

1 **RangeShifter 2.0: An extended and enhanced platform for modelling spatial eco-**  
2 **evolutionary dynamics and species' responses to environmental changes.**

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12 **Running title:** RangeShifter 2.0

13

14 **Abstract**

15 **1.** Process-based models are becoming increasingly used tools for understanding how  
16 species are likely to respond to environmental changes and to potential management options.

17 RangeShifter is one such modelling platform, which has been used to address a range of  
18 questions including identifying effective reintroduction strategies, understanding patterns of  
19 range expansion and assessing population viability of species across complex landscapes.

20 **2.** Here we introduce a new version, RangeShifter 2.0, which incorporates important new  
21 functionality. It is now possible to simulate dynamics over user-specified, temporally changing  
22 landscapes. Additionally, the genetic and evolutionary capabilities have been strengthened,  
23 notably by introducing an explicit genetic modelling architecture, which allows for simulation  
24 of neutral and adaptive genetic processes. Furthermore, emigration, transfer and settlement  
25 rules can now all evolve, allowing for sophisticated simulation of the evolution of dispersal. We  
26 illustrate the potential application of RangeShifter 2.0's new functionality by two examples.  
27 The first illustrates the range expansion of a virtual species across a dynamically changing UK  
28 landscape. The second demonstrates how the software can be used to explore the concept  
29 of evolving connectivity in response to land-use modification, by examining how movement  
30 rules come under selection over landscapes of different structure and composition.

31 **3.** RangeShifter 2.0 is built using object-oriented C++ providing computationally efficient  
32 simulation of complex individual-based, eco-evolutionary models. The code has been  
33 redeveloped to enable use across operating systems, including on high performance  
34 computing clusters, and the Windows GUI has been enhanced. Furthermore, the recoding of  
35 the package has supported the development of a new version running under the R platform,  
36 RangeShiftR.

37 **4.** RangeShifter 2.0 will facilitate the development of in-silico assessments of how species will  
38 respond to environmental changes and to potential management options for conserving or

39 controlling them. By making the code available open source, we hope to inspire further  
40 collaborations and extensions by the ecological community.

41 **Keywords**

42 Animal movement, dynamic landscapes, individual-based modelling, connectivity, population  
43 viability, distribution modelling, process-based modelling.

44

## 45 **Introduction**

46 Faced with an accelerating global biodiversity crisis caused by multiple interacting and often  
47 anthropogenic environmental changes (Ceballos et al., 2015; Urban, 2015; IPBES, 2019),  
48 biologists are striving to understand and predict how species will respond, in both ecological  
49 and evolutionary terms, to these threats and to management interventions (Urban et al., 2016;  
50 Urban, 2019). Policy makers, conservation biologists and land managers are relying more and  
51 more on such predictions to manage biodiversity on multiple fronts, including protecting  
52 threatened species, limiting invasive species, and targeting habitat restoration efforts to both  
53 enhance in-situ conservation and promoting range shifting (IPBES, 2019). Process-based  
54 models, also called dynamic or mechanistic models, have become increasingly popular  
55 following many calls urging the ecological community to move beyond correlative approaches  
56 towards models that explicitly incorporate the key processes underpinning eco-evolutionary  
57 responses to environmental changes (Franklin, 2010; Huntley et al., 2010; Schurr et al., 2012;  
58 Evans et al., 2013; Thuiller et al., 2013; Urban et al., 2016; Cabral et al., 2017; Connolly et al.  
59 2017; Briscoe et al., 2019; Peterson et al., 2019). Several models and platforms are actively  
60 being developed (e.g. Lurgi et al. 2015; Landguth et al. 2017; Okamoto & Amarasekare, 2018;  
61 Schumaker & Brookes, 2018; Cotto et al. 2020; Kearney & Porter, 2020; Visintin et al., 2020),  
62 benefits and shortcomings scrutinised (Dormann et al., 2012; Singer et al., 2016; Zurell et al.,  
63 2016; Fordham et al., 2018; Johnston et al., 2019), and a promising variety of applications is  
64 emerging (e.g. Synes et al., 2016).

