

1 **RangeShiftR: an R package for individual-based simulation of spatial** 2 **eco-evolutionary dynamics and species' responses to environmental** 3 **change**

4

5 Anne-Kathleen Malchow^{*1,2}, Greta Bocedi³, Stephen C. F. Palmer³, Justin M. J. Travis³, Damaris
6 Zurell^{1,2}

7

8 ¹ University of Potsdam, Institute of Biochemistry and Biology, Potsdam, Germany

9 ² Humboldt University of Berlin, Geography Department, Berlin, Germany

10 ³ School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue,
11 Aberdeen, AB24 2TZ UK

12

13 * malchow@uni-potsdam.de

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15 **Running title:** RangeShiftR

16

17 Abstract

18 1. Reliably modelling the demographic and distributional responses of a species to environmental
19 changes can be crucial for successful conservation and management planning. Process-based
20 models have the potential to achieve this goal, but so far they remain underused for predictions of
21 species' distributions. Individual-based models offer the additional capability to model inter-
22 individual variation and evolutionary dynamics and thus capture adaptive responses.

23

24 2. We present RangeShiftR, an R package that provides flexible and fast simulations of spatial
25 eco-evolutionary dynamics and species' responses to environmental changes. It implements the
26 individual-based simulation software RangeShifter for the widely used statistical programming
27 platform R. The package features additional auxiliary functions to support model specification and
28 analysis of results. We provide an outline of the package's functionality, describe the underlying
29 model structure with its main components and present a short example.

30

31 3. RangeShiftR offers substantial model complexity, especially for the demographic and dispersal
32 processes. It comes with comprehensive documentation and elaborate tutorials to provide a low
33 entry level. Thanks to the implementation of the core code in C++, the computations are fast. The
34 complete source code is published under a public licence, making adaptations and contributions
35 feasible.

36

37 4. The RangeShiftR package facilitates the application of individual-based and mechanistic
38 modelling to eco-evolutionary questions by operating a flexible and powerful simulation model from
39 R. It allows effortless interoperability with existing packages to create streamlined workflows that
40 can include data preparation, integrated model specification, and results analysis. Moreover, the
41 implementation in R strengthens the potential for coupling RangeShiftR with other models.

42

43 **Key-words**

44 connectivity, conservation, dispersal, evolution, individual-based modelling, population dynamics,

45 range dynamics, spatially explicit

46

47 Introduction

48 Under anthropogenic exploitation and rapid environmental changes, one of the most urgent
 49 challenges biologists face today is to understand and predict if and how species will persist, by
 50 adapting or undergoing changes in their geographic range (Brondizio et al., 2019; McGill et al.,
 51 2015). To infer a species' niche from data and make predictions in space and time, correlative
 52 species distribution models (SDMs) are commonly used tools (Elith & Leathwick, 2009; Guisan &
 53 Zimmermann, 2000; Qiao et al., 2015). The widespread use of SDMs has been facilitated by
 54 accessible and ready-to-use software, most notably Maxent (Phillips et al., 2017) and dedicated R
 55 packages such as biomod2 (Thuiller et al., 2009) and dismo (Hijmans et al., 2017). However, these
 56 methods often incorporate little ecological theory (Austin, 2007; Guisan & Thuiller, 2005) and
 57 usually require making assumptions that are routinely violated in natural observed systems (Elith et
 58 al., 2010; Jarnevich et al., 2015; Martínez-Minaya et al., 2018). For example, SDMs assume that
 59 species are at equilibrium with their environment and ignore any transient dynamics (Zurell et al.,
 60 2016). An alternative that avoids some of these drawbacks is the development and application of
 61 mechanistic models, which aim to simulate relevant eco-evolutionary processes such as dispersal,
 62 demography and evolution (Cabral et al., 2017; Urban et al., 2016). Despite repeated calls for
 63 more mechanistic understanding of range dynamics (Connolly et al., 2017; Kearney & Porter,
 64 2009; Schurr et al., 2012), such models remain underused, arguably due to challenges such as
 65 poor availability of the data needed for parametrisation and restricted accessibility of the required
 66 software (Briscoe et al., 2019; Dormann et al., 2012).

