1   Submission Type: Biodiversity research

2   **Geographic variation in dispersal and dispersal distance facilitate range expansion of a**

3   **lakeshore plant in response to climate change**

4

5   Authors: Elizabeth A. LaRue[1]*, Nancy C. Emery[2], Laura Briley[3], Mark R. Christie[1, 4]

6

7   [1]Department of Biological Sciences, Purdue University, 915 W. State Street, West Lafayette, IN

8   47907-2054

9   [2]Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Box 0334,

10 Boulder, CO, 80309-0334

11 [3]Great Lakes Integrated Sciences and Assessments, University of Michigan, 440 Church Street,

12 Dana Building, Ann Arbor, MI 48109-1041

13 [4]Department of Forestry and Natural Resources, 915 W. State Street, West Lafayette, IN 47907-

14 2054

15

16 *Corresponding author and current address: elarue@purdue.edu, 231.557.0047, Department of

17 Forestry and Natural Resources, 915 W. State Street, West Lafayette, IN 47907-2054

18

19 Running title: Geographic variation in dispersal

20

28

29 Biosketch: The goal of this research team is to further the understanding of how rapid evolution

30 influences range dynamics under environmental change through the combination of modelling

31 and empirical approaches. The team focuses on critical drivers underlying species distributions

32 such as dispersal, habitat specialization, and the evolution of domestication or invasion. This

33 study was the product of a doctoral dissertation project conducted at Purdue University by

34 E.A.L. Author contributions: E.A.L, N.C.E, and M.R.C. conceived the study idea; L.B. created

35 the climate data; E.A.L. and M.R.C. developed the individual-based model; E.A.L. collected the

36 data, analysed the data, and led the writing; all authors edited the manuscript.

1

2 DR ELIZABETH ANN LARUE (Orcid ID : 0000-0002-9535-0630)

3

4

6

7

9

10 **Geographic variation in dispersal and dispersal distance facilitate range expansion of a**

11 **lakeshore plant in response to climate change**

12

13 Authors: Elizabeth A. LaRue[1*], Nancy C. Emery[2], Laura Briley[3], Mark R. Christie[1, 4]

14

15 [1]Department of Biological Sciences, Purdue University, 915 W. State Street, West Lafayette, IN

16 47907-2054

17 [2]Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Box 0334,

18 Boulder, CO, 80309-0334

19 [3]Great Lakes Integrated Sciences and Assessments, University of Michigan, 440 Church Street,

20 Dana Building, Ann Arbor, MI 48109-1041

21 [4]Department of Forestry and Natural Resources, 915 W. State Street, West Lafayette, IN 47907-

22 2054

23

24 [*]Corresponding author and current address: elarue@purdue.edu, 231.557.0047, Department of

25 Forestry and Natural Resources, 915 W. State Street, West Lafayette, IN 47907-2054

26

28

31

32   Data availability statement: The habitat suitability maps and code for the individual-based model

33   used to generate all data in the manuscript are available from the Dryad Digital Repository.

34 **Abstract:**

35 Aim: Geographic variation in dispersal abilities is widespread and likely to affect species' range

36 dynamics in response to climate change. However, distribution models that predict climate-

37 induced range shifts do not account for spatial variation in dispersal. We developed an eco-

38 genetic model to investigate how variation in dispersal distances across a species' range could

39 interact with climate-induced selection and alter predicted range dynamics in a species with

40 documented variation in dispersal traits.

41 Location: We investigated the range of an annual plant, Cakile edentula var. lacustris, which

42 occupies beaches spanning a 555 km latitudinal gradient along the Laurentian Great Lakes.

43 Methods: We built a hybrid model that combines climatic niche modelling, based on decadal

44 climate projections, with an individual-based model that allows for evolutionary processes to act

45 upon a heritable dispersal kernel. We evaluated how spatial variation in dispersal distance and

46 dispersal evolution influenced range dynamics, spatial and temporal variation in dispersal, and

47 the distribution of neutral genetic variation. The model was parametrized with data on C.

48 *edentula's* distribution, life history, and dispersal characteristics.

49 Results: Geographic variation in dispersal distance, adaptive dispersal evolution, and dispersal

50 distance increased the potential for local populations of C. edentula to keep pace with changing

51 climatic conditions through range shifts. Dispersal distances always increased at the expanding

52 and contracting range edges when dispersal was allowed to evolve. Furthermore, scenarios where

53 dispersal distances were initially lower at the range edges resulted in the largest evolutionary

54 changes over 105 years (> 1.5 km increase in mean distance at northern edge). Adaptive

55 dispersal evolution always reduced neutral genetic diversity across the species' range.

56 Main conclusions: Variation in dispersal abilities across *C. edentula's* range and adaptive

57 evolution led to different predicted outcomes in range dynamics during climate change

58 illustrating the importance of including spatial variation in dispersal into species distribution

59 models.

