior to environmental change.

To produce the mean trait values in different parts of the range (the values that we report in the paper’s results, Table 1), we extracted, for each replicate, the 100 north-most, middle and south-most individuals from the file *Sim0\_Rep0\_Inds.txt* using the range margins reported in *Sim0\_Range.txt*. For each replicate and each group of 100 individuals, we calculated the mean emigration probability and the standard deviation, and then averaged both statistics across replicates. We did this for four points in time (years 500, 650, 800 and 1200) (note that

similar information, but already aggregated at the row level, can be extracted from the file *Sim0\_TraitsXrow.txt*, columns F and G above). The proportion of suitable occupied cells over time used to produce Figure 4e was extracted from the output *Sim0\_Range.txt*.

#### *Experiment b)*

Here we will investigate the same eco-evolutionary process of range shifting, but with fixed emigration probability and evolving dispersal distance. If you have not closed the program from the previous exercise, click *Refresh* and open the *Species Parameters* window. If you have closed the program, follow the same instructions as in Experiment (a). In the *Dispersal* page of the *Species Parameters* window, uncheck the *Individual variability* and *Evolving Traits* options for emigration and set  $d = 0.1$ . For the transfer phase, check the boxes *Individual variability* and *Evolving Traits*. Leave the mutation probability at 0.001 and set the following parameters: *Min. Mean distance I (m) = 100*; *Max. Mean distance I (m) = 400*; *Mutation Size = 30*. Click *OK* to save the parameters and close the window. Remember to change the *Simulation number* before running the simulation.

The same outputs as in Experiment (a) can be produced and the same analyses made. You will see how dispersal distances follow a similar pattern to emigration probability by increasing during range shifting, the increase starting from the front. However, notice that with a fixed emigration probability of 0.1, dispersal distances are not under such strong selection as emigration probability was, and more variability is maintained under a stationary range. This might explain why, when the environment starts to shift, the species does not decline as much as when only emigration probability evolves (Figure 4e in the paper). Moreover, after the shifting stops, the mean distances stay at the new level for a long time and do not evolve back down during the period of the simulation.

#### *Experiment c)*

Here, we want to model the simultaneous evolution of emigration probabilities and dispersal distances, as dispersal strategies in reality are likely to be determined by a suite of traits that come under selection. However, limited theoretical work has been done to look at the evolution of such ‘dispersal syndromes’ (Travis et al. 2012). In the *Dispersal* page of the *Species Parameters* window, set the emigration probability parameters as in Experiment (a) and the transfer parameters as in Experiment (b). Change the *Simulation number* and run the program. In this case, the individuals and the mean traits outputs will report values for both traits. The same spatial pattern for both traits emerges as in the previous two experiments.

Note that as reported in the companion paper the dispersal distances do not evolve to be as high during the range expansion period when the two traits evolve concurrently as they do when emigration probability is fixed.

As you run the simulations, you might notice that emigration probability and dispersal distances tend to be negatively correlated and perhaps that this is more pronounced during the shifting period. However, as you will notice when running the experiment, there is high variability between simulations, and some runs can even show positive correlations. This indicates how process other than evolution by mutation and selection are likely to be acting, including stochastic founder effects at the leading edge and surfing of genotypes backwards from the front. For this reason, the graphs depicted in the paper (Figure 4a-d) are from a single replicate. More work is needed to tease apart these different processes and understand their relative roles under environmental changes.

## 4.4 Exercise 4

### 4.4.1 Landscape-scale connectivity in batch mode

#### *Understanding the batch input files*

In this exercise, RangeShifter is used to reproduce the simulations in Exercise 2, but in [batch mode](#), i.e. all the parameters are provided to the program in a number of files, rather than having to repeatedly alter them through the GUI. Exercise 2 should be completed prior to attempting Exercise 4.

The *Inputs* folder for this exercise contains a number of template input files for this exercise. They have been set up to reproduce experiment (a) of Exercise 2. For additional information on how to specify parameters in these files, see the set of complementary spreadsheets (*.xlsx* files), which will be referred to here.

Firstly, open the file *Control\_exercise4.txt* in a text editor program (e.g. WordPad). This file is the *Control file* for the batch, within which certain parameters (fixed for the entire batch run) and batch file names are specified. Compare the parameter values in the file with the permissible values in the [model parameters table](#). Note that the *Control file* can accommodate comments about the batch run provided that they are placed at the end of the file. You may, if you wish, keep the file open for now as a reminder of the names of the other input files.

Now open the file *ParameterFile\_ex4.txt*, preferably with spreadsheet software such as *Excel* which can handle alignment of columns (the easiest way to do this is to right-click on the file name, then *Open with → Excel*). The file contains one header row and one data row specifying parameters for simulation no. 1. Note that the *ParameterFile* governs the content of all other input files (except the *LandFile*), which therefore must also specify parameters for a single simulation numbered 1. Some columns in the file hold the value -9; this is a place-holder for parameters which are not needed in this particular exercise, e.g. *GradSteep* is not needed because *Gradient* is 0 (there is no environmental gradient). Note also that it is not possible to visualise movements between patches on the screen in batch mode. Therefore, when setting up a new batch using SMS or CRW as the transfer method, it is advisable to try a few simulations first using the GUI to ensure that the population appears to be behaving as expected. Close the *ParameterFile* once you have familiarised yourself with the content.

Now open the next file listed in the *Control file*, i.e. the *LandFile*, named *LandFile\_ex4.txt*. Again, there is one header row and one data row. In order to illustrate that the landscape number is not tied to the simulation number, the landscape has been given an arbitrary number of 37. The next point to note is that the *LandscapeFile* is not the same one as was used in Exercise 2. This is because in batch mode, RangeShifter requires that habitat codes be sequentially numbered from 1. The file *landscape\_10m\_batch.txt* is identical with the original file *landscape\_10m.txt* except that the habitat codes 0, 1, 3, 5, 10, 20, 50 have been replaced by 1, 2, 3, 4, 5, 6, 7 respectively. The next difference from Exercise 2 is that the *LandFile* specifies an initial distribution file (*SpDistFile*), which is required because it is not possible to select initial patches manually. The file *patch30.txt* has the same effect as selecting patch 30 manually in Exercise 2. Close the *LandFile*, but note that there could be multiple landscapes specified within it if we had other sample landscapes on which to run this exercise, different configurations of patches or different initial species distributions; a new row would be required for each unique landscape / patch / distribution combination.

Now open the file *StageStructFile\_ex4.txt*, which specifies parameters required only for a stage-structured population, as we have here. The column *TransMatrixFile* specifies the name of a file holding the transition matrix for the population. Also open the file *TransitionMatrix\_ex4A.txt*. It corresponds to the transition matrix specified in Exercise 2, but with the addition of an extra column holding the minimum age for each stage of the population. Note that the *StageStructFile* indicates that the population exhibits density

dependence in fecundity (*FecDensDep*), but not in development or survival. Moreover, there are three columns in the *StageStructFile* which contain the text ‘NULL’. These are for optional weighting matrices if there is stage-dependent density dependence in fecundity, development or survival (none of which is applied here). Close the two open files.

Next open the *EmigrationFile\_ex4.txt* file. Here, we immediately see a difference in the file structure. Because the population from Exercise 2 exhibits stage-dependent differences in emigration rules, we need to include a separate row for each stage. The column *StageDep* must be 1 in each row to indicate stage dependency, and the column *Stage* indicates to which stage each row refers. There are non-zero values only for stage 0 (juveniles), as that is the only stage which emigrates (according to a density-dependent reaction norm). If the emigration behaviour were also sex-dependent, the column *SexDep* would need to be 1 in each row, and we would need six rows for the simulation, one for each stage/sex combination. For a full set of possible combinations, depending on whether the population is stage-structured or has sexes modelled separately, and, if so, exhibits stage- and/or sex-dependent emigration, see the file *EmigrationFile.xlsx*.