67
 68 The ambition for a more prominent representation of process-based models in ecological research
 69 led to the development of RangeShifter (Bocedi et al., 2014), an implementation of a flexible
 70 individual-based model (IBM) which simulates eco-evolutionary dynamics in a spatially explicit way.
 71 It models population dynamics, dispersal, and evolution as interacting processes, organised within
 72 a modular structure in which each process has a number of modelling options. This makes

RangeShifter a highly adaptable platform with a wide range of applications, including conducting population viability or connectivity analyses (Aben et al., 2016; Henry et al., 2017) and assessing the dynamics of genetic variation across complex landscapes. RangeShifter is a Windows application that can be used via a graphical user interface (GUI) or in a batch mode. The new version 2.0 (Bocedi et al. 2020) adds novel features including the option for dynamic landscapes and a completely revised genetics module. Here, we present RangeShiftR, a package that implements the RangeShifter 2.0 simulation in R (R Core Team, 2020), making it a multi-platform software.

With the RangeShiftR package, we take a step towards a more effortless and accessible use of mechanistic individual-based models. It extends the existing suite of R packages for ecological modelling, which comprises software like the spatially explicit population models steps (Visintin et al., 2020) and demoniche (Nenzén et al., 2012), by a complete and flexible IBM with detailed dispersal dynamics. The package augments the RangeShifter platform with functionality to assist in model specification and output visualisation. As part of the R environment, RangeShiftR offers the powerful potential to interoperate with other packages in order to form integrated workflows, drawing on the extensive functionality for data preparation, output analysis, and easy reporting that is available for R. The actual numeric simulation is implemented entirely in C++ and accessed via Rcpp (Eddelbuettel et al., 2011), thus ensuring high computational performance. RangeShiftR is published under the public license GPLv3 and hence is free to use, modify and share. In order to provide easy access for all users, the package includes extensive built-in documentation and comes with elaborate tutorials presented on the accompanying website (<https://rangeshifter.github.io/RangeshiftR-tutorials/>).