60

61   Keywords: Cakile edentula, climate change, dispersal evolution, expanding range limit,

62   geographic range, genetic diversity

63   **Introduction:**

64   Recent empirical and theoretical work has demonstrated that diverse taxa may be able to rapidly

65   adapt to environmental changes, such as those presented by habitat modification (Bosse et al.,

66   2017) and climate change (Palkovacs et al., 2012; Siepielski et al., 2017). Climate change is

67   already acting as an important selective agent for many species, but it remains challenging to

68   predict which species will be able to keep pace with changing conditions (Bateman et al., 2013;

69   Siepielski et al., 2017). One way that populations may respond to climate change is through

70   dispersal evolution – the heritable change in a dispersal kernel due to the selection on dispersal

71   traits (Hargreaves & Eckert 2014). Distribution models that are used to predict species'

72   responses to climate change do not often include scenarios where dispersal can evolve as the

73   geographic range changes (Bateman et al., 2013; but see Dytham et al., 2009; Hargreaves et al.,

74   2015 for examples of general species models). However, recent empirical studies have shown

75   that dispersal traits often exhibit heritable genetic variation and may be able to quickly respond

76   to selection (e.g., Phillips et al., 2006; Weiss-Lehman et al., 2017). Such rapid changes in

77   dispersal could facilitate metapopulation persistence by influencing the rate at which new habitat

78   can be colonized as it becomes available (Bell & Gonzalez, 2011; Boeye et al., 2013; Kubisch et

79   al., 2013; Hargreaves et al., 2015).

80   The dynamics of dispersal evolution are expected to be shaped by the distribution of

81   genetic variation in dispersal traits across a species' range (Travis et al., 1998), and prior studies

82   have established that mean dispersal distances often vary geographically among populations

83   within a species' range (Hargreaves & Eckert, 2014). For example, mean dispersal distances are

84   sometimes shorter at the edges of a species' range compared to the interior (Talavera et al., 2011;

85   LaRue et al., 2018). Furthermore, the evolutionary responses of dispersal traits may vary at

86   different positions within the species' range, such as the range edges vs. the interior, due to the

87   genetic composition of individual populations (Bridle, 2007). For example, edge populations

88   may have low additive genetic variation in dispersal traits due to founder effects (Eckert et al.,

89   2008; Razgour et al., 2013), which in turn may limit the potential for dispersal-related traits to

90   quickly respond to selection. Nevertheless, the strength of selection imposed by climate change

91   may be stronger in marginal populations that are near rapidly changing habitat (Hargreaves &

92   Eckert, 2014), and the failure for dispersal traits to adaptively evolve may hinder metapopulation

93   persistence. Furthermore, evolutionary processes may influence a species' ability to respond to

94   changing patterns of selection by shaping the amount and distribution of genetic variation in

95   traits that influence organismal performance within habitat patches (Edmonds et al., 2004;

96   Klopfstein et al., 2006). Genetic bottlenecks during colonization events can cause reduced

97   variation in populations that are expanding into new habitat patches (e.g., neutral genetic

98   variation), which in turn may limit the evolutionary potential of those populations during and

99   after establishment (Bridle & Vines, 2004; Gaston et al., 2009). Currently, we lack models that

100   evaluate how preexisting geographic variation and evolutionary change in dispersal strategies

101   directly influence species' range dynamics and neutral genetic variation in response to climate

102   change (Johnson et al., 2019).

103   The diversity of dispersal mechanisms documented across the globes' species results in

104   orders of magnitude of differences in their dispersal distances, making it critical that models of

105   range shifts in response to climate change are grounded in taxa-specific dispersal properties. For

106   example, plants and animals can be widely different in the extent of their maternal control on

107   their offspring's dispersal (Starrfelt & Kokko, 2010). Maternal plant traits directly influence

108   dispersal of their offspring by determining how they are released into the environment (e.g., the

109   height at which wind-dispersed seeds are released) and their external characteristics (e.g., seed

110   morphology) (Donohue, 1999); in contrast, the dispersal kernel of mammals tends to be

111   dominated by the phenotype of the offspring (Starrfelt & Kokko, 2010). These differences can

112   have implications for range dynamics: for example, dispersal kernels determined by offspring

113   can result in more rapid range expansion than those determined by the maternal phenotype

114   (Starrfelt & Kokko, 2010). Similarly, in organisms that engage in passive dispersal, geographic

115   variation in the dispersal vectors that they rely upon can lead to drastically different range

116   dynamics. Seeds that disperse by water, such as floating seeds, lead to more rapid colonization

117   and range expansion than seeds that fall directly to the ground and are pulled down by gravity as

118   they fall (Nathan et al., 2006). Collectively, the diversity of dispersal mechanisms in nature

119   raises the need to fine-tune distribution models that incorporate dispersal variation to represent

120   the dispersal properties of the studied organism.