65         RangeShifter is a process-based models that we initially developed (Bocedi, Palmer,  
66 et al., 2014), in response to the many calls for moving towards integrated dynamic modelling  
67 approaches. The main objective was to provide an individual-based, spatially-explicit  
68 modelling platform that integrated population dynamics with sophisticated dispersal behaviour,  
69 and that could be used for a variety of applications, from theory development to in-silico testing  
70 of management interventions. Indeed, since its release, RangeShifter has been used in  
71 studies addressing a range of issues, including testing the effectiveness of alternative

72 management interventions to improve connectivity and population persistence (Aben et al.,  
73 2016; Henry et al., 2017), facilitating range expansion (Synes et al., 2015, 2020), improving  
74 reintroduction success (Heikkinen et al., 2015; Ovenden et al., 2019), investigating range  
75 dynamics of invasive (Fraser et al., 2015; Dominguez Almela et al., 2020) and recovering  
76 species (Sun et al., 2016) and theoretically investigating how different traits and processes  
77 affect rate of range expansion (Bocedi, Zurell et al. 2014; Henry et al., 2014; Barros et al.,  
78 2016; Santini et al., 2016). RangeShifter has also been coupled with CRAFTY (Murray-Rust  
79 et al., 2014), an agent-based model designed to explore the impact of land managers'  
80 behaviours on land-use change, showing that, in the example context of predicting interactions  
81 between crops and their pollinators in a changing agricultural landscape, models that integrate  
82 ecological processes with land managers' behaviours, together with their interactions and  
83 feed-backs can reveal important dynamics in land use change which might otherwise be  
84 missed (Synes et al., 2019; Willemen et al., 2019).

85         Here, we present the new RangeShifter 2.0, which, among various additions and  
86 improvements, includes two major novelties: the option for implementing temporally dynamic  
87 landscapes and a module for the explicit modelling of neutral and adaptive genetics  
88 (controlling dispersal traits). RangeShifter is written in C++; it has been completely recoded  
89 from its original release following object-oriented programming principles and is now open  
90 source, thus facilitating wider usage and enhancements by the ecological community.  
91 Additionally, we provide a dedicated website (<https://rangeshifter.github.io/>) and updated  
92 tutorials for learning to use RangeShifter, and a forum page for more effective communication  
93 among users. In addition to the original and improved Windows graphical user interface (GUI),  
94 RangeShifter can now be compiled to run in batch-mode on Linux computer clusters. Below  
95 we briefly describe, and illustrate with examples, the two major additions of dynamic  
96 landscapes and explicit genetics, while we refer to the RangeShifter 2.0 User Manual  
97 (<https://github.com/RangeShifter/RangeShifter-software-and-documentation>) for smaller  
98 changes and new features.

## 99 **Model enhancements**

### 100 DYNAMIC LANDSCAPES

101 Considering dynamically changing landscapes is crucial for scenario-based simulations (e.g.  
102 climate change or land-used change scenarios), for implementing landscape processes  
103 through time (e.g. ongoing habitat fragmentation) and for testing dynamic management  
104 interventions accounting for time lags from their deployment (e.g. creating a new woodland)  
105 to the realization of their full potential (Watts et al., 2020). In RangeShifter 2.0, the landscape  
106 may be changed any number of times during a simulation, but always at the start of the year,  
107 i.e. prior to reproduction. The changes may comprise any of: alterations to the habitat  
108 structure; addition, removal or changes of patches in a patch-based model; and modifications  
109 of the cost map when using the stochastic movement simulator (SMS; Palmer, Coulon, &  
110 Travis, 2011).

### 111 EXPLICIT GENETICS

112 A new module is provided to define the genetic architecture of a species in a flexible and  
113 explicit way. Individuals may carry one or more chromosomes, to which neutral loci and  
114 adaptive loci controlling dispersal traits are mapped. It is possible to model unlimited neutral  
115 markers, thus allowing tracking of population structure and neutral diversity, as well as  
116 simulating spatial genetic patterns emerging from the interaction between demographic and  
117 spatial processes, e.g. for in-silico applications of landscape genetics (Manel et al., 2003). The  
118 dispersal traits have been extended to cover density-dependent emigration and settlement  
119 reaction norms, which may optionally differ between the sexes. Additionally, if SMS is selected  
120 as the movement model in the transfer phase, the parameters controlling directional  
121 persistence and the dispersal bias and its decay (see the User Manual) can be modelled as  
122 evolving traits. Each dispersal or movement trait can be controlled by a separate single  
123 chromosome, akin to RangeShifter v1 (Bocedi, Palmer, et al., 2014), or through a highly  
124 flexible mapping of traits to chromosomes, which enables the degree of linkage between traits

125 to be controlled and, optionally, pleiotropy to be incorporated, thus allowing for complex  
126 genetic architectures underlying evolution of dispersal strategies (Saastamoinen et al., 2018).  
127 The whole genome of each individual may be output in a separate file if required, e.g. for the  
128 calculation of landscape genetic indices.