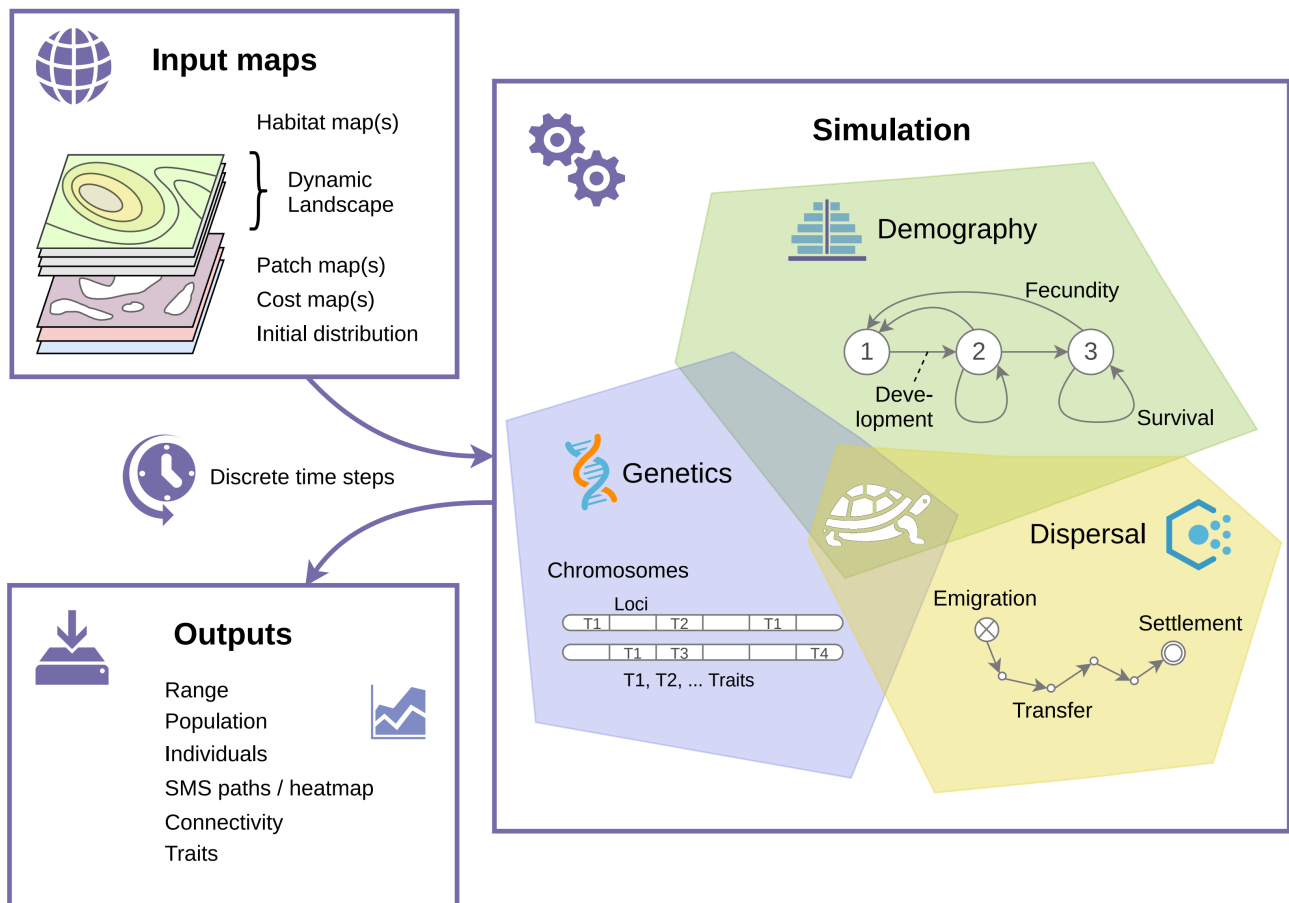


Figure 1: Conceptual overview of a RangeShiftR simulation. The user provides input maps to characterise the landscape, and specifies parameter options that define the three interacting processes of demography, dispersal, and genetics. One option for representing each process is symbolised here as an exemplary model configuration. Different outputs are generated during the simulation and stored in files.

97 Package Structure

98 The RangeShiftR package inherits its model structure from the underlying RangeShifter platform
 99 (Fig. 1). The model requires inputs that include information about the study species and the
 100 landscape. These are provided in the form of model choices, parameters and raster maps. The
 101 simulation itself is based on a regularly gridded landscape and runs over discrete time steps. It
 102 models three main, interacting processes: demography, dispersal, and genetics. Various levels of
 103 output can be generated during the simulation and used for analyses. The functions and classes

104 comprising the RangeShiftR package (Fig. 2) reflect this conceptual workflow and can be
105 categorised into the following three groups.

106 **Model functions**

107 A RangeShiftR model is defined by its structure as well as its parameters. The model structure is
108 formed by the assembly of various modules that define the different processes and sub-processes,
109 such as demography or emigration. Each module is represented in R by its own class, whose
110 instances hold the (numeric) values of all model parameters relevant to the respective module.
111 These instances are constructed via the model functions (Fig. 2).
112 Among the modules exists a number of interdependencies, which are induced by the hierarchy of
113 processes and their sub-processes as well as compatibility restrictions with some options (Bocedi
114 et al., 2014). To reflect this, all modules are organised in a 'ParameterMaster' class, that
115 consolidates all components of the model and gives informative error messages or warnings to the
116 user in case of incompatible parameter combinations. An object of this class defines the entire
117 RangeShiftR model and is used for running the simulation.

118 **Helper functions**

119 Most modules in a RangeShiftR simulation influence each other either directly or indirectly, and the
120 specification of a certain parameter might have implications in various places. Therefore, it can
121 prove challenging to express knowledge about the system by directly specifying numerical
122 parameter values. To aid parameter specification, RangeShiftR includes helper functions to
123 estimate or visualise the effect of some parameters (Fig. 2). For example, they can be used to plot
124 density-dependent demographic or dispersal relationships, whose shape may vary by stage and
125 sex. RangeShiftR also contains the novel functionality to estimate the combined effect of density-
126 dependent population dynamics on a closed population (cf. example below), to guide the choice of
127 adequate levels of demographic rates.

128 **Output functions**

129 All simulation output is written to text files in the formats provided by RangeShifter. The
130 RangeShiftR package includes dedicated output functions that facilitate the inspection of these
131 results by processing and visualising the output files. This includes, for example, the creation of
132 dispersal heatmaps, which show the number of dispersers that passed through each location, and
133 the computation of statistics such as the occupancy probability and the time to colonisation.
134

135 **Simulation Modules**

136 In the modular structure of RangeShiftR, each module represents a different aspect or process of
137 the simulation (Fig. 2), allowing for adaptable levels of model complexity. Below, the main modules
138 are described briefly. For comprehensive documentation, covering all parameters and options, we
139 refer to the package documentation and the RangeShifter manual (Bocedi et al., 2014)(2020).

