1 **RangeShiftR: an R package for individual-based simulation of spatial**

2 **eco-evolutionary dynamics and species' responses to environmental**

3 **change**

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15 **Running title:** RangeShiftR

16

Abstract

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

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

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

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

43 **Key-words**

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

45 range dynamics, spatially explicit

46

Introduction

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

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

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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 assesing

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

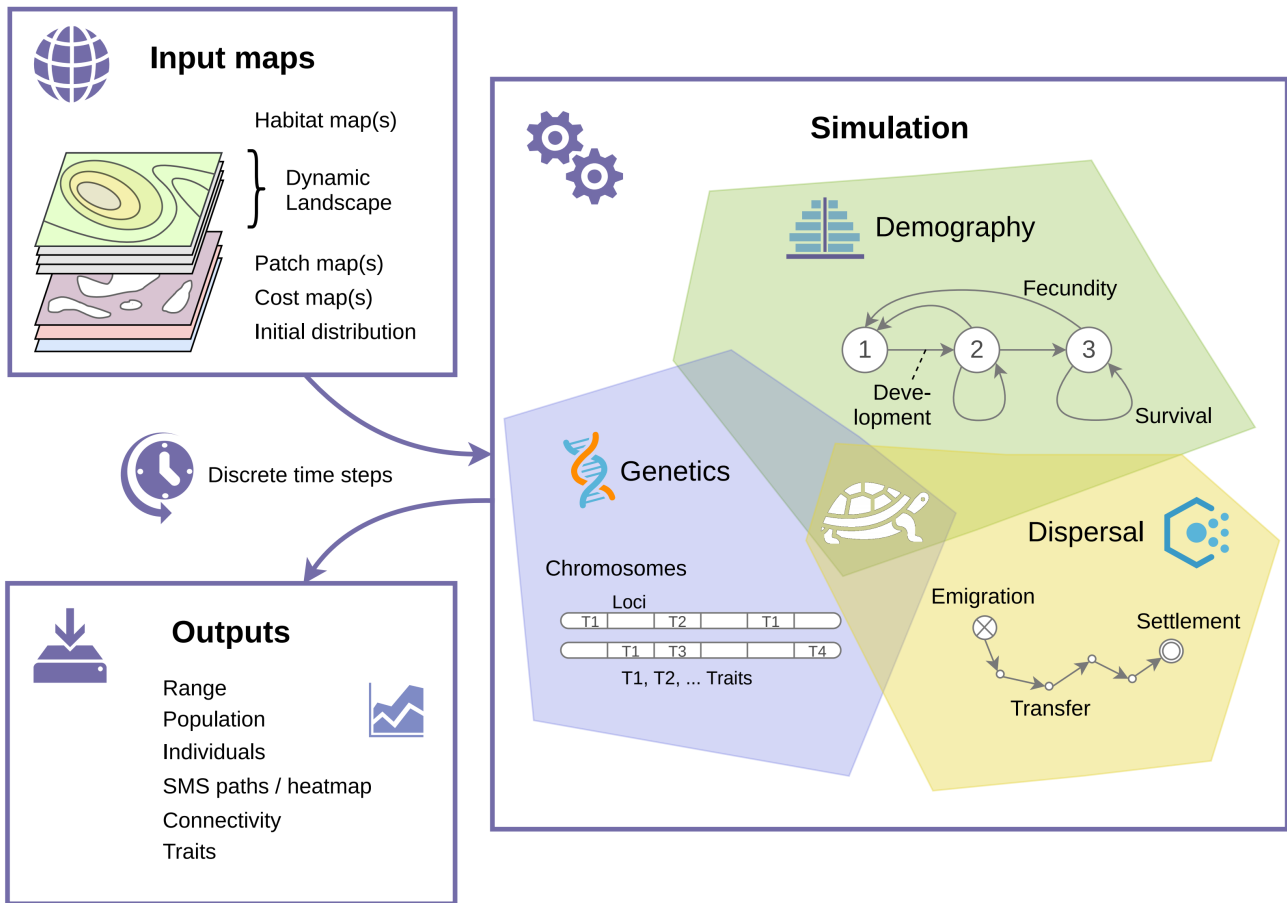95 (https://rangeshifter.github.io/RangeshiftR-tutorials/).