## 129 **Example applications**

### 130 EFFECTIVENESS OF WOODLAND CREATION STRATEGIES TO FACILITATE RANGE 131 EXPANSION

132 We illustrate the application of dynamic landscapes using the example of woodland creation  
133 in a real UK landscape introduced by Synes et al. (2015, 2020), who compared the effects of  
134 various realistic management scenarios for improving functional connectivity for a range of  
135 exemplar virtual woodland species on both species' persistence in existing patches and range  
136 expansion ability. They compared persistence and expansion rates under the management  
137 scenarios with a baseline rate for the original landscape. However, as the landscape changes  
138 were 'instant', i.e. the new habitat was assumed to be immediately fully suitable, the  
139 differences they observed could be over-estimated, as newly planted woodland would in reality  
140 take many decades to develop into the equivalent of existing woodland in terms of its suitability  
141 as breeding habitat for many species (Watts et al., 2020). Rather, newly planted areas might  
142 be expected firstly to provide increased structure which might aid movement of woodland  
143 species, and then gradually increase in quality as breeding habitat as canopy cover develops.

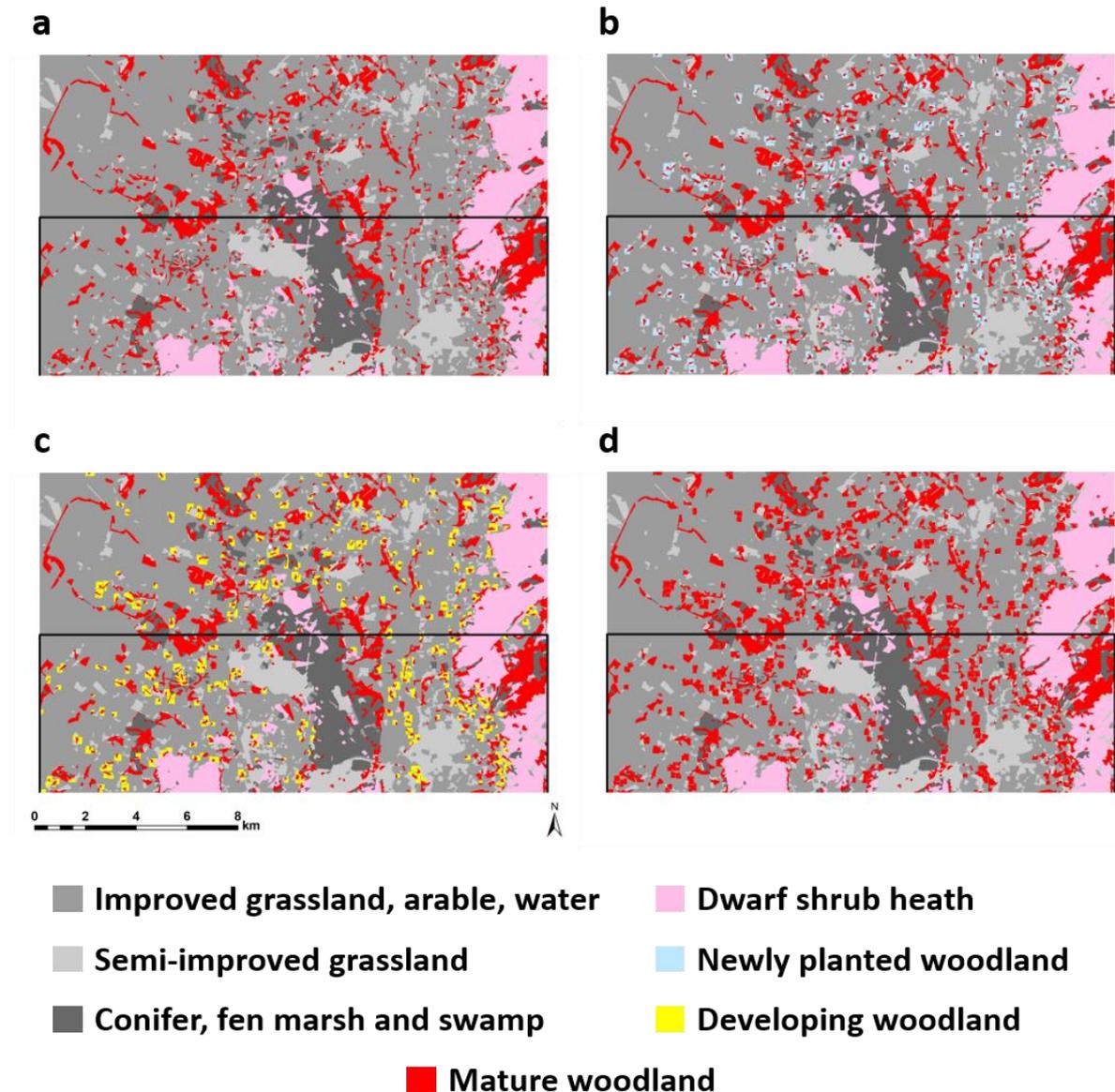
144 We assume as in Synes et al. (2015, 2020) that the locations of all new woodlands are  
145 allocated immediately and on land previously used as improved grassland or arable, and that  
146 planting of saplings occurs instantly in all locations. However, rather than instantly becoming  
147 mature woodland habitat, planted areas develop gradually over a period of 40 years (Table 1,  
148 Fig. 1). We compared the dynamic landscape approach with the 'instant' landscape approach  
149 on the basis of the two most successful scenarios identified by Synes et al. (2015), namely  
150 'CreateRandom' (new patches created anywhere) and 'CreateSmallAdjacent' (new planting to