140 **Landscape**

141 A RangeShiftR simulation runs on a cartesian grid in which each cell holds information about its
142 cover. This is characterised either by a land type index or by a habitat quality score. The landscape
143 map can be imported from an ASCII raster file or it can be artificially created by a built-in function.
144 Imported landscapes have additional options: they can be patch-based, in which case a second
145 raster file is required to indicate each cell's patch ID. Additionally, a raster of dispersal resistance
146 values and a presence-absence raster of the initial distribution can be loaded.

147 **Demography**

148 The modelled demography is determined by two main choices: 1) The population can have
149 overlapping or non-overlapping generations, meaning it can be stage-structured or not. A stage-
150 structure is a sub-module that is represented by its own class and that can be added to the
151 demography module. 2) The population can be modelled using either both sexes or females only.
152 In the former case, various parameters can be sex-specific and the reproductive dynamics may
153 optionally include an explicit mating system.

154 **Dispersal**

155 The dispersal module has three obligatory sub-modules: 'Emigration', 'Transfer', and 'Settlement',
156 which represent the three explicitly modelled phases of dispersal (Travis et al. 2012). Emigration
157 and settlement can be density-dependent and, if applicable, sex- and stage-specific.

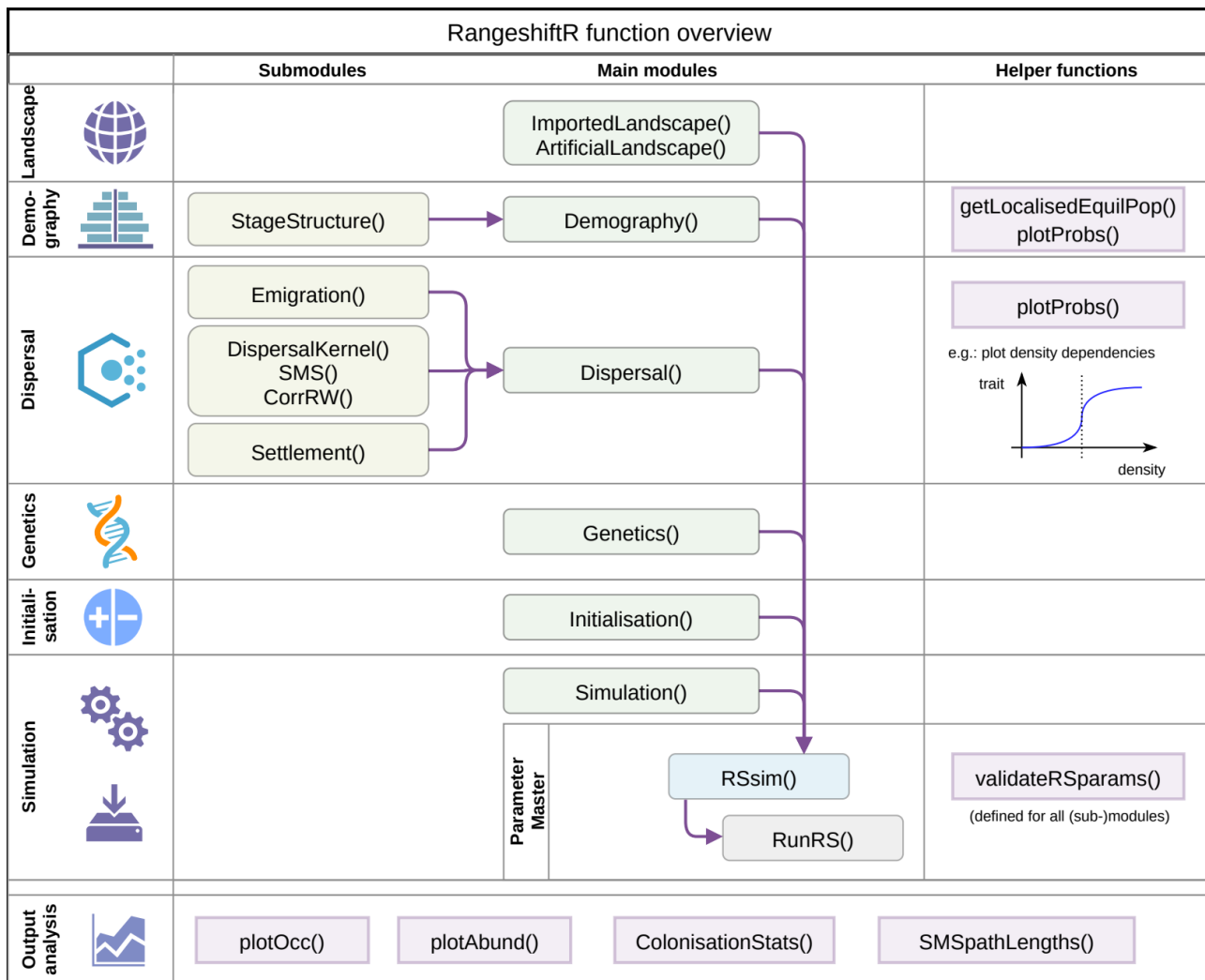


Figure 2: RangeShiftR function overview. The first column introduces the various modules with their respective icons, as reference to Fig. 1. The rounded boxes and arrows in columns 2 and 3 indicate model functions and their respective hierarchical relations. They are class constructors used to define the sub-modules (column 2, yellow) and main modules (column 3, green), which can be combined to a parameter master (blue) to compose the RangeShiftR model. The function RunRS (grey) then starts the simulation. The angled boxes in the last column indicate helper functions that are related to their respective modules. The angled boxes in the bottom row are separate from the columns and itemise the output functions that can be used for processing the simulation results.

159 The transfer sub-module offers three options: it can be modelled with a dispersal kernel or with
160 explicit consideration of the movement processes using either the stochastic movement simulator
161 (SMS) (Palmer et al., 2011) or a correlated random walk.

162 **Genetics**

163 Individuals can carry a genome that they inherit from their parents at birth. The genome may
164 consist of multiple autosomal loci that can either be neutral or coding for traits (Bocedi et al. 2020).
165 Most dispersal parameters can optionally be treated as heritable traits thus allowing evolution of
166 dispersal strategies. The genetic architecture is highly flexible and processes such as
167 recombination, mutation and pleiotropy can be explicitly modelled. Modelling of neutral loci allows