In neither of the subsequent phases of dispersal do we need to specify stage-dependent or sex-dependent behaviour (only juveniles can disperse anyway), and therefore the files *TransferFile\_ex4.txt* and *SettlementFile\_ex4.txt* each contain only one data row for simulation 1. However, we need to be careful in other ways when setting up these two files, as their format depends on the kind of transfer model being applied. Take a look also at the files *TransferFile.xlsx* and *SettlementFile.xlsx*. In this exercise, the transfer phase of dispersal uses the movement model SMS, and we therefore need to apply the file formats specified in the worksheets *Description SMS* and *Description Movt Process* respectively; different formats would apply if transfer were by the kernel or CRW methods. In the *TransferFile* for SMS, we need to specify the cost values associated with each of the seven habitat categories, and these are given in the columns *CostHab1*...*CostHab7*. It is also necessary to include the same number of *MortHab* columns, even though in this exercise, step-dependent mortality risk is not habitat-dependent. Note that the number of *MortHab* and *CostHab* columns depends on the parameter *MaxHabitats* in the *Control file*, which may be greater than the number of habitats in any particular *LandscapeFile*. This is to allow a batch to be run against multiple landscapes which do not all have the same number of habitat categories defined.

Finally, take a look at the *InitialisationFile\_ex4.txt* file. This is relatively straightforward to understand, but note that its format depends on whether the model is cell- or patch-based and on whether the population is stage-structured or not, as detailed in the *InitialisationFile.xlsx* file.

Close any input files before moving on to the next step.

#### *Running Experiment (a)*

Double-click on the RangeShifter executable file to start the program. Click on *File* → *Set Directory* and select the working directory, **RS\_Example4**, in the same way as for the previous exercises. Click on *File* a second time, and then on *Batch Mode*. Select the file *Control\_exercise4.txt* and then click on *Open*. You should immediately see an error message box appear. This is because mistakes have deliberately been included in the template input files in order to demonstrate how to deal with input errors. Note the details of the error message, and then click on *OK* to cancel the message. It is not necessary to close RangeShifter at this point. Instead, take a look at the file *BatchLog.txt* which has been created in the Outputs folder of the *RS\_Example4* working directory. It indicates that there is an error (unless you already noticed and corrected it!) in the *PropMales* column of line 1 of the *ParameterFile*. Open the file *ParameterFile\_ex4.txt*, change the value of 0 for *PropMales* to the correct value of 0.5 for the balanced sex-ratio population being simulated in this exercise, and save the file. Note that any errors in the *ParameterFile* must be corrected before other files are checked (as the number and identity of simulations is taken from the *ParameterFile*).

Return to RangeShifter, click on *File* → *Batch Mode* again, and as previously select and run the *Control\_exercise4.txt* file. The same error message should appear, despite having corrected the *ParameterFile*. Take another look at the *BatchLog.txt* file. This time, the *ParameterFile* should be reported as OK, but there are error messages relating (1) to the resolution of the *SpDistFile* and (2) to the *TransferFile*.

Inspection of the initial species distribution file *patch30.txt* reveals that it has a *cellsize* of 10 (metres), the same as the other two landscape files. In fact, the error lies in the *Control\_exercise4.txt* file, where *DistResolution* was set to 100 instead of to 10. It is in fact possible to have a species distribution file having a cell size which is an integer multiple of the landscape cell size (as in Exercise 1), but it is not the case in this exercise. So, change the value from 100 to 10 and save the *Control\_exercise4.txt* file.

The error in *TransferFile\_ex4.txt* is more straightforward. *PRmethod* should be 1 rather than 0. Edit and save the file accordingly.

Now repeat the procedure to select and run the *Control file* for this exercise. This time, if you have corrected the mistakes as described, there should be no error box, and the message “Control file valid” should appear in the information panel in the RangeShifter main window. If that is the case, *Run* the model; if not, identify and correct the outstanding error(s) before repeating the batch validation procedure. When the model is running, nothing will appear on the screen except for short messages regarding each replicate in the information panel.

All being well, the batch will run until completion, when the only option is to close RangeShifter. Now take a look at the output files in the *Outputs* folder for this exercise. The files should be similar to those created from Exercise 2, except that the file names start with the batch number *Batch1* and contain reference to the landscape number, in this case *land37*. If multiple landscapes had been included in the *LandFile*, there would be a separate set of files for each landscape.

#### *Including the other experiments in the batch*

The batch mode can be used in just the way described above, namely to run a single simulation; it saves having to specify all the parameters again through the GUI if you want to run the same simulation again. However, the real advantage of the batch mode lies in setting up a whole series of simulations in one batch to perform a virtual experiment, e.g. where one or more parameters is varied systematically to examine its effect on a population (for example, in terms of the range expansion rate or probability of extinction).

Here, we will extend the batch example for Experiment (a) to incorporate the additional experiments from Exercise 2. However, there is one important constraint. Experiment (c) cannot be combined in the same batch run as the other experiments, as it requires an asexual population, whereas the other experiments require sexual populations. It will therefore need to be run as a separate batch.

Open the file *ParameterFile\_ex4.txt* for editing as previously, and add a second data line, which should be a copy of the first. The only change to make is that the *Simulation* column must be changed to 2 in the second line (simulations must be sequentially numbered). Then save the file. Repeat this procedure for the *StageStructFile*, *TransferFile* and *InitialisationFile*. In the *EmigrationFile*, all three lines must be copied and changed to

*Simulation 2.* So far, the second simulation is the same as the first; the critical change is in the *SettlementFile*, where we now need to specify different behaviour for the two sexes. Copy the existing single line twice, and change both new lines to *Simulation 2*. Then, on the first of these new lines change *SexDep* to 1 and *SettleType* to 0, and on the second new line change *SexDep* to 1 and *Sex* to 1. Note that in the batch input, *Sex 0* is for females and *Sex 1* is for males. The file should now appear as follows:

A	B	C	D	E	F	G	H	I	J	K	L
1	Simulation	StageDep	SexDep	Stage	Sex	SettleType	MinSteps	MaxSteps	MaxStepsYear	Slope	InflPoint
2	1	0	0	0	0	2	0	0	0	0	0
3	2	0	1	0	0	0	0	0	0	0	0
4	2	0	1	0	1	2	0	0	0	0	0
5											

so that, for *Simulation 2*, females will settle in any suitable patch, and males will settle only if there is a female present.

Save the *SettlementFile*, and then run the batch again. There is no need to make any changes to the *Controlfile*, as none of its parameters or file names is altered, unless you wish to change *BatchNum*, so that the previous output is not overwritten. Once the batch run has completed, the *Outputs* folder will contain two sets of files, one for each simulation.

Following similar editing procedures, the parameters for Experiment (d) may be added by again copying from *Simulation 1* and renumbering as *Simulation 3* (note that there will be just one line for *Simulation 3* in the *SettlementFile*). The key change for Experiment (d) is to specify habitat-dependent mortality risk, and so in the *TransferFile*, the *SMtype* column must be changed to 1, and the seven *MortHab* columns must be set to 0, 0, 0, 0.01, 0.01, 0.02 and 0.05 in sequence.

For Experiment (c), it is important to ensure that the output data from the other experiments are not overwritten. This can be achieved either by creating a separate working directory for Experiment (c) (complete with its own *Inputs*, *Outputs* and *Output\_maps* folders), or, in the

same working directory, by allocating a different *BatchNum* to Experiment (c). Here, we will follow the second option.

Make copies of all the batch input files (except the *LandFile* and the raster files), and name them ...\_ex4C.txt. In the new *Control file*, set *BatchNum* to some previously unused number, e.g. 99, set *Reproduction* to 0, and add ‘C’ to all the file names (except the *LandFile*) to ensure that the new input files are processed. Edit each of the new files, removing all but the line(s) from *Simulation 1*. Also make the following edits: change *K1* from 10 to 5 in the *ParameterFile*; change the name of the *TransMatrixFile* in the *StageStructFile*, and in the new *TransMatrixFile* itself, set the fecundity of stage 2 to 2.5; change *SettleType* to 0 in the *SettlementFile*; change *IndsHa* to 5 in the *InitialisationFile*. Run the batch, taking care to select the new *Control file*, and, provided that there are no errors, at the end of the batch run, a further set of output files for *Batch99\_Sim0\_...* will have been created in the Outputs folder.