151 increase the size of existing patches of under 3 ha), applied to 4% of the landscape. For  
152 illustrative purposes we consider one virtual woodland species with simple sexual, stage-  
153 structured demography and good dispersal abilities (Bird\_D<sup>+</sup>P<sup>-</sup>S<sup>+</sup> in Synes et al. 2015; see  
154 Table S1 for the model parameters). We modelled dispersal movements through the  
155 landscape with SMS. To ensure that the species was in equilibrium before management  
156 commenced, we ran simulations for 50 years on the original landscape before applying the  
157 first landscape change, and then continued for a further 100 years during which range  
158 expansion was allowed to occur under the management scenario. Simulations were run on  
159 the baseline landscape and on all the 10 replicate landscapes for each scenario generated by  
160 Synes et al. (2015), and each simulation was replicated 10 times.

161 **Table 1.** Temporal development of newly planted woodland, where  $1/b$  is the fecundity  
 162 density-dependent coefficient (individuals / ha) (which largely determines the equilibrium  
 163 density of the population), *Cost* is the perceived movement cost applied in modelling the  
 164 transfer phase of dispersal by SMS and *Mort* is the per-step habitat-specific mortality  
 165 probability.

<b>Years</b>	<b><math>1/b</math></b>	<b><i>Cost</i></b>	<b><i>Mort</i></b>	<b>Description</b>
0 - 4	0	100	0.05	<b>Permeable habitat</b> – the planting of new woodland provides enhanced movement potential (with lower movement costs). However, the limited canopy cover has no impact on mortality or breeding potential: <i>treat as similar to semi-improved grassland</i>
5 - 9	0	10	0.005	<b>Permeable and safe habitat</b> – as the new woodland develops, it provides increased structural cover for movement and reduced mortality, but it is still too young to provide suitable breeding habitat: <i>treat as dwarf shrub heath</i>
10 - 19	5	5	0.002	<b>Low quality breeding habitat</b> – the new woodland starts to provide a degree of reduced quality breeding habitat and settlement starts to occur, but there are still movement costs and a small mortality risk
20 - 29	10	2	0.001	<b>Medium quality breeding habitat</b> – movement and mortality risks decrease further as canopy cover develops and breeding quality is enhanced
30 - 39	15	1	0.0	<b>High quality breeding habitat</b> – further canopy closure removes movement costs and mortality risk and patch quality moves towards that of established woodland
40 - 100	21	1	0.0	<b>Very high quality breeding habitat</b> – optimal high quality woodland habitat is achieved in year 40 as previously Synes et al. (2015) implemented from year 0

166



167

168 **Figure 1.** Example of dynamic landscape development: (a) initial landscape, (b) after 5 years  
169 when newly planted woodland adjacent to small patches is treated as dwarf shrub heath for  
170 dispersal modelling, (c) after 20 years as canopy closure develops, (d) final landscape after  
171 40 years when newly planted woodland is fully mature. The black line shows the northern limit  
172 of the initial range.