168 explicit and individual-based population genetic simulations to address questions on how
169 environmental features and processes, in interaction with population dynamics and dispersal
170 behaviours, shape the genetic structure and diversity of populations (Manel et al., 2003).

171 **Initialisation**

172 The initial state of the simulation in the starting year can be defined in three different ways: with an
173 initial distribution map, with a list of individuals and their location, or at a given density in randomly
174 selected locations.

175 **Simulation**

176 This module specifies the general simulation settings like the number of simulated time steps
177 (years) and replicates, the types of generated output, and some more specialised options, such as
178 imposing a (shifting) gradient or enabling environmental stochasticity.

179

180 Using RangeShiftR

181 As widely applicable simulation software, RangeShiftR aims to provide easy access via a range of
 182 resources to support the user: all functions are comprehensively documented on R help pages, an
 183 extensive user manual is available online, and the webpage (<https://rangeshifter.github.io>) features
 184 a support forum as well as a collection of detailed tutorials that illustrate the model's scope and
 185 introduce the available modelling options. The tutorials include adaptations of the three original
 186 RangeShifter examples (Bocedi et al., 2014), accompanied by sample code for analysis and
 187 visualisation. Additionally, we provide a fourth tutorial that demonstrates novel features of
 188 RangeShifter 2.0 (Bocedi et al. 2020) by simulating the range dynamics of a species in a changing
 189 landscape. Here, we present its shortened form to introduce the RangeShiftR syntax.

190 Landscape

191 When using the novel feature of dynamic landscapes, we specify the file names of the changing
 192 habitat maps, their corresponding patch files, and the order of years in which these become
 193 effective. All maps are imported as ASCII rasters by the function 'ImportedLandscape()'. Further
 194 arguments are the number of land cover types 'Nhabitats', their respective density-dependence
 195 'K_or_DensDep', and the initial distribution map. The value of 'K_or_DensDep' depends on the
 196 demography: for a non-structured population it is interpreted as carrying capacity (K) whereas for a
 197 stage-structured population it represents the strength of demographic density dependence (1/b).

```
198 landnames <- c("map_01.asc", "map_02.asc", "map_03.asc", "map_04.asc")
199 patchnames <- c("patch01.asc", "patch02.asc", "patch03.asc", "patch03.asc")
200 land <- ImportedLandscape(LandscapeFile = landnames,
201                           PatchFile = patchnames,
202                           DynamicLandYears = c(0,80,110,140),
203                           Nhabitats = 5,
204                           Resolution = 10,
205                           K_or_DensDep = c(125,0,150,75,0),
206                           SpDistFile = "init_dist.asc",
207                           SpDistResolution = 10
208
```