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.

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

6

104 comprising the RangeShiftR package (Fig. 2) reflect this conceptual workflow and can be

105 categorised into the following three groups.

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.

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

Simulation Modules

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

Landscape

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

Demography

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

Dispersal

The dispersal module has three obligatory sub-modules: 'Emigration', 'Transfer', and 'Settlement', which represent the three explicitly modelled phases of dispersal (Travis et al. 2012). Emigration and settlement can be density-dependent and, if applicable, sex- and stage-specific.
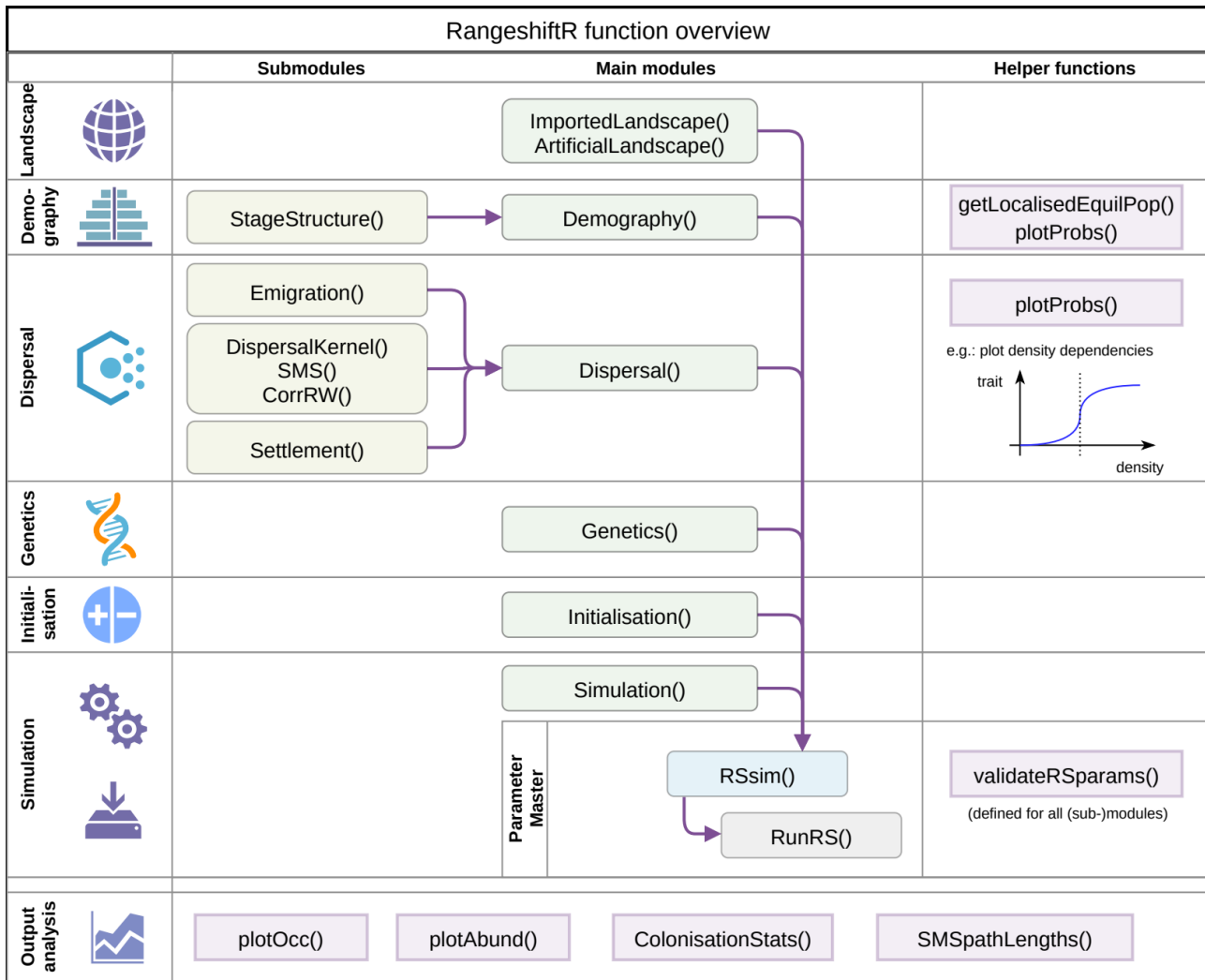
Figure 2: RangeShiftR function overview. The first column introduces the various modules with their respective icons, as reference to Fig. 1. The rounded boxes and arrows in columns 2 and 3 indicate model functions and their respective hierarchical relations. They are class constructors used to define 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