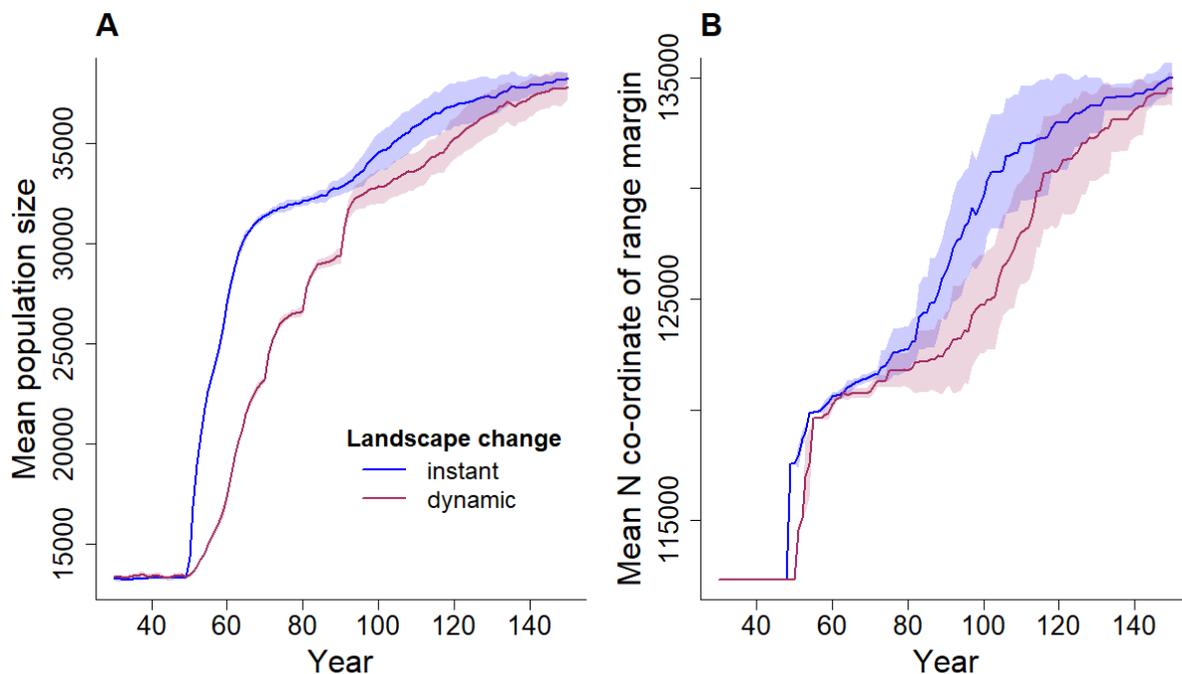
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For the instant landscape approach (Synes et al. 2015), the mean rate of range expansion for the CreateRandom scenario was 187 m/year over 100 years (standard error s.e. 2.34 m/year), 2.0 times the rate on the baseline landscape. Similarly, for the

176 CreateSmallAdjacent scenario, the mean rate of range expansion was 201 m/year  
177 (s.e. 2.90 m/year), 2.1 times faster than the baseline. By applying the dynamic landscape  
178 approach to the CreateRandom scenario, the mean rate of range expansion was reduced  
179 negligibly to 184 m/year (s.e. 2.64 m/year; relative reduction 1.6%). In contrast, for the  
180 CreateSmallAdjacent scenario, the mean rate of range expansion was increased slightly to  
181 216 m/year (s.e. 2.69 m/year; relative increase 7.5%). Despite rather similar total expansion  
182 rates over a period of 100 years, the temporal trajectories differed considerably between the  
183 instant and the dynamic landscape approach, as is illustrated for a single landscape replicate  
184 of the CreateSmallAdjacent scenario (Fig. 2). The total population size on the dynamic  
185 landscape lagged behind that on the instant landscape by up to 25% during the first 40 years  
186 after planting (Fig. 2A), and the location of the northern range margin on the dynamic  
187 landscape was up to 5 km further south during the succeeding 40 years (Fig. 2B).



188

189 **Figure 2.** Consideration of dynamic landscape restoration affects predictions on species'  
190 range expansion dynamics. (A) Mean total population size and (B) mean location of species'  
191 northern range margin for the instant (blue) and dynamic (red) landscape change methods