209 Demography

210 The population model is set up to use explicit sexes and a stage-structure, i.e. generations are
 211 overlapping. In the 'Demography()' module the coded argument 'ReproductionType' determines

whether both sexes are modelled. The 'StageStructure()' sub-module takes the transition matrix and sets optional density-dependencies on the sub-processes of fecundity, survival and development.

```

TraMa <- matrix( c(0.0, 0.0, 0.0, 5.0 ,
                  1.0, 0.1, 0.0, 0.0 ,
                  0.0, 0.6, 0.2, 0.0 ,
                  0.0, 0.0, 0.45, 0.85),
                ncol = 4, byrow = TRUE)

demog <- Demography(ReproductionType = 1,
                   StageStruct = StageStructure(Stages = 4,
                                                TransMatrix = TraMa,
                                                FecDensDep = T,
                                                SurvDensDep = T,
                                                SurvDensCoeff = 0.4))

```

The helper function 'getLocalisedEquilPop()' can assist in understanding how the demographic rates of the 'Demography()' module and the local density-dependence ($1/b$) affect the simulated abundances:

```

getLocalisedEquilPop(demog = demog, DensDep_values = seq(50,300,50))

```

It simulates a time series of the density (in individuals per hectare) of a single closed population for varying values of $1/b$ (given by 'DensDep_values'). This is achieved by repeated matrix multiplication with the density-dependent transition matrix until an equilibrium is reached. The function returns these equilibrium densities by stages at the given density-dependence values and generates a bar graph (Fig. 3a). The generated densities approximate the equilibrium densities of a closed patch in the RangeShiftR simulation, and can thus be used to guide the choice of the parameter $1/b$. However, the matrix approach neglects stochasticity, the scheduling of survival and reproduction, and the integer units of abundance, so that the quality of the estimate is lower for smaller populations.

Dispersal

The three phases of dispersal are defined as sub-modules before assembling them in the dispersal module. The emigration probability is modelled as stage- and density-dependent, therefore we

246 provide a matrix with one row per stage containing three parameters each, which define how
247 emigration probability relates to population density:

```
248   emig <- Emigration(StageDep = T,  
249                     DensDep = T,  
250                     EmigProb = cbind(0:3, c(0.55,0.45,0,0),  
251                                     c(5,5,0,0), c(1,1,0,0) ))
```

252
253 The transition phase uses SMS, setting a dispersal bias (entire second line), habitat-specific
254 dispersal resistances, and a constant per-step mortality:

```
255   tran <- SMS(DP = 1.8, MemSize = 4,  
256              GoalType = 2, GoalBias = 2.5, AlphaDB = .4, BetaDB = 10,  
257              Costs = c(3,5,1,2,30),  
258              StepMort = 0.01)
```

259
260 The settlement module defines the minimum and maximum number of steps permitted and sets
261 the mate-finding requirement:

```
262   sett <- Settlement(MaxSteps = 80, MinSteps = 15, MaxStepsYear = 20,  
263                     FindMate = T) )
```

264
265 Now, the previously defined sub-modules can be combined in the 'Dispersal()' module:

```
266   disp <- Dispersal(Emigration = emig,  
267                    Transfer    = tran,  
268                    Settlement  = sett)
```

270 **Genetics**

271 The genetics module is optional and we leave it disabled here (but see Bocedi et al. 2020 for an
272 example of this functionality). Although this implies missing inter-individual variation in dispersal
273 traits, individuals are still characterised by their sex, stage and age.

274 **Initialisation**

275 The simulation is initialised in all locations indicated by the initial distribution map (in the landscape
276 module) at a given density. Further, the stage- and age-distributions of the initial population are set.

```
277   init <- Initialise(InitType = 1,  
278                     SpType = 0,  
279                     InitDens = 2,  
280                     IndsHaCell = 75,  
281                     PropStages = c(0,0.6,0.2,0.2),  
282                     InitAge = 2)
```

283

284 **Simulation**

285 The simulation runs for 200 years and over twenty replicates. The population, range and SMS
286 paths outputs are enabled and will be generated at the given time intervals:

```
287     simul <- Simulation(Years = 200,  
288                       Replicates = 20,  
289                       OutIntPop = 10,  
290                       OutIntRange = 5,  
291                       OutIntPaths = 10)  
292
```