Using RangeShiftR

180

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.

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
```

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

12

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)

221    demog <- Demography(ReproductionType = 1,
222                    StageStruct = StageStructure(Stages = 4,
223                                                 TransMatrix = TraMa,
224                                                 FecDensDep = T,
225                                                 SurvDensDep = T,
226                                                 SurvDensCoeff = 0.4))
```

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))
```

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

13

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)
269
```

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
```

14

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
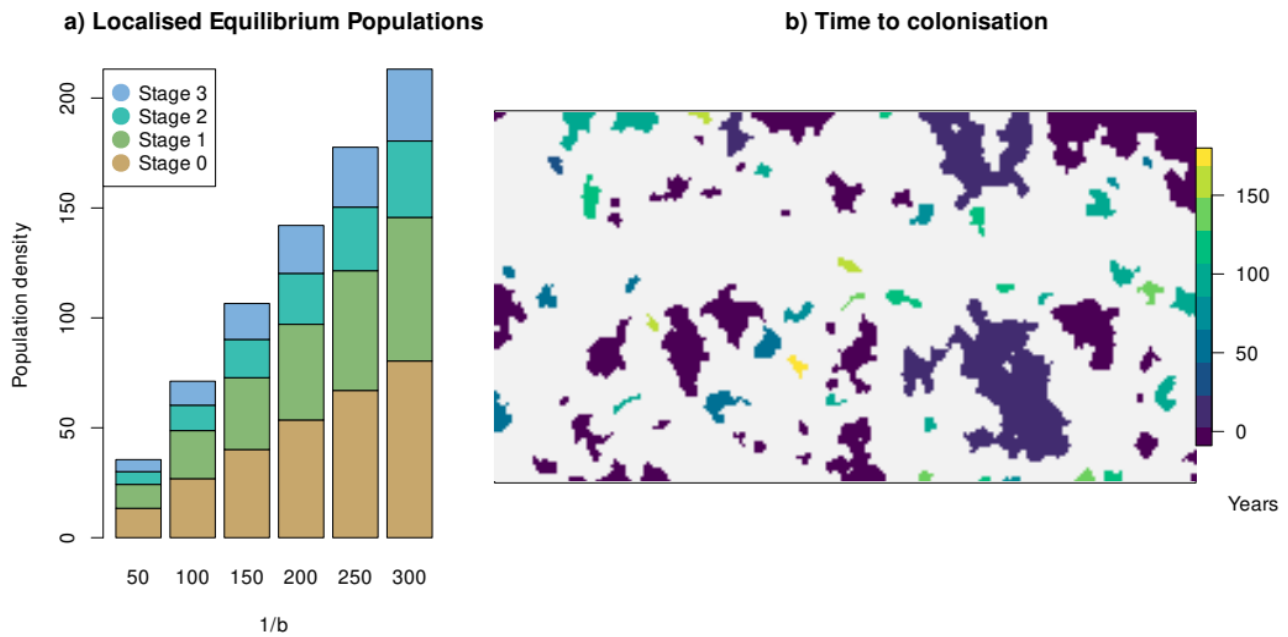
312 ones.

15

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.

Discussion

313 RangeShiftR provides, for the first time, an open-source eco-evolutionary numerical simulation

314

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 demoniche 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

Acknowledgements

371

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

379 **References**

Aben, J., Bocedi, G., Palmer, S. C. F., Pellikka, P., Strubbe, D., Hallmann, C., Travis, J. M. J., Lens, L., & Matthysen, E. (2016). The importance of realistic dispersal models in conservation planning: Application of a novel modelling platform to evaluate management scenarios in an Afrotropical biodiversity hotspot. *Journal of Applied Ecology*, *53*(4), 1055–1065. https://doi.org/10.1111/1365-2664.12643

Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, *200*(1), 1–19. https://doi.org/10.1016/j.ecolmodel.2006.07.005

Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K., & Travis, J. M. J. (2014). RangeShifter: A platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology and Evolution*, *5*(4), 388–396. https://doi.org/10.1111/2041-210X.12162

Briscoe, N. J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J. J., Camac, J. S., Giljohann, K. M., Holden, M. H., Hradsky, B. A., Kearney, M. R., McMahon, S. M., Phillips, B. L., Regan, T. J., Rhodes, J. R., Vesk, P. A., Wintle, B. A., Yen, J. D. L., & Guillera-Arroita, G. (2019). Forecasting species range dynamics with process-explicit models: Matching methods to applications. *Ecology Letters*, *22*(11), 1940–1956. https://doi.org/10.1111/ele.13348

Brondizio, E., Settele, J., Díaz, S., & others. (2019). IPBES. 2019 Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *Bonn, Germany*.

Cabral, J. S., Valente, L., & Hartig, F. (2017). Mechanistic simulation models in macroecology and biogeography: State-of-art and prospects. *Ecography*, *40*(2), 267–280. https://doi.org/10.1111/ecog.02480