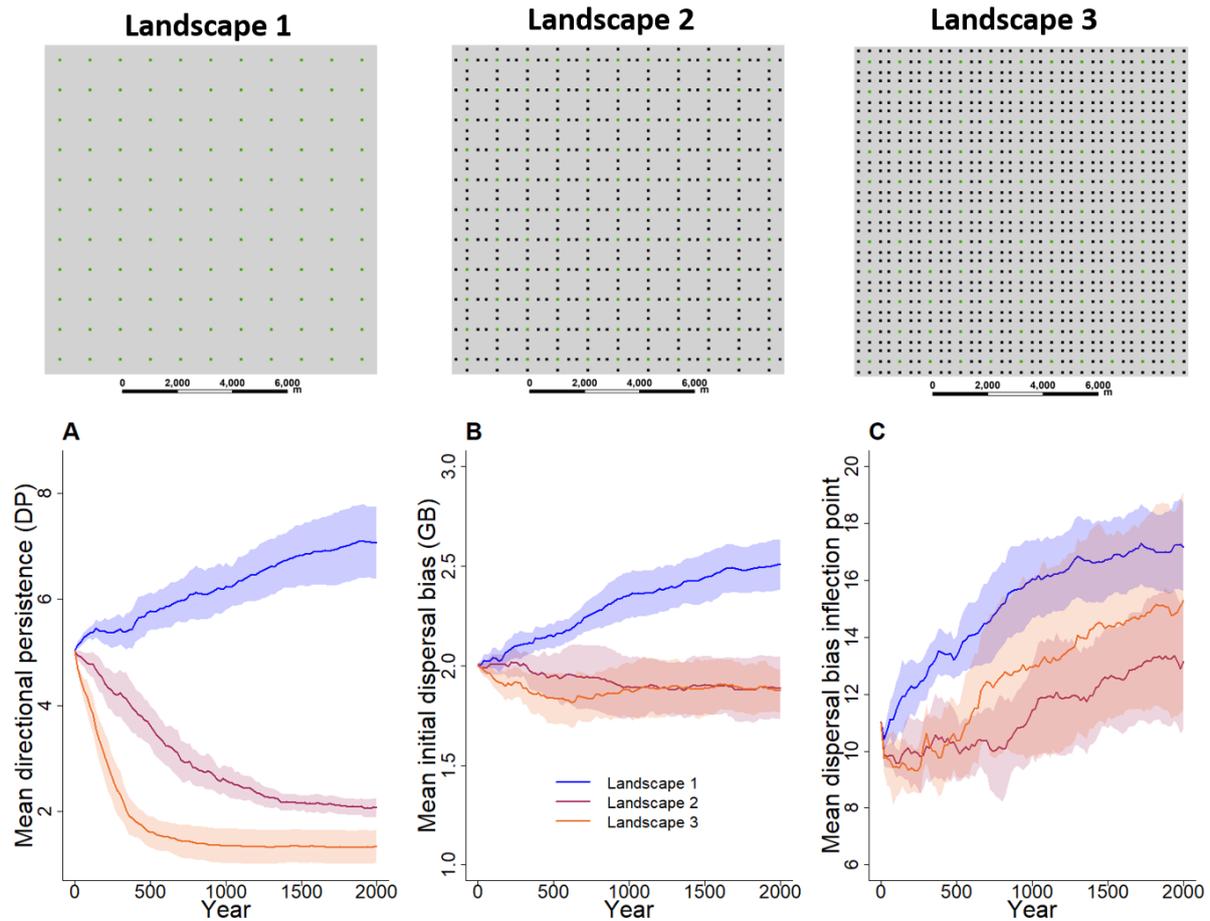
192 commencing at year 50 for a single landscape replicate of the CreateSmallAdjacent scenario.  
193 Shades show 95% confidence intervals from 10 replicates.

## 194 EVOLUTION OF MULTIPLE DISPERSAL TRAITS

195 We illustrate how RangeShifter 2.0 can be used to model evolution of complex dispersal  
196 strategies, which involve evolution of multiple traits defining all three phases of dispersal  
197 (emigration, transfer through the landscape and settlement in a new habitat patch) on  
198 landscapes that differ in their structure and composition. We modelled the evolution of  
199 dispersal traits of an annual sexual species on a set of three stylised landscapes of 121 rows  
200 x 121 columns differing in the degree to which movement was inhibited by the presence of  
201 high-cost cells in the landscape (Fig. 3). Temporally uncorrelated local environmental  
202 stochasticity was applied in two forms in order to promote dispersal evolution: as annual  
203 variability in carrying capacity and as a small probability of local patch extinction. The  
204 parameters controlling all three phases of dispersal, namely emigration (density-dependent),  
205 transfer and settlement (density-dependent), evolved independently of one another, each trait  
206 being determined by a separate autosome having three unlinked loci. Emigration and  
207 settlement traits were modelled as sex-dependent, thus having sex-limited phenotypic  
208 expression. Further, sex differences were assumed in settlement: while for both sexes  
209 settlement probability could evolve density dependence, males had the additional fixed  
210 settlement condition of requiring the presence of a mate in the patch.