293 **Model run and results**

294 All defined model components are combined into the parameter master with 'RSsim()'. Every
295 RangeShiftR simulation is defined by an instance of this class and the path to its directory and is
296 run using 'RunRS()':

```
297     s <- RSsim(land = land, demog = demog, dispersal = disp, init = init,  
298              simul = simul)  
299  
300     RunRS(s, dirpath = dirpath)  
301
```

302 The simulation output is written to text files in the 'Outputs' folder of the directory, which can be
303 visualised and processed using the auxiliary output functions. For example, Fig. 3b shows the
304 result of the following function that calculates, among other things, the time to colonisation and
305 maps it onto the landscape:

```
306     col <- ColonisationStats(s, dirpath, maps=T)  
307     plot(col$map_col_time)  
308
```

309 In the resulting plot, the non-suitable landscape matrix appears grey and all habitat
310 patches are coloured according to their averaged time to colonisation over all
311 replicates. In this example, smaller patches tend to get colonised later than larger
312 ones.

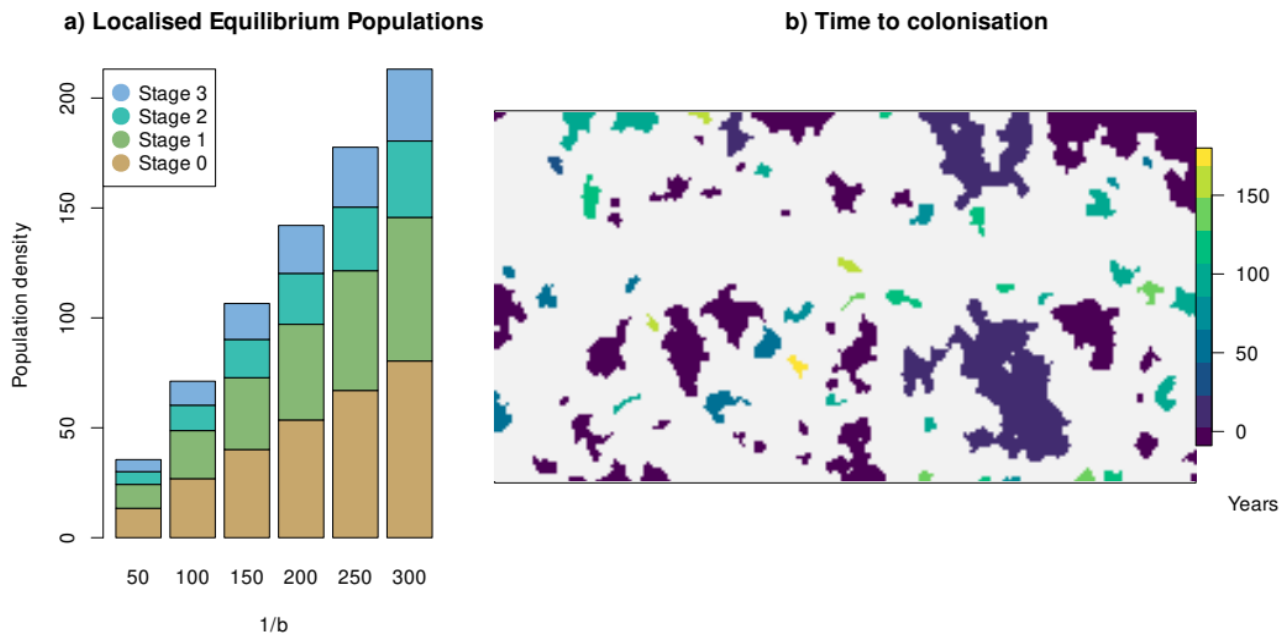


Figure 3: RangeShiftR example. (a) Bar graph generated by the helper function 'getLocalisedEquilPop()', showing the approximated equilibrium densities classified by stages over the parameter $1/b$ (both in units of Inds/ha). They serve as a quick approximation to assess the effect of density-dependent demographic rates. (b) Raster generated by the output function 'ColonisationStats()', showing the average time to colonisation.

313 Discussion

314 RangeShiftR provides, for the first time, an open-source eco-evolutionary numerical simulation
 315 platform that can be controlled and analysed entirely from R. Building on the established
 316 RangeShifter platform (Bocedi et al., 2014)(2020), it offers a high degree of model complexity,
 317 especially for the demographic and dispersal processes. Despite this complexity, straightforward
 318 use of the software is provided through the provision of helper functions and comprehensive
 319 documentation.