## 5 References

---

- Aben, J., Strubbe, D., Adriaensen, F., Palmer, S.C.F., Travis, J.M.J., Lens, L. & Matthysen, E. (2014). Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *Journal of Applied Ecology*, 51, 693–702.
- Adriaensen, F., Chardon, J., De Blust, G., Swinnen, E., Villalba, S., Gulink, H., et al. (2003). The application of “least-cost”modelling as a functional landscape model. *Landscape and Urban Planning*, 64, 233–247.
- Altwegg, R., Collingham, Y.C., Erni, B. & Huntley, B. (2013). Density-dependent dispersal and the speed of range expansions. *Diversity and Distributions*, 19, 60–68.
- Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W., et al. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1415–20.
- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011). Climate change threatens European conservation areas. *Ecology Letters*, 14, 484–92.
- Araújo, M.B., Whittaker, R.J., Ladle, R.J. & Erhard, M. (2005). Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, 14, 529–538.
- Armsworth, P.R. (2008). Conditional dispersal, clines, and the evolution of dispersiveness. *Theoretical Ecology*, 2, 105–117.
- Armsworth, P.R. & Roughgarden, J.E. (2008). The structure of clines with fitness-dependent dispersal. *The American Naturalist*, 172, 648–57.
- Atkins, K.E. & Travis, J.M.J. (2010). Local adaptation and the evolution of species’ ranges under climate change. *Journal of Theoretical Biology*, 266, 449–57.
- Bach, L. & Ripa, J. (2007). On the evolution of conditional dispersal under environmental and demographic stochasticity. *Evolutionary Ecology Research*, 1–22.
- Baguette, M. (2003). Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography*, 2, 153–160.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, 88, 310–26.
- Baguette, M. & Van Dyck, H. (2007). Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology*, 22, 1117–1129.
- Baker, M.B. & Rao, S. (2004). Incremental costs and benefits shape natal dispersal: theory and example with *Hemilepistus reaumuri*. *Ecology*, 85, 1039–1051.
- Balčiauskas, L. & Kawata, Y. (2009). Estimation of carrying capacity and growth rate of wolf in Lithuania. *Acta Zoologica Lituanica*, 19, 79–84.

- Bartoń, K. A., Hovestadt, T., Phillips, B.L. & Travis, J.M.J. (2012). Risky movement increases the rate of range expansion. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1194–202.
- Bartoń, K. A., Phillips, B.L., Morales, J.M. & Travis, J.M.J. (2009). The evolution of an “intelligent” dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos*, 118, 309–319.
- Beaumont, M.A. (2010). Approximate Bayesian Computation in Evolution and Ecology. *Annual Review of Ecology, Evolution, and Systematics*, 41, 379–406.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377.
- Benton, T.G. & Bowler, D. (2012). Dispersal in invertebrates: influences on individual decisions. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). Oxford University Press, pp. 41–49.
- Benton, T.G., Solan, M., Travis, J.M.J. & Sait, S.M. (2007). Microcosm experiments can inform global ecological problems. *Trends in Ecology & Evolution*, 22, 516–21.
- Bessa-Gomes, C., Legendre, S. & Clobert, J. (2010). Discrete two-sex models of population dynamics: On modelling the mating function. *Acta Oecologica*, 36, 439–445.
- Best, A.S., Johst, K., Münkemüller, T. & Travis, J.M.J. (2007). Which species will successfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. *Oikos*, 116, 1531–1539.
- Bian, L. (2003). The representation of the environment in the context of individual-based modeling. *Ecological Modelling*, 159, 279–296.
- Bitume, E. V, Bonte, D., Ronce, O., Bach, F., Flaven, E., Olivieri, I., et al. (2013). Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecology Letters*, 16, 430–7.
- De Block, M., Pauwels, K., Van Den Broeck, M., De Meester, L. & Stoks, R. (2013). Local genetic adaptation generates latitude-specific effects of warming on predator-prey interactions. *Global Change Biology*, 19, 689–696.
- Bocedi, G., Atkins, K.E., Liao, J., Henry, R., Travis, J. & Hellmann, J.J. (2013). Effects of local adaptation and interspecific competition on species’ responses to climate change. *Annals of the New York Academy of Sciences*, 1297, 83–97.
- Bocedi, G., Heinonen, J. & Travis, J.M.J. (2012a). Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *The American Naturalist*, 179, 606–20.
- Bocedi, G., Pe'er, G., Heikkinen, R.K., Matsinos, Y. & Travis, J.M.J. (2012b). Projecting species’ range expansion dynamics: sources of systematic biases when scaling up patterns and processes. *Methods in Ecology and Evolution*, 3, 1008–1018.

- Boeye, J., Travis, J.M.J., Stoks, R. & Bonte, D. (2013). More rapid climate change promotes evolutionary rescue through selection for increased dispersal distance. *Evolutionary Applications*, 6, 353–364.
- Bonenfant, C., Gaillard, J.-M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., et al. (2009). Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research*, 41, 313–357.
- Bonte, D., Borre, J. Vanden & Lens, L. (2006). Geographical variation in wolf spider dispersal behaviour is related to landscape structure. *Animal Behaviour*, 72, 655–662.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., et al. (2012). Costs of dispersal. *Biological Reviews of the Cambridge Philosophical Society*, 87, 290–312.
- Bonte, D., Hovestadt, T. & Poethke, H.-J. (2009). Sex-specific dispersal and evolutionary rescue in metapopulations infected by male killing endosymbionts. *BMC Evolutionary Biology*, 9, 16.
- Bonte, D., Hovestadt, T. & Poethke, H.-J. (2010). Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos*, 119, 560–566.
- Boulangeat, I., Gravel, D. & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, 15, 584–93.
- Bowler, D.E. & Benton, T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society*, 80, 205–25.
- Bridle, J.R. & Vines, T.H. (2007). Limits to evolution at range margins: when and why does adaptation fail? *Trends in ecology & evolution*, 22, 140–7.
- Brooker, R.W., Travis, J.M.J., Clark, E.J. & Dytham, C. (2007). Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, 245, 59–65.
- Broquet, T. & Petit, E.J. (2009). Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology, Evolution, and Systematics*, 40, 193–216.
- Bullock, J.M. & Clarke, R.T. (2000). Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia*, 124, 506–521.
- Cagnacci, F., Boitani, L., Powell, R.A. & Boyce, M.S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365, 2157–62.
- Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates.
- Caswell, H., Takada, T. & Hunter, C.M. (2004). Sensitivity analysis of equilibrium in density-dependent matrix population models. *Ecology Letters*, 7, 380–387.