211         The transfer phase of dispersal was modelled using SMS, which models the dispersal  
212 trajectory on a stepwise basis whilst accounting for perceived movement costs and a tendency  
213 to follow a correlated path, as determined by the directional persistence (DP) and the dispersal  
214 bias parameters. The dispersal bias determines the tendency of moving in a straight line away  
215 from the natal patch and is subject to a decay in strength as a function of the accumulated  
216 number of steps taken (see Supplementary Information). DP and the parameters defining the  
217 decay function of the dispersal bias were modelled as evolving traits, thus allowing for

218 evolution of movement rules. In the baseline Landscape 1 (Fig. 3), there were no inhibitory  
219 cells in the matrix (Cost = 10; per-step mortality = 0.01), and therefore we would expect  
220 relatively straight movement to evolve (Zollner & Lima, 1999). However, in Landscape 2, it is  
221 much less clear what would be the best movement strategy, as the orthogonal paths between  
222 patches are inhibited by high-cost cells (Cost = 1000; per-step mortality = 0.5), whereas the  
223 diagonal movements are not. Finally, in Landscape 3, both orthogonal and diagonal paths are  
224 impeded, and dispersers must therefore evolve strategies to reach a new patch whilst avoiding  
225 as much as possible the high-risk inhibitory cells. We ran ten replicate simulations of 2000  
226 years on each landscape. All model parameters and initialisation conditions are reported in  
227 Table S2. Equations defining reaction norms are also reported in the Supplementary  
228 Information.



229

230 **Figure 3.** Stylised landscapes used to model evolution of dispersal traits (upper panels).

231 Landscape 1 comprises evenly distributed breeding habitat patches of 100 m x 100 m (green)

232 set in a homogenous matrix (grey). In Landscape 2 high-cost cells inhibitory to movement

233 (black) are added orthogonally between the patches. In Landscape 3 additional inhibitory cells

234 are added to the diagonals between patches. **(A-C)** Evolution of mean transfer traits,

235 directional persistence (A), initial dispersal bias (B) and dispersal bias inflection point

236 (measured in steps taken; C), on the three landscapes. Phenotypic values are averaged over

237 all individuals and 10 replicate simulations.

238 As expected from the spatial and temporal configuration of the selective environments,

239 the dispersal strategies that evolved on the different landscapes differed mainly in their

240 movement rules (Fig. 3A-C), whereas they evolved similar reaction norms for the emigration

241 and settlement phases (Figs. S1-S2, S4-S5). In the absence of inhibitory features in

242 Landscape 1, very straight movement trajectories evolved (Fig. S6A): both mean directional  
243 persistence (DP) and mean dispersal bias (the tendency to move in a direction away from the  
244 natal patch) reached high values of  $\sim 7.0$  and  $2.5$  respectively after 2000 years (Fig. 3A-B),  
245 and indeed there was some indication that they were still increasing slightly. In contrast, when  
246 orthogonal movement became inhibited in Landscape 2, much less direct movement evolved  
247 (Fig. S6B), as determined by low mean DP (Fig. 3A). Mean dispersal bias initially remained  
248 relatively high at around  $2.0$  (Fig. 3B), but its mean inflection point (the number of steps at  
249 which dispersal bias decreases most rapidly) decreased from around 16 steps on  
250 Landscape 1 to around 12 steps (Fig. 3C). Thus, dispersers having evolved in Landscape 2  
251 would be following a much less straight path sooner after having left the natal patch compared  
252 to dispersers having evolved in the more benign Landscape 1 (Fig. S3), thereby enabling them  
253 to respond to the appearance of a suitable (low cost) cell within the perceptual range by  
254 moving towards it. The addition of inhibitory features to diagonal movement further developed  
255 this trend: dispersal bias altered little, but DP decreased to a very low level of around  $1.3$  on  
256 average (Fig. 3A).

257 Emigration probability generally evolved to be male-biased. Mean male emigration  
258 probability decreased as the occurrence of inhibitory cells in the landscape increased  
259 (Landscapes 2 and 3) because the cost of dispersal effectively increased (Fig. S1-S2). Male-  
260 biased emigration would be expected, given the loosely polygynous mating system (i.e. males  
261 can mate with multiple females but each female mates only with one male) and the high  
262 environmental and demographic stochasticity (Table S2), which increase between-patch  
263 variance in male reproductive success (Henry et al., 2016; Li & Kokko, 2019). Density-  
264 dependent settlement evolved similarly in the two sexes, so that individuals were likely to settle  
265 at the first suitable patch encountered unless it was substantially above carrying capacity  
266 (Fig. S4-S5).