Connolly, S. R., Keith, S. A., Colwell, R. K., & Rahbek, C. (2017). Process, Mechanism, and Modeling in Macroecology. *Trends in Ecology & Evolution*, *32*(11), 835–844. https://doi.org/10.1016/j.tree.2017.08.011

Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., & Singer, A. (2012). Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography*, *39*(12), 2119–2131. https://doi.org/10.1111/j.1365-2699.2011.02659.x

Eddelbuettel, D., François, R., Allaire, J., Ushey, K., Kou, Q., Russel, N., Chambers, J., & Bates, D. (2011). Rcpp: Seamless R and C++ integration. *Journal of Statistical Software*, *40*(8), 1–18.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

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*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*(2–3), 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Hartig, F., Minunno, F., Paul, S., Cameron, D., & Ott, T. (2017). BayesianTools: General-purpose MCMC and SMC samplers and tools for Bayesian statistics. *R Package Version. R Package Version 0.1*, *3*.

Henry, R. C., Palmer, S. C. F., Watts, K., Mitchell, R. J., Atkinson, N., & Travis, J. M. J. (2017). Tree loss impacts on ecological connectivity: Developing models for assessment. *Ecological Informatics*, *42*, 90–99. https://doi.org/10.1016/j.ecoinf.2017.10.010

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). dismo: Species distribution modeling. *R Package Version*, *1*(4), 1–1.

Hijmans, R. J., & van Etten, J. (2016). raster: Geographic data analysis and modeling. *R Package Version*, *2*(8).

Jarnevich, C. S., Stohlgren, T. J., Kumar, S., Morisette, J. T., & Holcombe, T. R. (2015). Caveats for correlative species distribution modeling. *Ecological Informatics*, *29*, 6–15. https://doi.org/10.1016/j.ecoinf.2015.06.007

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Lacy, R. C. (1993). VORTEX: A computer simulation model for population viability analysis. *Wildlife Research*, *20*(1), 45–65. https://doi.org/10.1071/wr9930045

Lurgi, M., Brook, B. W., Saltré, F., & Fordham, D. A. (2015). Modelling range dynamics under global change: Which framework and why? *Methods in Ecology and Evolution*, *6*(3), 247–256. https://doi.org/10.1111/2041-210X.12315

Manel, S., Schwartz, M. K., Luikart, G., & Taberlet, P. (2003). Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, *18*(4), 189–197. https://doi.org/10.1016/S0169-5347(03)00008-9

Martínez-Minaya, J., Cameletti, M., Conesa, D., & Pennino, M. G. (2018). Species distribution modeling: A statistical review with focus in spatio-temporal issues. *Stochastic Environmental Research and Risk Assessment*, *32*(11), 3227–3244. https://doi.org/10.1007/s00477-018-1548-7

McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution*, *30*(2), 104–113. https://doi.org/10.1016/j.tree.2014.11.006