- Caswell, H. & Weeks, D.E. (1986). Two-Sex Models: Chaos, Extinction, and Other Dynamic Consequences of Sex. *The American Naturalist*, 128, 707–735.
- Chaine, A.S., Legendre, S. & Clobert, J. (2013). The co-evolution of multiply-informed dispersal: information transfer across landscapes from neighbors and immigrants. *PeerJ*, 1, e44.
- Chaput-Bardy, A., Grégoire, A., Baguette, M., Pagano, A. & Secondi, J. (2010). Condition and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*. *PloS one*, 5, e10694.
- Chardon, J.P., Adriaensen, F. & Matthysen, E. (2003). Incorporating landscape elements into a connectivity measure: a case study for the speckled wood butterfly (*Pararge aegeria* L.). *Landscape Ecology*, 18, 561–573.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–6.
- Chipperfield, J.D., Dytham, C. & Hovestadt, T. (2011). An updated algorithm for the generation of neutral landscapes by spectral synthesis. *PloS one*, 6, e17040.
- Clark, J., Fastie, C., Hurt, G., Jackson, S. & Johnson, C. (1998). Reid's paradox of rapid plant migration. *BioScience*, 48, 13–24.
- Clark, J.S., Lewis, M. & Horvath, L. (2001). Invasion by extremes: population spread with variation in dispersal and reproduction. *The American Naturalist*, 157, 537–54.
- Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (2012). *Dispersal Ecology and Evolution*. Oxford University Press.
- Clobert, J., Danchin, E., Dhondt, A. & Nichols, J. (2001). *Dispersal*. Oxford University Press.
- Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S. & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12, 197–209.
- Clotuche, G., Mailleux, A.-C., Yano, S., Detrain, C., Denebourg, J.-L. & Hance, T. (2013). Settlement decisions by the two-spotted spider mite *Tetranychus urticae*. *Comptes Rendus Biologies*, 336, 93–101.
- Codling, E. a, Plank, M.J. & Benhamou, S. (2008). Random walk models in biology. *Journal of the Royal Society*, 5, 813–34.
- Comins, H., Hamilton, W. & May, R.. (1980). Evolutionarily stable dispersal strategies. *Journal of Theoretical Biology*, 82, 205–230.
- Conlisk, E., Syphard, A.D., Franklin, J., Flint, L., Flint, A. & Regan, H. (2013). Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Global Change Biology*, 19, 858–69.

- Cote, J. & Clobert, J. (2007). Social information and emigration: lessons from immigrants. *Ecology Letters*, 10, 411–7.
- Coulson, T., Ezard, T.H.G., Pelletier, F., Tavecchia, G., Stenseth, N.C., Childs, D.Z., et al. (2008). Estimating the functional form for the density dependence from life history data. *Ecology*, 89, 1661–1674.
- Coumou, D. & Rahmstorf, S. (2012). A decade of weather extremes. *Nature Climate Change*, 2, 491–496.
- Davis, M.B. & Shaw, R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292, 673–9.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011). Beyond predictions: biodiversity conservation in a changing climate. *Science*, 332, 53–8.
- Delattre, T., Burel, F., Humeau, A., Stevens, V.M., Vernon, P. & Baguette, M. (2010). Dispersal mood revealed by shifts from routine to direct flights in the meadow brown butterfly *Maniola jurtina*. *Oikos*, 119, 1900–1908.
- Delgado, M.M., Penteriani, V., Revilla, E. & Nams, V.O. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology*, 79, 620–32.
- Denno, R., Roderick, G. & Peterson, M. (1996). Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecological*, 66, 389–408.
- Doerr, V.A.J., Barrett, T. & Doerr, E.D. (2011). Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. *Journal of Applied Ecology*, 48, 143–147.
- Doligez, B., Pärt, T., Danchin, E., Clobert, J. & Gustafsson, L. (2004). Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology*, 73, 75–87.
- Dormann, C.F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, 16, 129–138.
- Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., et al. (2012). Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, 39, 2119–2131.
- Dover, J. & Settele, J. (2008). The influences of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation*, 13, 3–27.
- Driezen, K., Adriaensen, F. & Rondinini, C. (2007). Evaluating least-cost model predictions with empirical dispersal data: A case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). *Ecological Modelling*, 209, 314–322.
- Duckworth, R.A. (2008). Adaptive dispersal strategies and the dynamics of a range expansion. *The American Naturalist*, 172 Suppl , S4–17.

- Van Dyck, H. & Matthysen, E. (1999). Habitat fragmentation and insect flight: a changing “design” in a changing landscape? *Trends in ecology & evolution*, 14, 172–174.
- Dytham, C. (2009). Evolved dispersal strategies at range margins. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1407–13.
- Dytham, C. & Travis, J.M.J. (2006). Evolving dispersal and age at death. *Oikos*, 113, 530–538.
- Easterling, D.R. (2000). Climate extremes: Observations, modeling, and impacts. *Science*, 289, 2068–2074.
- Edelaar, P., Siepielski, A.M. & Clobert, J. (2008). Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution*, 62, 2462–72.
- Elith, J. & Leathwick, J.R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.
- Enfjäll, K. & Leimar, O. (2009). The evolution of dispersal - the importance of information about population density and habitat characteristics. *Oikos*, 118, 291–299.
- Engler, R. & Guisan, A. (2009). MigClim: Predicting plant distribution and dispersal in a changing climate. *Diversity and Distributions*, 15, 590–601.
- Excoffier, L., Foll, M. & Petit, R.J. (2009). Genetic consequences of range expansions. *Annual Review of Ecology, Evolution, and Systematics*, 40, 481–501.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515.
- Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, 21, 1003–1015.
- Fellous, S., Duncan, A., Coulon, A. & Kaltz, O. (2012). Quorum sensing and density-dependent dispersal in an aquatic model system. *PloS one*, 7, e48436.
- Fischer, J. & Lindenmayer, D.B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, 16, 265–280.
- Fletcher, R.J. (2006). Emergent properties of conspecific attraction in fragmented landscapes. *The American Naturalist*, 168, 207–19.
- Fletcher, R.J. (2007). Species interactions and population density mediate the use of social cues for habitat selection. *The Journal of Animal Ecology*, 76, 598–606.
- Fowler, M.S. & Ruokolainen, L. (2013). Confounding environmental colour and distribution shape leads to underestimation of population extinction risk. *PloS one*, 8, e55855.
- Frankham, R. (2009). Where are we in conservation genetics and where do we need to go? *Conservation Genetics*, 11, 661–663.

- Franklin, J. (2010). Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, 16, 321–330.
- Franks, S.J. & Hoffmann, A.A. (2012). Genetics of Climate Change Adaptation. *Annual Review of Genetics*, 46, 185–208.
- Friedenberg, N.A. (2003). Experimental evolution of dispersal in spatiotemporally variable microcosms. *Ecology Letters*, 6, 953–959.
- Fronhofer, E.A., Sperr, E.B., Kreis, A., Ayasse, M., Poethke, H.J. & Tschapka, M. (2013). Picky hitch-hikers: vector choice leads to directed dispersal and fat-tailed kernels in a passively dispersing mite. *Oikos*, 122, 1254–1264.
- Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., et al. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19114–9.
- Le Galliard, J.-F., Massot, M. & Clobert, J. (2012a). Dispersal and range dynamics in changing climates: a review. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). pp. 317–336.
- Le Galliard, J.-F., Rémy, A., Ims, R. a & Lambin, X. (2012b). Patterns and processes of dispersal behaviour in arvicoline rodents. *Molecular Ecology*, 21, 505–23.
- Gallien, L., Münkemüller, T., Albert, C.H., Boulangeat, I. & Thuiller, W. (2010). Predicting potential distributions of invasive species: where to go from here? *Diversity and Distributions*, 16, 331–342.
- Gardner, R.H. & Gustafson, E.J. (2004). Simulating dispersal of reintroduced species within heterogeneous landscapes. *Ecological Modelling*, 171, 339–358.
- Gaston, K.J. (2009). Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1395–406.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A framework for community interactions under climate change. *Trends in ecology & evolution*, 25, 325–31.
- Gilroy, J.J. & Lockwood, J.L. (2012). Mate-finding as an overlooked critical determinant of dispersal variation in sexually-reproducing animals. *PloS one*, 7, e38091.
- Greenman, J. V & Benton, T.G. (2005). The impact of environmental fluctuations on structured discrete time population models: resonance, synchrony and threshold behaviour. *Theoretical Population Biology*, 68, 217–35.
- Greenwood, P. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28, 1140–1162.
- Grimm, V. & Railsback, S.F. (2005). *Individual-based Modeling And Ecology*. Princeton University Press.

