

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

4

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14

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 interoperation 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

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

81

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

96

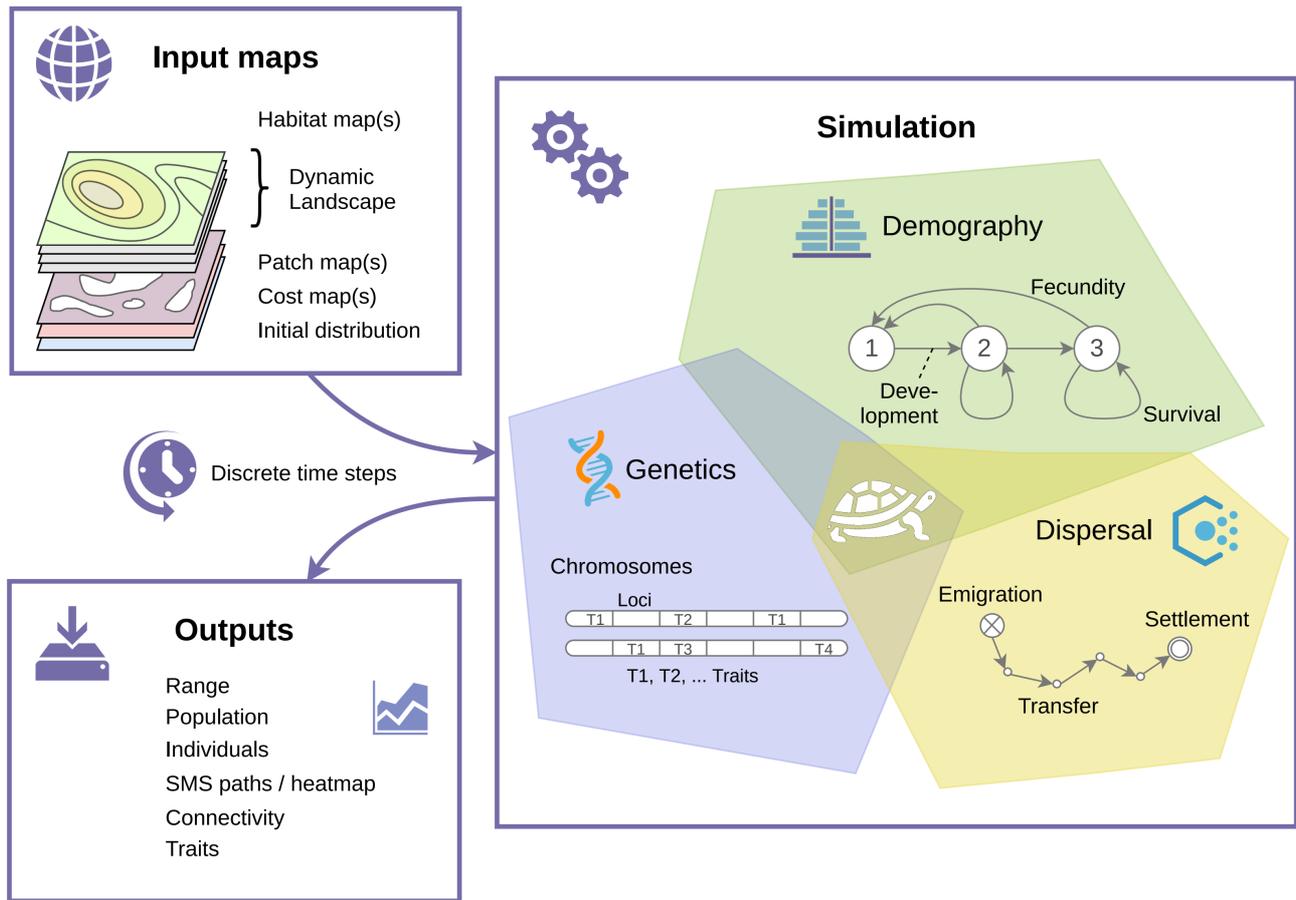


Figure 1: Conceptual overview of a RangeShiftR simulation. The user provides input maps to characterise the landscape, and specifies parameter options that define the three interacting processes of demography, dispersal, and genetics. One option for representing each process is symbolised here as an 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.