## 267 **Discussion**

268 RangeShifter 2.0 provides enhancements and substantial extensions to the RangeShifter  
269 software (Bocedi, Palmer, et al., 2014) expanding its potential range of applications. The  
270 flexible and spatially-explicit demography and dispersal modules that are distinctive of this  
271 platform (Lurgi et al., 2015) can be now combined with a flexible genetically-explicit  
272 representation of neutral markers and/or multiple dispersal traits, allowing for diverse  
273 applications focussed on combining population genetic processes with ecological and  
274 environmental processes (Manel et al., 2003; Epperson et al., 2010) and accounting for  
275 evolution of complex and multi-trait dispersal strategies (Cote et al., 2017; Legrand et al.,  
276 2017; Saastamoinen et al., 2018). This is further combined with the ability of incorporating  
277 dynamic landscapes, enabling applications that explicitly aim to predict species' genetic,  
278 ecological and evolutionary responses to ongoing environmental changes. Such applications  
279 include in-silico testing of management interventions which need to account for the occurrence  
280 of ecological time-lags when targeting and evaluating conservation actions (Watts et al.,  
281 2020).

282         Importantly, and in contrast with the previous release, RangeShifter 2.0 source code  
283 is now open source (<https://github.com/rangeshifter>), published under the GNU general public  
284 license (GPLv3). It is hence free for the wider community to use, modify and share.  
285 Furthermore, RangeShifter 2.0 is also the core of the new package RangeShiftR (Malchow et  
286 al., 2020), which allows running RangeShifter from the R environment (R Core Team, 2020)  
287 while maintaining the high performance of the C++ code, and includes functions assisting with  
288 the set-up of the simulations, the parameterisation and output analyses. RangeShiftR, in  
289 addition to improving and broadening RangeShifter accessibility, makes it easily available for  
290 multiple platforms, has access to R's infrastructure for parallel and cluster computing and  
291 offers many opportunities for interoperation with other R packages.

292         RangeShifter 2.0 additionally comes with an enhanced Windows graphical user  
293 interface (GUI) as freeware (<https://github.com/RangeShifter/RangeShifter-GUI>). From  
294 current users, and from workshops that we are running worldwide, we are able to appreciate

295 the value of the RangeShifter GUI: it is particularly useful for non-modellers to explore eco-  
296 evolutionary dynamics and their conservation implications, to recognise data gaps in empirical  
297 systems, to communicate with stakeholders, and for teaching purposes across grades. It also  
298 provides easily accessible and free software for countries with little funding for conservation  
299 and research. Further, to improve accessibility, the User Manual has now been translated into  
300 Spanish (<https://github.com/RangeShifter/RangeShifter-software-and-documentation>).

301 RangeShifter is in continuous development, and there are key areas for future  
302 progress, which we hope, by making it open source and integrating it with R, will be addressed  
303 by a common effort to move towards a fully-integrated dynamic platform that includes all the  
304 key and necessary processes for predicting species' eco-evolutionary responses to global  
305 changes. For example, RangeShifter 2.0 currently remains a single-species model, while  
306 inter-specific interactions are often key in determining species' persistence to global changes  
307 (Gilman et al., 2010; Norberg et al., 2012; Urban et al., 2012; Urban et al., 2019; Bocedi et al.,  
308 2013; Svenning et al., 2014; Thompson & Fronhofer, 2019). Although we made a first  
309 important step in including explicit genetics, and we are actively prioritising this area of  
310 development, RangeShifter 2.0 does not yet include the level of sophistication that  
311 characterises much forward-time population genetic software (Guillaume & Rougemont, 2006;  
312 Haller & Messer, 2019), in terms of genetic processes, structures and outputs, and adaptive  
313 traits. For example, the possibility of modelling adaptation to multiple environmental variables  
314 will be a crucial addition. However, RangeShifter 2.0 holds an advantage in terms of the  
315 ecological, demographic and dispersal complexity it can represent, which, combined with  
316 explicit genetics, opens possibilities for sophisticated landscape genetics applications and for  
317 fully accounting for evolution of dispersal behaviours (not just emigration rates) which are likely  
318 to be critical for species' inhabiting or moving through complex, human-modified landscapes.

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## 327 **Author's contributions**

328 GB, SCFP and JMJT mainly developed the model structure, implemented the C++ core code,  
329 developed the GUI and wrote the documentation. AM contributed to code testing and cleaning,  
330 and DZ developed the accompanying website. KW provided the landscape data for the first  
331 example. GB, SCFP and JMJT wrote the initial manuscript and all authors contributed critically  
332 to the drafts and gave final approval for publication.

## 333 **Data Availability**

334 RangeShifter C++ core code for the batch implementation is open source under the GNU  
335 general public license (GPLv3). The code, as well as the compiled Windows package, the  
336 User Manual and the data for the tutorials are available from GitHub  
337 <https://github.com/RangeShifter>.

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