- Gros, A., Hovestadt, T. & Poethke, H.J. (2008). Evolution of sex-biased dispersal: The role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecological Modelling*, 219, 226–233.
- Gros, A., Poethke, H.J. & Hovestadt, T. (2009). Sex-specific spatio-temporal variability in reproductive success promotes the evolution of sex-biased dispersal. *Theoretical population biology*, 76, 13–8.
- Guillaume, F. & Perrin, N. (2009). Inbreeding load, bet hedging, and the evolution of sex-biased dispersal. *The American Naturalist*, 173, 536–41.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.
- Hansen, J., Sato, M. & Ruedy, R. (2012). Perception of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 109, E2415–23.
- Hanski, I., Erälahti, C., Kankare, M., Ovaskainen, O. & Sirén, H. (2004). Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters*, 7, 958–966.
- Hanski, I. & Mononen, T. (2011). Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecology Letters*, 14, 1025–34.
- Hartig, F., Calabrese, J.M., Reineking, B., Wiegand, T. & Huth, A. (2011). Statistical inference for stochastic simulation models - theory and application. *Ecology Letters*, 14, 816–27.
- Hartig, F., Dyke, J., Hickler, T., Higgins, S.I., O'Hara, R.B., Scheiter, S., et al. (2012). Connecting dynamic vegetation models to data - an inverse perspective. *Journal of Biogeography*, 39, 2240–2252.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., et al. (2005). The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters*, 8, 91–101.
- Haughland, D. & Larsen, K. (2004). Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. *Journal of Animal Ecology*, 1024–1034.
- Hawkes, C. (2009). Linking movement behaviour, dispersal and population processes: is individual variation a key? *The Journal of Animal Ecology*, 78, 894–906.
- Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W. & Martin, T.S. (2006). Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, 30, 1–27.
- Heino, M. & Hanski, I. (2001). Evolution of migration rate in a spatially realistic metapopulation model. *The American Naturalist*, 157, 495–511.
- Heino, M., Ripa, J. & Kaitala, V. (2009). Extinction Risk under Coloured Environmental Noise. *Ecography*, 23, 177–184.

- Heinz, S.K. & Strand, E. (2006). Adaptive Patch Searching Strategies in Fragmented Landscapes. *Evolutionary Ecology*, 20, 113–130.
- Hellmann, J.J., Prior, K.M. & Pelini, S.L. (2012). The influence of species interactions on geographic range change under climate change. *Annals of the New York Academy of Sciences*, 1249, 18–28.
- Henry, R.C., Bocedi, G. & Travis, J.M.J. (2013). Eco-evolutionary dynamics of range shifts: Elastic margins and critical thresholds. *Journal of Theoretical Biology*, 321, 1–7.
- Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist*, 173, 579–588.
- Higgins, S.I., O'Hara, R.B. & Römermann, C. (2012). A niche for biology in species distribution models. *Journal of Biogeography*, 39, 2091–2095.
- Hoban, S., Bertorelle, G. & Gaggiotti, O.E. (2011). Computer simulations: tools for population and evolutionary genetics. *Nature Reviews. Genetics*, 13, 110–22.
- Hobbs, N. & Swift, D. (1985). Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *The Journal of Wildlife Management*, 49, 814–822.
- Hodgson, J.A., Moilanen, A., Wintle, B.A. & Thomas, C.D. (2011). Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*, 48, 148–152.
- Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. (2009). Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology*, 46, 964–969.
- Hodgson, J.A., Thomas, C.D., Dytham, C., Travis, J.M.J. & Cornell, S.J. (2012). The speed of range shifts in fragmented landscapes. *PloS one*, 7, e47141.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., et al. (2008). Assisted colonization and rapid climate change. *Science*, 321, 345–6.
- Hoffmann, A. a & Sgrò, C.M. (2011). Climate change and evolutionary adaptation. *Nature*, 470, 479–85.
- Holt, R.D. (2003). On the evolutionary ecology of species ' ranges. *Evolutionary Ecology Research*, 5, 159–178.
- Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A. & Taper, M.L. (2005). Theoretical models of species ' borders: single species approaches. *Oikos*, 108, 18–27.
- Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. & Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19060–5.

- Hovestadt, T., Binzenhöfer, B., Nowicki, P. & Settele, J. (2011). Do all inter-patch movements represent dispersal? A mixed kernel study of butterfly mobility in fragmented landscapes. *The Journal of Animal Ecology*, 80, 1070–7.
- Hovestadt, T., Bonte, D., Dytham, C. & Poethke, H.J. (2012). Evolution and emergence of dispersal kernels—a brief theoretical evaluation. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). Oxford University Press, pp. 211–221.
- Hovestadt, T., Kubisch, A. & Poethke, H.J. (2010). Information processing in models for density-dependent emigration: A comparison. *Ecological Modelling*, 221, 405–410.
- Hovestadt, T., Messner, S. & Poethke, H.J. (2001). Evolution of reduced dispersal mortality and “fat-tailed” dispersal kernels in autocorrelated landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 268, 385–91.
- Hughes, C.L., Dytham, C. & Hill, J.K. (2007). Modelling and analysing evolution of dispersal in populations at expanding range boundaries. *Ecological Entomology*, 32, 437–445.
- Hughes, C.L., Hill, J.K. & Dytham, C. (2003). Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proceedings of the Royal Society B: Biological Sciences*, 270 Suppl , S147–50.
- Huntley, B., Barnard, P., Altwegg, R., Chambers, L., Coetzee, B.W.T., Gibson, L., et al. (2010). Beyond bioclimatic envelopes: dynamic species’ range and abundance modelling in the context of climatic change. *Ecography*, 33, 621–626.
- Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., et al. (2013). Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, 1, 6.
- Johst, K., Brandl, R. & Eber, S. (2002). Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos*, 98, 263–270.
- Johst, K. & Wissel, C. (1997). Extinction risk in a temporally correlated fluctuating environment. *Theoretical Population Biology*, 52, 91–100.
- Jongejans, E., Skarpaas, O. & Shea, K. (2008). Dispersal, demography and spatial population models for conservation and control management. *Perspectives in Plant Ecology, Evolution and Systematics*, 9, 153–170.
- Keith, D. a, Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., et al. (2008). Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, 4, 560–3.
- Kendall, B. & Fox, G. (2003). Unstructured individual variation and demographic stochasticity. *Conservation Biology*, 17, 1170–1172.
- Knowlton, J.L. & Graham, C.H. (2010). Using behavioral landscape ecology to predict species’ responses to land-use and climate change. *Biological Conservation*, 143, 1342–1354.

- Kokko, H. & López-Sepulcre, A. (2006). From individual dispersal to species ranges: perspectives for a changing world. *Science*, 313, 789–91.
- Kramer-Schadt, S., Revilla, E., Wiegand, T. & Breitenmoser, U. (2004). Fragmented landscapes , road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, 41, 711–723.
- Krosby, M., Tewksbury, J., Haddad, N.M. & Hoekstra, J. (2010). Ecological connectivity for a changing climate. *Conservation Biology*, 24, 1686–9.
- Kubisch, A., Degen, T., Hovestadt, T. & Poethke, H.J. (2013). Predicting range shifts under global change: the balance between local adaptation and dispersal. *Ecography*, 36, 873–882.
- Kubisch, A., Hovestadt, T. & Poethke, H.-J. (2010). On the elasticity of range limits during periods of expansion. *Ecology*, 91, 3094–9.
- Kubisch, A. & Poethke, H.-J. (2011). Range border formation in a world with increasing climatic variance. *Evolutionary Ecology Research*, 13, 159–169.
- Kubisch, A., Poethke, H.-J. & Hovestadt, T. (2011). Density-dependent dispersal and the formation of range borders. *Ecography*, 34, 1002–1008.
- Kun, A. & Scheuring, I. (2006). The evolution of density-dependent dispersal in a noisy spatial population model. *Oikos*, 115, 308–320.
- Lambin, X., Le Bouille, D., Oliver, M.K., Sutherland, C., Tedesco, E. & Douglas, A. (2012). High connectivity despite high fragmentation: iterated dispersal in a vertebrate metapopulation. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M.). Oxford University Press, pp. 406–412.
- Lande, R., Engen, S., Sæther, B.E. & Coulson, T. (2006). Estimating Density Dependence from Time Series of Population Age Structure. *The American Naturalist*, 168, 76–87.
- Lawson Handley, L.J. & Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, 16, 1559–78.
- Legendre, S. (2004). Age structure, mating system and population viability. In: *Evolutionary Conservation Biology* (eds. Ferrière, R., Dieckmann, U. & Couvet, D.). Cambridge University Press, pp. 41–58.
- Lenoir, J., Gégout, J.C., Marquet, P. a, de Ruffray, P. & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–71.
- Lesser, M.R. & Jackson, S.T. (2013). Contributions of long-distance dispersal to population growth in colonising *Pinus ponderosa* populations. *Ecology Letters*, 16, 380–9.
- Lima, S. & Zollner, P. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, 11, 131–135.