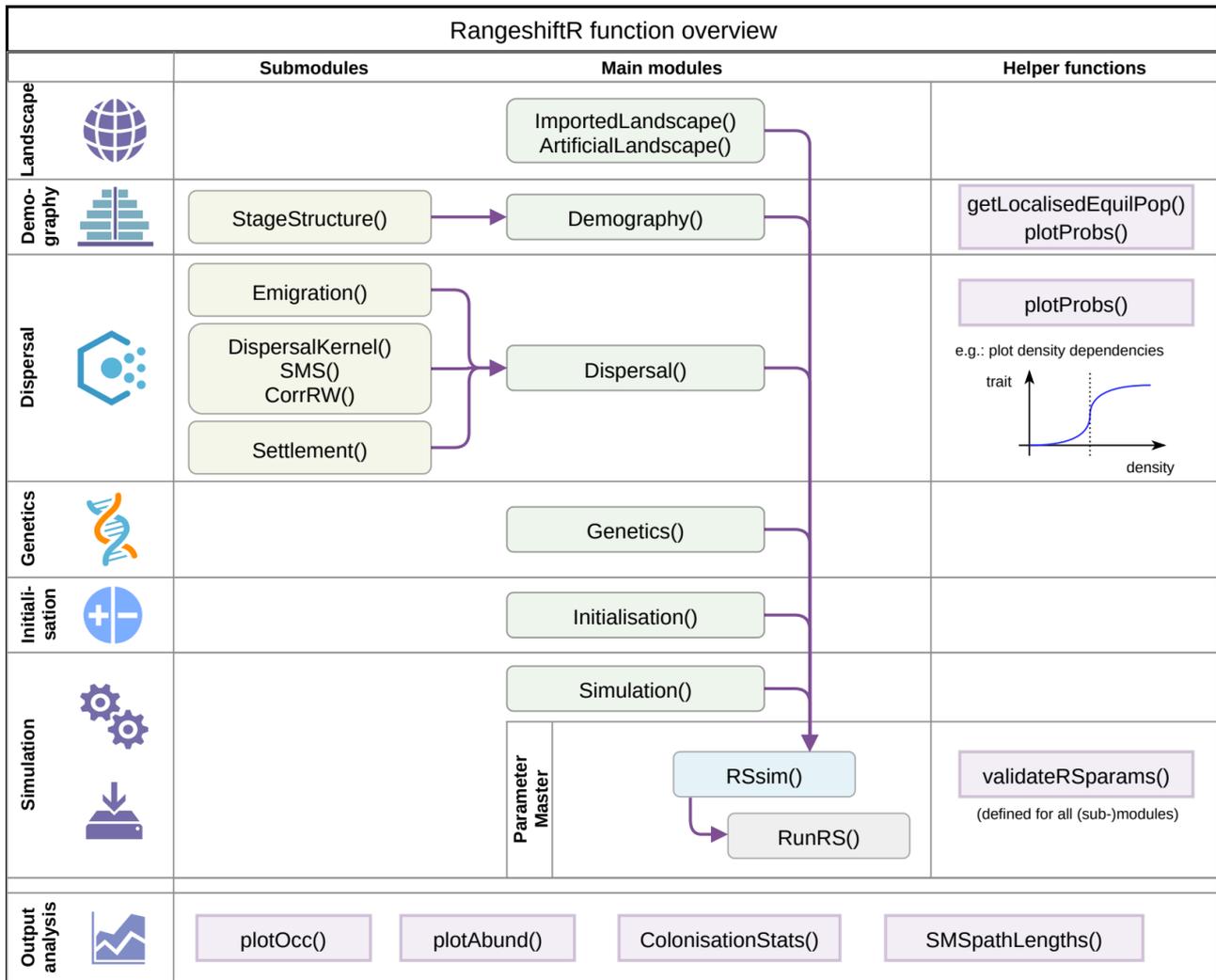


Figure 2: RangeShiftR function overview. The first column introduces the various modules with their respective icons, as reference to Fig. 1. The rounded boxes and arrows in columns 2 and 3 indicate model functions and their respective hierarchical relations. They are class constructors used to define 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

