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

Abstract

1. Process-based models are becoming increasingly used tools for understanding how species are likely to respond to environmental changes and to potential management options. RangeShifter is one such modelling platform, which has been used to address a range of questions including identifying effective reintroduction strategies, understanding patterns of range expansion and assessing population viability of species across complex landscapes.

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

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

4. RangeShifter 2.0 will facilitate the development of in-silico assessments of how species will 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

Introduction

45

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

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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$^+$P$^-$S$^+$ 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.

| Years	*1/b*	*Cost*	*Mort*	Description
0 - 4	0	100	0.05	**Permeable habitat** – 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: *treat as similar to semi-improved grassland*
5 - 9	0	10	0.005	**Permeable and safe habitat** – 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: *treat as dwarf shrub heath*
10 - 19	5	5	0.002	**Low quality breeding habitat** – 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	**Medium quality breeding habitat** – movement and mortality risks decrease further as canopy cover develops and breeding quality is enhanced
30 - 39	15	1	0.0	**High quality breeding habitat** – further canopy closure removes movement costs and mortality risk and patch quality moves towards that of established woodland
40 - 100	21	1	0.0	**Very high quality breeding habitat** – optimal high quality woodland habitat is achieved in year 40 as previously Synes et al. (2015) implemented from year 0

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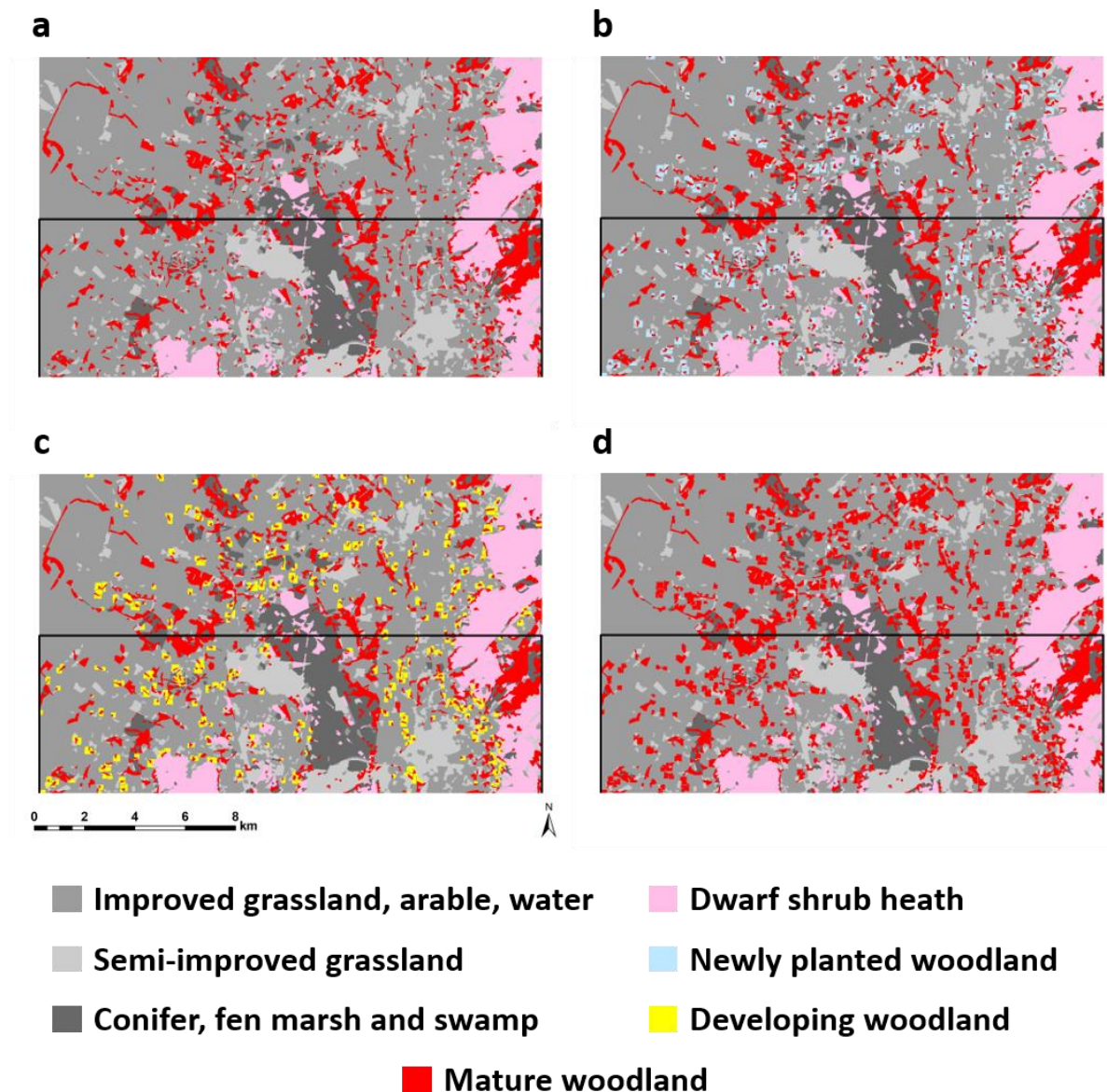
Figure 1. Example of dynamic landscape development: (a) initial landscape, (b) after 5 years when newly planted woodland adjacent to small patches is treated as dwarf shrub heath for dispersal modelling, (c) after 20 years as canopy closure develops, (d) final landscape after 40 years when newly planted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