- Lindström, J. & Kokko, H. (1998). Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. *Proceedings of the Royal Society B: Biological Sciences*, 265, 483–8.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009). The velocity of climate change. *Nature*, 462, 1052–5.
- Loss, S.R., Terwilliger, L.A. & Peterson, A.C. (2011). Assisted colonization: Integrating conservation strategies in the face of climate change. *Biological Conservation*, 144, 92–100.
- Mathias, A., Kisdi, E. & Olivieri, I. (2001). Divergent evolution of dispersal in a heterogeneous landscape. *Evolution*, 55, 246–259.
- Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography*, 28, 403–416.
- Matthysen, E. (2012). Multicausality of dispersal: a review. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). Oxford University Press, pp. 3–18.
- Maynard-Smith, J. & Slatkin, M. (1973). The stability of predator-prey systems. *Ecology*, 54, 384–391.
- McInerny, G., Travis, J.M.J. & Dytham, C. (2007). Range shifting on a fragmented landscape. *Ecological Informatics*, 2, 1–8.
- McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. & Ehrlich, P.R. (2002). Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 6070–4.
- McPeek, M. & Holt, R.D. (1992). The evolution of dispersal in spatially and temporally varying environments. *The American Naturalist*, 140, 1010–1027.
- De Meester, N. & Bonte, D. (2010). Information use and density-dependent emigration in an agrobiont spider. *Behavioral Ecology*, 21, 992–998.
- Merckx, T. & Van Dyck, H. (2006). Landscape structure and phenotypic plasticity in flight morphology in the butterfly Pararge aegeria. *Oikos*, 113, 226–232.
- Merckx, T., Van Dyck, H., Karlsson, B. & Leimar, O. (2003). The evolution of movements and behaviour at boundaries in different landscapes: a common arena experiment with butterflies. *Proceedings of the Royal Society B: Biological Sciences*, 270, 1815–21.
- Metz, J. a & Gyllenberg, M. (2001). How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proceedings of the Royal Society B: Biological Sciences*, 268, 499–508.
- Midgley, G.F., Davies, I.D., Albert, C.H., Altweig, R., Hannah, L., Hughes, G.O., et al. (2010). BioMove - an integrated platform simulating the dynamic response of species to environmental change. *Ecography*, 33, 612–616.

- Miller, T.E.X. & Inouye, B.D. (2013). Sex and stochasticity affect range expansion of experimental invasions. *Ecology Letters*, 16, 354–61.
- Miller, T.E.X., Shaw, A.K., Inouye, B.D. & Neubert, M.G. (2011). Sex-biased dispersal and the speed of two-sex invasions. *The American Naturalist*, 177, 549–61.
- Mitikka, V., Moilanen, A. & Hanski, I. (2010). The effect of landscape structure on range expansion of the map butterfly in Finland. In: *The range expansion of the European map butterfly in Finland. PhD Thesis* (ed. Mitikka, V.).
- Morales, J. & Ellner, S. (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology*, 83, 2240–2247.
- Morales, J.M. (2002). Behavior at habitat boundaries can produce leptokurtic movement distributions. *The American Naturalist*, 160, 531–538.
- Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R. a, et al. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society of London. Series B*, 365, 2289–301.
- Muñoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R. & Martínez, I. (2004). Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science*, 304, 1144–7.
- Murrell, D., Travis, J. & Dytham, C. (2002). The evolution of dispersal distance in spatially-structured populations. *Oikos*, 97, 229–236.
- Mustin, K., Benton, T.G., Dytham, C. & Travis, J.M.J. (2009). The dynamics of climate-induced range shifting; perspectives from simulation modelling. *Oikos*, 118, 131–137.
- Mustin, K., Dytham, C., Benton, T.G. & Travis, J.M.J. (2013). Red noise increases extinction risk during rapid climate change. *Diversity and Distributions*, 19, 815–824.
- Nathan, R., Getz, W., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., et al. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105, 19052–19059.
- Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F.M. & Katul, G.G. (2011). Spread of North American wind-dispersed trees in future environments. *Ecology Letters*, 14, 211–9.
- Nathan, R., Klein, E., Robledo-Arnuncio, J.J. & Revilla, E. (2012). Dispersal kernels: review. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). Oxford University Press, pp. 187–210.
- Neubert, M.G. & Caswell, H. (2000). Density-dependent vital rates and their population dynamic consequences. *Journal of Mathematical Biology*, 41, 103–121.
- Norberg, J., Urban, M.C., Vellend, M., Klausmeier, C.A. & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*, 2, 747–751.
- North, A., Cornell, S. & Ovaskainen, O. (2011). Evolutionary responses of dispersal distance to landscape structure and habitat loss. *Evolution*, 65, 1739–51.

- Olden, J.D., Schooley, R.L., Monroe, J.B. & Poff, N.L. (2004). Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology*, 73, 1190–1194.
- Opdam, P. & Wascher, D. (2004). Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, 117, 285–297.
- Ovaskainen, O. (2004). Habitat-Specific Movement Parameters Estimated Using Mark–Recapture Data and a Diffusion Model. *Ecology*, 85, 242–257.
- Ovaskainen, O. & Cornell, S.J. (2003). Biased movement at a boundary and conditional occupancy times for diffusion processes. *Journal of Applied Probability*, 40, 557–580.
- Ovaskainen, O. & Crone, E.E. (2010). Modeling animal movement with diffusion. In: *Spatial Ecology* (eds. Cantrell, S., Cosner, C. & Ruan, S.). Chapman & Hall, pp. 63–84.
- Ovaskainen, O., Luoto, M., Ikonen, I., Rekola, H., Meyke, E. & Kuussaari, M. (2008a). An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *The American Naturalist*, 171, 610–9.
- Ovaskainen, O., Smith, A.D., Osborne, J.L., Reynolds, D.R., Carreck, N.L., Martin, A.P., et al. (2008b). Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19090–5.
- Pagel, J. & Schurr, F.M. (2012). Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography*, 21, 293–304.
- Palmer, S.C.F., Coulon, A. & Travis, J.M.J. (2011). Introducing a “stochastic movement simulator” for estimating habitat connectivity. *Methods in Ecology and Evolution*, 2, 258–268.
- Palmer S.C.F., Coulon A. & Travis J.M.J. (2014). Inter-individual variability in dispersal behaviours impacts connectivity estimates. *Oikos*, 123, 923–932.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hillk, J.K., Thomas, C.D., Descimon, H., et al. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology & Evolution*, 23, 87–94.
- Pe'er, G., Henle, K., Dislich, C. & Frank, K. (2011). Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. *PLoS one*, 6, e22355.