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

```
215 TraMa <- matrix( c(0.0, 0.0, 0.0, 5.0 ,  
216                   1.0, 0.1, 0.0, 0.0 ,  
217                   0.0, 0.6, 0.2, 0.0 ,  
218                   0.0, 0.0, 0.45, 0.85),  
219                 ncol = 4, byrow = TRUE)  
220  
221 demog <- Demography(ReproductionType = 1,  
222                   StageStruct = StageStructure(Stages = 4,  
223                                               TransMatrix = TraMa,  
224                                               FecDensDep = T,  
225                                               SurvDensDep = T,  
226                                               SurvDensCoeff = 0.4))  
227  
228
```

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

```
232 getLocalisedEquilPop(demog = demog, DensDep_values = seq(50,300,50))  
233
```

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

## 243 **Dispersal**

244 The three phases of dispersal are defined as sub-modules before assembling them in the dispersal  
245 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 The transition phase uses SMS, setting a dispersal bias (entire second line), habitat-specific  
253 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 The settlement module defines the minimum and maximum number of steps permitted and sets  
260 the mate-finding requirement:

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

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

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

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

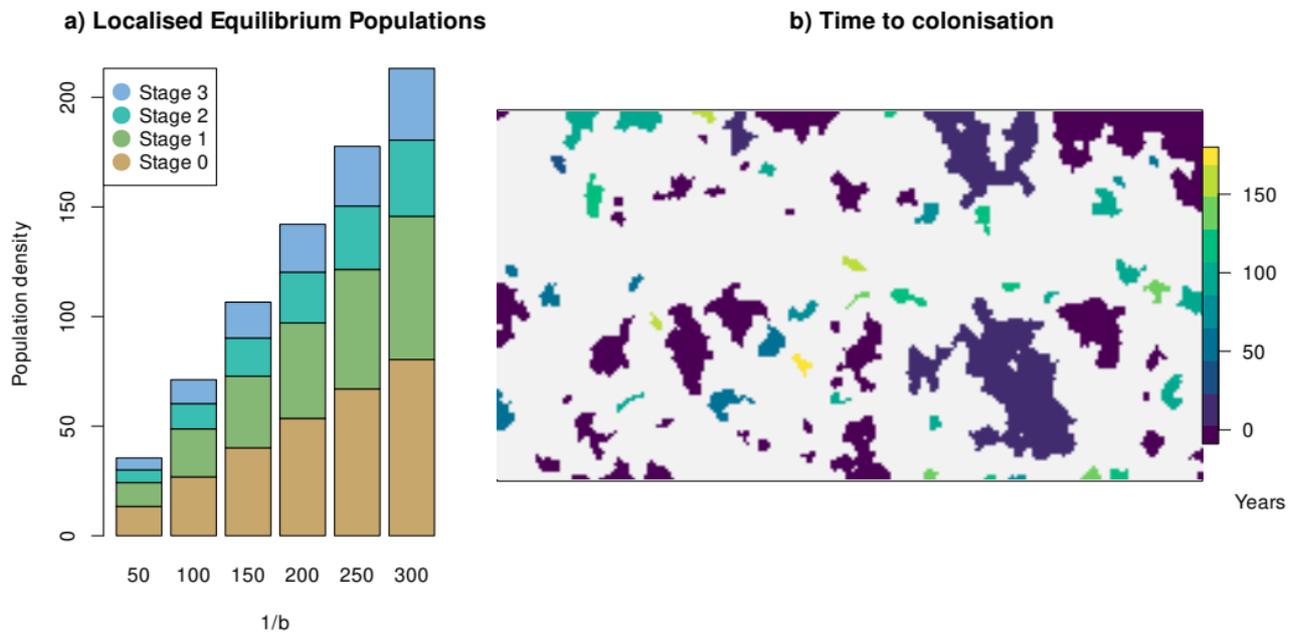


Figure 3: RangeShiftR example. (a) Bar graph generated by the helper function 'getLocalisedEquilPop()', showing the approximated equilibrium densities classified by stages over the parameter  $1/b$  (both in units of Inds/ha). They serve as a quick approximation to assess the effect of density-dependent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

### 368 **Acknowledgements**

369 AM and DZ were supported by Deutsche Forschungsgemeinschaft (DFG) under grant agreement  
370 No. ZU 361/1-1. GB was supported by the Royal Society University Research Fellowship.

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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