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

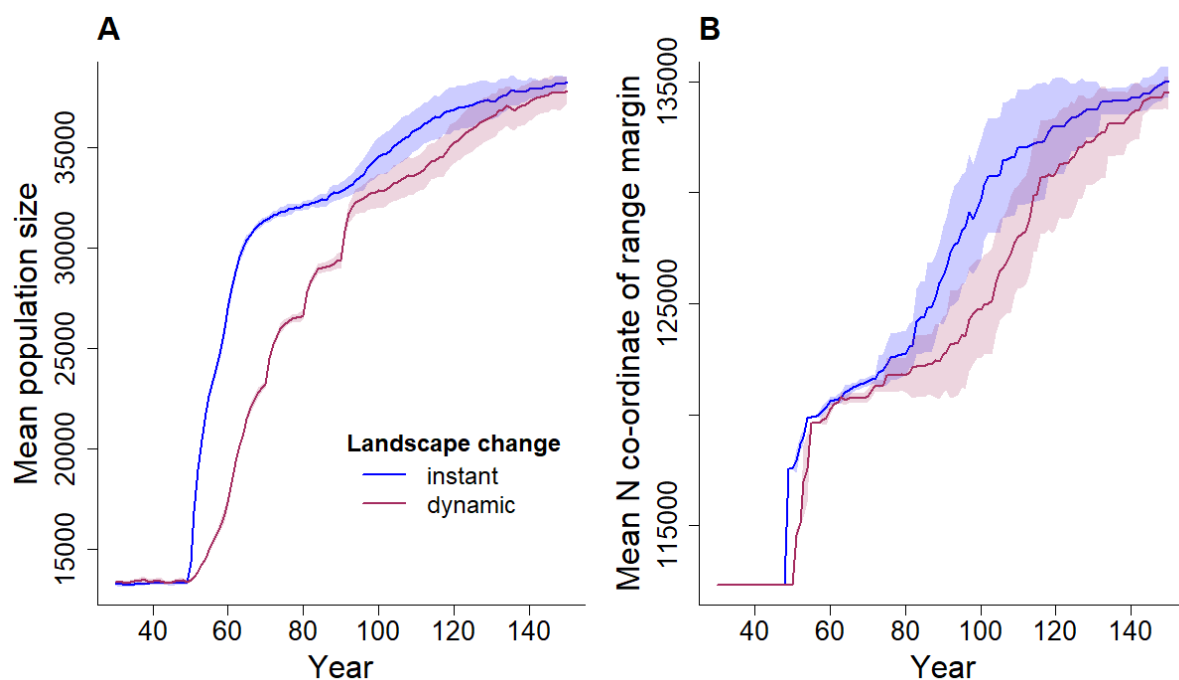187 landscape was up to 5 km further south during the succeeding 40 years (Fig. 2B).