- Pe'er, G. & Kramer-Schadt, S. (2008). Incorporating the perceptual range of animals into connectivity models. *Ecological Modelling*, 213, 73–85.
- Pe'er, G., Zurita, G.A., Schober, L., Bellocq, M.I., Strer, M., Müller, M., et al. (2013). Simple process-based simulators for generating spatial patterns of habitat loss and fragmentation: A review and introduction to the G-RaFFe model. *PLoS ONE*, 8, e64968.
- Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12, 361–371.
- Perrin, N. & Mazalov, V. (1999). Dispersal and inbreeding avoidance. *The American Naturalist*, 154, 282–292.
- Perrin, N. & Mazalov, V. (2000). Local competition, inbreeding, and the evolution of sex-biased dispersal. *The American Naturalist*, 155, 116–127.
- Petit, S. & Pors, L. (1996). Survey of columnar cacti and carrying capacity for nectar-feeding bats on Curaçao. *Conservation Biology*, 10, 769–775.
- Phillips, B., Brown, G. & Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology*, 91, 1617–1627.
- Phillips, B.L. (2012). Range shift promotes the formation of stable range edges. *Journal of Biogeography*, 39, 153–161.
- Phillips, B.L., Brown, G.P., Travis, J.M.J. & Shine, R. (2008). Reid's paradox revisited: the evolution of dispersal kernels during range expansion. *The American Naturalist*, 172 Suppl , S34–48.
- Plotnick, R.E. & Gardner, R.H. (2002). A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns. *Ecological Modelling*, 147, 171–197.
- Poethke, H.J., Gros, A. & Hovestadt, T. (2011). The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance. *Journal of Theoretical Biology*, 282, 93–9.
- Poethke, H.J. & Hovestadt, T. (2002). Evolution of density- and patch-size-dependent dispersal rates. *Proceedings of the Royal Society B: Biological Sciences*, 269, 637–45.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, 15, 732–743.
- Revilla, E. & Wiegand, T. (2008). Individual movement behaviour, matrix heterogeneity, and the dynamics of spatially structured populations. *Proceedings of the National Academy of Sciences*, 105, 19120–19125.
- Revilla, E., Wiegand, T., Palomares, F., Ferreras, P. & Delibes, M. (2004). Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. *The American Naturalist*, 164, E130–53.

- Ricketts, T.H. (2001). The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, 158, 87–99.
- Ripa, J. & Lundberg, P. (1996). Noise colour and the risk of population extinctions. *Proceedings of the Royal Society B: Biological Sciences*, 263, 1751–1753.
- Robert, A., Sarrazin, F. & Couvet, D. (2003). Variation among individuals, demographic stochasticity, and extinction: Response to Kendall and Fox. *Conservation Biology*, 17, 1166–1169.
- Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, 38, 231–253.
- Ronce, O. & Clobert, J. (2012). Dispersal syndrome. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M.). Oxford University Press.
- Ronce, O., Perret, F. & Olivieri, I. (2000). Landscape dynamics and evolution of colonizer syndromes: interactions between reproductive effort and dispersal in a metapopulation. *Evolutionary Ecology*, 14, 233–260.
- Rousset, F. & Gandon, S. (2002). Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *Journal of Evolutionary Biology*, 515–523.
- Ruokolainen, L., Lindén, A., Kaitala, V. & Fowler, M.S. (2009). Ecological and evolutionary dynamics under coloured environmental variation. *Trends in Ecology & Evolution*, 24, 555–63.
- Ruxton, G.D. & Rohani, P. (1998). Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. *Journal of Animal Ecology*, 67, 530–539.
- Saupe, D. (1988). Algorithms for random fractals. In: *The Science of Fractal Images* (eds. Pietgen, H.O. & Saupe, D.). Springer, New York, pp. 71–113.
- Scheiner, S.M., Barfield, M. & Holt, R.D. (2012). The genetics of phenotypic plasticity. XI. Joint evolution of plasticity and dispersal rate. *Ecology and evolution*, 2, 2027–39.
- Schiffers, K., Bourne, E.C., Lavergne, S., Thuiller, W. & Travis, J.M.J. (2013). Limited evolutionary rescue of locally adapted populations facing climate change. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 368, 20120083.
- Schtickzelle, N. & Baguette, M. (2003). Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration – patch area relationships in fragmented landscapes. *Journal of Animal Ecology*, 72, 533–545.
- Schtickzelle, N., Mennechez, G. & Baguette, M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology*, 87, 1057–1065.
- Schtickzelle, N., Turlure, C. & Baguette, M. (2012). Temporal variation in dispersal kernels in a metapopulation of the bog fritillary butterfly (*Boloria eunomia*). In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). Oxford University Press, pp. 231–239.

- Schultz, C. & Crone, E. (2001). Edge-mediated dispersal behavior in a prairie butterfly. *Ecology*, 82, 1879–1892.
- Schurr, F.M. (2012). How random is dispersal? From stochasticity to process in the description of seed movement. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M.). Oxford University Press, pp. 240–247.
- Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O’Hara, R.B., et al. (2012). How to understand species’ niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography*, 39, 2146–2162.
- Schwager, M., Johst, K. & Jeltsch, F. (2006). Does red noise increase or decrease extinction risk? Single extreme events versus series of unfavorable conditions. *The American Naturalist*, 167, 879–88.
- Schymanski, S.J., Dormann, C.F., Cabral, J., Chuine, I., Graham, C.H., Hartig, F., et al. (2013). Process, correlation and parameter fitting in species distribution models: a response to Kriticos et al. *Journal of Biogeography*, 40, 612–613.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009). Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, 40, 415–436.
- Shreeve, T.G. & Dennis, R.L.H. (2010). Landscape scale conservation: resources, behaviour, the matrix and opportunities. *Journal of Insect Conservation*, 15, 179–188.
- Simmons, A.D. & Thomas, C.D. (2004). Changes in dispersal during species’ range expansions. *The American Naturalist*, 164, 378–95.
- Sinclair, S.J., White, M.D. & Newell, G.R. (2010). How useful are species distribution models for managing biodiversity under future climates ? *Ecology And Society*, 15, 8.
- Singer, A., Travis, J.M.J. & Johst, K. (2012). Interspecific interactions affect species and community responses to climate shifts. *Oikos*, 122, 358–366.
- Smouse, P.E., Focardi, S., Moorcroft, P.R., Kie, J.G., Forester, J.D. & Morales, J.M. (2010). Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 365, 2201–11.
- Spear, S.F., Balkenhol, N., Fortin, M.-J., McRae, B.H. & Scribner, K. (2010). Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology*, 19, 3576–91.
- Stamps, J. (1998). Conspecific attraction and aggregation in territorial species. *The American Naturalist*, 131, 329–347.
- Stamps, J. (2001). Habitat selection by dispersers: integrating proximate and ultimate approaches. In: *Dispersal* (eds. Clobert, J., Danchin, E., Dhondt, A. & Nichols, J.). Oxford University Press.
- Stamps, J., Krishnan, V. V & Willits, N.H. (2009). How different types of natal experience affect habitat preference. *The American Naturalist*, 174, 623–30.

- Stamps, J. & Blozis, S. (2006). Effects of natal experience on habitat selection when individuals make choices in groups: a multilevel analysis. *Animal Behaviour*, 71, 663–672.
- Stamps, J.A., Krishnan, V. & Reid, M.L. (2005). Search costs and habitat selection by dispersers. *Ecology*, 86, 510–518.
- Starrfelt, J. & Kokko, H. (2010). Parent-offspring conflict and the evolution of dispersal distance. *The American Naturalist*, 175, 38–49.
- Stenseth, N. & Lidicker, W. (1992). *Animal dispersal: small mammals as a model*. Springer.
- Stevens, V.M. & Coulon, A. (2012). Landscape effects on dispersal dynamics: the natterjack toad as a case study. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). Oxford University Press, pp. 280–289.
- Stevens, V.M., Leboulengé, E., Wesselingh, R. a & Baguette, M. (2006a). Quantifying functional connectivity: experimental assessment of boundary permeability for the natterjack toad (*Bufo calamita*). *Oecologia*, 150, 161–71.
- Stevens, V.M., Polus, E., Wesselingh, R.A., Schtickzelle, N. & Baguette, M. (2004). Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack toad (*Bufo calamita*). *Landscape Ecology*, 19, 829–842.
- Stevens, V.M., Turlure, C. & Baguette, M. (2010). A meta-analysis of dispersal in butterflies. *Biological Reviews of the Cambridge Philosophical Society*, 85, 625–42.
- Stevens, V.M., Verkenne, C., Vandewoestijne, S., Wesselingh, R.A & Baguette, M. (2006b). Gene flow and functional connectivity in the natterjack toad. *Molecular Ecology*, 15, 2333–44.
- Thomas, C.D. (2010). Climate, climate change and range boundaries. *Diversity and Distributions*, 16, 488–495.
- Thomas, C.D. (2011). Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in ecology & evolution*, 26, 216–21.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., et al. (2004). Extinction risk from climate change. *Nature*, 427, 145–8.
- Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., et al. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 9, 137–152.
- Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009). BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography*, 32, 369–373.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 8245–50.