Murray-Rust, D., Brown, C., van Vliet, J., Alam, S. J., Robinson, D. T., Verburg, P. H., & Rounsevell, M. (2014). Combining agent functional types, capitals and services to model land use dynamics. *Environmental Modelling & Software*, *59*, 187–201. https://doi.org/10.1016/j.envsoft.2014.05.019

Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*(4), 368–375. https://doi.org/10.1111/ecog.01881

Nenzén, H. K., Swab, R. M., Keith, D. A., & Araújo, M. B. (2012). Demoniche – an R-package for simulating spatially-explicit population dynamics. *Ecography*, *35*(7), 577–580. https://doi.org/10.1111/j.1600-0587.2012.07378.x

Pacioni, C., & Mayer, F. (2017). vortexR: An R package for post Vortex simulation analysis. *Methods in Ecology and Evolution*, *8*(11), 1477–1481. https://doi.org/10.1111/2041-210X.12786

Pagel, J., & Schurr, F. M. (2012). Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography*, *21*(2), 293–304. https://doi.org/10.1111/j.1466-8238.2011.00663.x

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*(3), 258–268. https://doi.org/10.1111/j.2041-210X.2010.00073.x

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*(7), 887–893. https://doi.org/10.1111/ecog.03049

Qiao, H., Soberón, J., & Peterson, A. T. (2015). No silver bullets in correlative ecological niche modelling: Insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution*, *6*(10), 1126–1136. https://doi.org/10.1111/2041-210X.12397

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., Hartig, F., Kissling, W. D., Linder, H. P., Midgley, G. F., Schröder, B., Singer, A., & Zimmermann, N. E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, *39*(12), 2146–2162. https://doi.org/10.1111/j.1365-2699.2012.02737.x

Synes, N. W., Brown, C., Palmer, S. C. F., Bocedi, G., Osborne, P. E., Watts, K., Franklin, J., & Travis, J. M. J. (2019). Coupled land use and ecological models reveal emergence and feedbacks in socio-ecological systems. *Ecography*, *42*(4), 814–825. https://doi.org/10.1111/ecog.04039

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, *32*(3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Urban, M. C., Bocedi, ... Palmer, S. C. F., … Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304). https://doi.org/10.1126/science.aad8466

Visintin, C., Briscoe, N. J., Woolley, S. N. C., Lentini, P. E., Tingley, R., Wintle, B. A., & Golding, N. (2020). steps: Software for spatially and temporally explicit population simulations. *Methods in Ecology and Evolution*, *11*(4), 596–603. https://doi.org/10.1111/2041-210X.13354

Zurell, D., Thuiller, W., Pagel, J., Cabral, J. S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., Schiffers, K. H., Moore, K. A., & Zimmermann, N. E. (2016). Benchmarking novel approaches for modelling species range dynamics. *Global Change Biology*, *22*(8), 2651–2664. https://doi.org/10.1111/gcb.13251