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
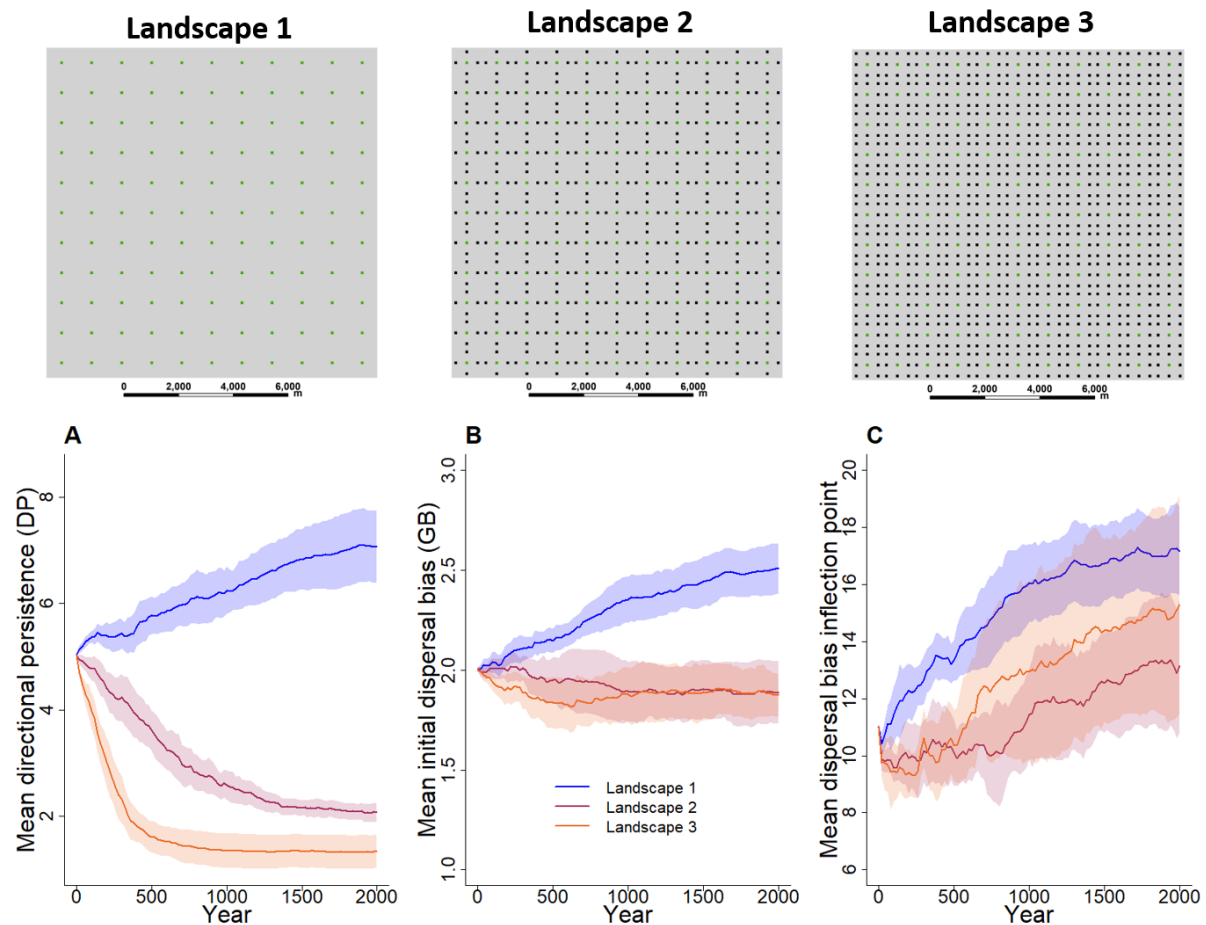
228   Information.

Figure 3. Stylised landscapes used to model evolution of dispersal traits (upper panels). Landscape 1 comprises evenly distributed breeding habitat patches of 100 m x 100 m (green) set in a homogenous matrix (grey). In Landscape 2 high-cost cells inhibitory to movement (black) are added orthogonally between the patches. In Landscape 3 additional inhibitory cells are added to the diagonals between patches. **(A-C)** Evolution of mean transfer traits, directional persistence (A), initial dispersal bias (B) and dispersal bias inflection point (measured in steps taken; C), on the three landscapes. Phenotypic values are averaged over all individuals and 10 replicate simulations.

As expected from the spatial and temporal configuration of the selective environments, the dispersal strategies that evolved on the different landscapes differed mainly in their movement rules (Fig. 3A-C), whereas they evolved similar reaction norms for the emigration and settlement phases (Figs. S1-S2, S4-S5). In the absence of inhibitory features in

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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 ~ 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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Author's contributions

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

Data Availability

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

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