320 The RangeShifter GUI and the RangeShiftR package constitute two complementary entities, as
 321 they represent alternative interfaces to the same software core. The GUI version offers an intuitive
 322 handling of the model and visual tracking of simulation outcomes, making it particularly suited for
 323 the use by stakeholders or for undergraduate education. The RangeShiftR package, on the other
 324 hand, is especially useful for research purposes. It offers transparent, reproducible workflows, as
 325 the entire simulation can be scripted in R, along with the visualisation and post-analysis of
 326 simulation results. This also facilitates large-scale parameter comparisons, as in sensitivity and
 327 robustness analyses. The use of Rcpp (Eddelbuettel et al., 2011) allows running of the simulation
 328 in a C++ module and thereby yields high performance, while the integration in R makes
 329 RangeShiftR available for multiple platforms and provides the infrastructure for parallel and cluster
 330 computing without having to adapt the C++ backend.

331 RangeShiftR holds many opportunities for interoperation with other R packages. Firstly, it can be
 332 readily integrated with packages for describing the landscape context (e.g. raster; (Hijmans & van
 333 Etten, 2016)) or species distribution modelling (e.g. biomod2; (Thuiller et al., 2009), sdm; (Naimi &
 334 Araújo, 2016)). Secondly, it permits coupling of different model types, as exemplified by coupling
 335 RangeShifter with the land-use model CRAFTY (Murray-Rust et al., 2014; Synes et al., 2019).
 336 Thirdly, it enables integrated use with existing methodological devices, like inverse
 337 parameterisation through Bayesian inference, for example using the package BayesianTools
 338 (Hartig et al., 2017)

339 RangeShiftR complements the existing toolbox of R packages for ecological simulations by a
 340 powerful individual-based eco-evolutionary modelling platform. It offers some important features
 341 that have not been available so far. Existing R implementations of spatially-explicit population
 342 modelling frameworks, such as the recently published package steps (Visintin et al., 2020) or the
 343 *demonic* package (Nenzén et al., 2012), are population-based. By contrast, RangeShiftR is
 344 individual-based and hence allows for an explicit representation of genetics and evolutionary
 345 dynamics. The package *vortexR* (Pacioni & Mayer, 2017) implements post-analysis functions for
 346 the prominent Vortex model (Lacy, 1993) that is also individual-based and commonly applied for
 347 population viability analysis (PVA). Here, RangeShiftR provides a useful alternative that allows
 348 conducting spatially-explicit PVA under more complex dispersal assumptions.

349 RangeShiftR can help overcome some of the challenges that have prevented more widespread
 350 use of mechanistic range models (Briscoe et al., 2019) by offering high accessibility. In the future,
 351 we plan to enhance the platform further to improve forecasts under global change. For example,
 352 RangeShiftR is currently restricted to modelling a single species only and does not incorporate
 353 species interactions. Moreover, the model operates on a single habitat layer that contains either
 354 land types or habitat quality. Therefore, demographic rates are related to the environment only
 355 indirectly via the user-defined carrying capacities or density dependence coefficients. Lastly, the
 356 genetics module is currently restricted to modelling evolution of dispersal traits while demographic
 357 traits cannot evolve. Thus, potential future extensions of the platform will involve explicitly
 358 modelling species interactions, demography-environment relationships (Pagel & Schurr, 2012) and
 359 genetic evolution of demographic traits. As the code is open source, there is now an opportunity for
 360 a broad community of researchers and modellers to contribute to representing these important
 361 processes in future versions of the platform.

362 The RangeShiftR package constitutes an important step towards making frameworks for modelling
 363 range dynamics under global change accessible to a wider audience (Lurgi et al., 2015; Schurr et
 364 al., 2012; Zurell et al., 2016). We hope that this will inspire a more widespread use of mechanistic

365 distribution models, for example to guide conservation efforts and ecosystem management, and
366 facilitate more seamless integration with other modelling tools.

367

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371

372 **Authors' contributions**

373 AM and DZ conceptualised the modular RangeShiftR package design. GB and SP mainly
374 developed the C++ core code. All authors were involved in key decisions taken during the
375 development of the package. AM primarily wrote, documented and published the RangeShiftR
376 package and led the writing of the manuscript. All authors contributed critically to the drafts and
377 gave final approval for publication.

378

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