- Thuiller, W., Münkemüller, T., Lavergne, S., Mouillot, D., Mouquet, N., Schiffers, K., et al. (2013). A road map for integrating eco-evolutionary processes into biodiversity models. *Ecology Letters*, 16, 94–105.
- Travis, J.M.J. (2001). The color of noise and the evolution of dispersal. *Ecological Research*, 16, 157–163.
- Travis, J.M.J. (2003). Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B: Biological Sciences*, 270, 467–73.
- Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., et al. (2014). Dispersal and species' responses to climate change. *Oikos*, 122, 1532–1540.
- Travis, J.M.J. & Dytham, C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society B: Biological Sciences*, 266, 723–728.
- Travis, J.M.J. & Dytham, C. (2002). Dispersal evolution during invasions. *Evolutionary Ecology Research*, 4, 1119–1129.
- Travis, J. & Dytham, C. (2004). A method for simulating patterns of habitat availability at static and dynamic range margins. *Oikos*, 104, 410–416.
- Travis, J. & Dytham, C. (2012). Dispersal and climate change: a review of theory. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.). Oxford University Press, pp. 337–348.
- Travis, J.M.J., Harris, C.M., Park, K.J. & Bullock, J.M. (2011). Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. *Methods in Ecology and Evolution*, 2, 477–488.
- Travis, J.M.J., Murrell, D.J. & Dytham, C. (1999). The evolution of density-dependent dispersal. *Proceedings of the Royal Society B: Biological Sciences*, 266, 1837–1842.
- Travis, J.M.J., Mustin, K., Bartoń, K.A., Benton, T.G., Clobert, J., Delgado, M.M., et al. (2012). Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution*, 3, 628–641.
- Travis, J.M.J., Mustin, K., Benton, T.G. & Dytham, C. (2009). Accelerating invasion rates result from the evolution of density-dependent dispersal. *Journal of Theoretical Biology*, 259, 151–8.
- Travis, J.M.J., Smith, H.S. & Ranwala, S.M.W. (2010). Towards a mechanistic understanding of dispersal evolution in plants: conservation implications. *Diversity and Distributions*, 16, 690–702.
- Turlure, C., Baguette, M., Stevens, V.M. & Maes, D. (2011). Species- and sex-specific adjustments of movement behavior to landscape heterogeneity in butterflies. *Behavioral Ecology*, 22, 967–975.

- Turner, M.G., Arthaud, G.J., Engstrom, R.T., Hejl, S.J. & Liu, J. (1995). Usefulness of spatially explicit population models in land management. *Ecological Applications*, 5, 12–16.
- Urban, M.C., Zarnetske, P.L. & Skelly, D.K. (2013). Moving forward: dispersal and species interactions determine biotic responses to climate change. *Annals of the New York Academy of Sciences*, 1297, 44–60.
- Vandermeer, J. & Carvajal, R. (2001). Metapopulation dynamics and the quality of the matrix. *The American Naturalist*, 158, 211–220.
- Vasseur, D.A. & Yodzis, P. (2004). The color of environmental noise. *Ecology*, 85, 1146–1152.
- Verheyen, G., De Bruyn, L., Adriaensen, F. & Matthysen, E. (2003). Does matrix resistance influence Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? *Landscape Ecology*, 18, 791–805.
- Verboom, J., Schippers, P., Cormont, A., Sterk, M., Vos, C.C. & Opdam, P.F.M. (2010). Population dynamics under increasing environmental variability: implications of climate change for ecological network design criteria. *Landscape Ecology*, 25, 1289–1298.
- Vercken, E., Sinervo, B. & Clobert, J. (2012). The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment. *Behavioral Ecology*, 23, 1059–1067.
- Vitt, P., Havens, K. & Hoegh-Guldberg, O. (2009). Assisted migration: part of an integrated conservation strategy. *Trends in Ecology & Evolution*, 9, 473–474.
- Vuilleumier, S. & Metzger, R. (2006). Animal dispersal modelling: Handling landscape features and related animal choices. *Ecological Modelling*, 190, 159–170.
- Vuilleumier, S. & Perrin, N. (2006). Effects of cognitive abilities on metapopulation connectivity. *Oikos*, 113, 139–147.
- Wang, R., Ovaskainen, O., Cao, Y., Chen, H., Zhou, Y., Xu, C., et al. (2011). Dispersal in the Glanville fritillary butterfly in fragmented versus continuous landscapes: comparison between three methods. *Ecological Entomology*, 36, 251–260.
- Warren, M., Hill, J., Asher, T. & Fox, R. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414, 65–69.
- Watts, K., Eycott, A.E., Handley, P., Ray, D., Humphrey, J.W. & Quine, C.P. (2010). Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. *Landscape Ecology*, 25, 1305–1318.
- Weeks, A.R., Sgro, C.M., Young, A.G., Frankham, R., Mitchell, N.J., Miller, K. a, et al. (2011). Assessing the benefits and risks of translocations in changing environments: a genetic perspective. *Evolutionary applications*, 4, 709–725.

- Wiegand, T., Revilla, E. & Moloney, K.A. (2005). Effects of Habitat Loss and Fragmentation on Population Dynamics. *Conservation Biology*, 19, 108–121.
- Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S., et al. (2009a). Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conservation Letters*, 2, 46–52.
- Willis, S.G., Thomas, C.D., Hill, J.K., Collingham, Y.C., Telfer, M.G., Fox, R., et al. (2009b). Dynamic distribution modelling: predicting the present from the past. *Ecography*, 32, 5–12.
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., et al. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological reviews of the Cambridge Philosophical Society*, 88, 15–30.
- With, K.A. (1997). The application of neutral landscape models in conservation biology. *Conservation Biology*, 11, 1069–1080.
- With, K.A. & King, A.W. (1999). Extinction Thresholds for Species in Fractal Landscapes. *Conservation Biology*, 13, 314–326.
- Zheng, C., Ovaskainen, O. & Hanski, I. (2009a). Modelling single nucleotide effects in phosphoglucose isomerase on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Philosophical Transactions of the Royal Society of London. Series B*, 364, 1519–32.
- Zheng, C., Pennanen, J. & Ovaskainen, O. (2009b). Modelling dispersal with diffusion and habitat selection: Analytical results for highly fragmented landscapes. *Ecological Modelling*, 220, 1495–1505.
- Zollner, P. & Lima, S. (1999). Search strategies for landscape-level interpatch movements. *Ecology*, 80, 1019–1030.
- Zollner, P.A. & Lima, S.L. (1997). Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos*, 80, 51–60.
- Zollner, P.A. & Lima, S.L. (2005). Behavioral tradeoffs when dispersing across a patchy landscape. *Oikos*, 108, 219–230.
- Zurell, D., Grimm, V., Rossmanith, E., Zbinden, N., Zimmermann, N.E. & Schröder, B. (2012). Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps. *Ecography*, 35, 590–603.
- Zurell, D., Jeltsch, F., Dormann, C.F. & Schröder, B. (2009). Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography*, 32, 733–744.