121   Here we present a spatially-explicit, individual-based model that evaluates the interplay

122   between geographic variation in dispersal and subsequent evolution in response to climate

123   change. Given that model outcomes would be highly dependent on the dispersal kernels, we

124   chose to base model parameters on the biology of Cakile edentula subsp. edentula var. lacustris

125   (Brassicaceae; Fig. 1A), because extensive information about its dispersal strategy (Donohue,

126   1998; 1999), geographic variation in dispersal traits (LaRue et al., 2018), and its geographic

127   range was readily available (Rodman, 1973; LaRue et al., 2018). This annual herb occupies

128   beach habitats that outline the shores of the Great Lakes, with a geographic range that spans 555

129   km from 41 to 46 degrees of latitude north (Rodman, 1973) (Fig. 1B, C). Cakile edentula

130   reproduces predominantly via self-pollination, so seed dispersal likely accounts for most of the

131   gene flow within and among populations (Rodman, 1973). Individual plants produce dimorphic

132   fruits that disperse locally by wind or longer distances by water (Rodman, 1973). Previous work

133   has documented heritable variation in wind and water dispersal traits across the species' range,

134   including reduced potential for water dispersal at the range edges (LaRue et al., 2018). While our

135   analyses were based on the biology of C. edentula, we expect that our results may be relevant to

136   organisms that exhibit passive, long-distance dispersal (e.g., many plant, insect, and marine

137   organisms). In our analysis, we first evaluated how existing patterns of dispersal distance and

138   geographic variation in dispersal properties can influence our predictions for how a species'

139   range will shift in response to climate change. Next, we evaluated how the adaptive evolution of

140   dispersal traits over time altered these predictions. We also tracked variation at neutral loci to

141   monitor how dispersal variation and evolution alters the distribution of genetic diversity as a

142   species' range adjusts with climate change. To do this, we used neutral markers as a proxy for

143   genetic variation that does not influence dispersal genotypes, but instead is shaped by the

144   patterns of colonization and gene flow that result from the dispersal patterns that drive range

145   expansion and contraction under climate change. Our results revealed that the initial dispersal

146   distance and spatial distribution of dispersal distances across the range of C. edentula had large

147   effects on species' range dynamics, and that dispersal trait evolution facilitated metapopulation

148   persistence. More generally, these results demonstrate that incorporating variation in dispersal

149   traits, both across a species' range and through time, can substantially alter the predictions of

150   species' distribution models as climate change proceeds.

151   **Methods:**

152   We evaluated how geographic variation in dispersal and dispersal trait evolution can alter

153   predictions for range dynamics under climate change by combining the projected habitat

154   suitability from a C. edentula-specific species distribution model with an eco-genetic, individual-

155   based model (Fig. 1D). Future climate change projections of air temperature were obtained

156   monthly for the decades 2020 to 2090 and used as climate change projections for input into

157   MaxEnt. To obtain these projections, we used the NorESM1-M model from the CMIP5 multi-

158   model ensemble (Coupled Model Intercomparison Project; Taylor et al., 2012) with the

159   Intergovernmental Panel on Climate Change (IPCC) representative concentration pathways of

160   RCP 2.6 (low emission) and RCP 8.5 (high emission) (IPCC, 2014). We chose to use the

161   NorESM1-M as our climate change framework because it represents a medium amount of future

162   projected change in temperature for the Great Lakes region. We relied on a simple delta method

163   to produce future temperature values (Prudhomme et al., 2002) by calculating changes between

164   the projected future decade and modeled historical period (1971- 2000) on a monthly basis, and

165   then adding those changes to an observed data set of historical temperature. By applying the

166   delta method, we did not have to correct for global circulation model biases, because we

167   compensated for differences between the historical and projected future temperatures at specific

168   locations. It is important to note that our method does not eliminate model bias, but it does allow

169   us to initialize our climate data from a realistic starting point based on historical temperature

170   observations. The historical data consisted of the University of Delaware Air Temperature and

171   Precipitation observations (Willmott & Matsuura, 2001) obtained from the NOAA/OAR/ESRL

172   PSD website (Boulder, Colorado, USA; http://www.esrl.noaa.gov/psd/).

173   We used the program MaxEnt to predict future habitat suitability under present and future

174   climate change scenarios (Phillips et al., 2004; 2006; Elith et al., 2011) (e.g., Fig. 1B, C).

175   MaxEnt estimates the potential distribution of a species' habitat suitability based on maximum

176   entropy distribution, which requires species presence data and treats the remaining spatial points

177   as background data as opposed to absences. Documented occurrences of C. edentula were

178   obtained from the published literature (Gormally et al., 2011; LaRue et al., 2018) and the GBIF

179   database (Lane, 2008). We used the SDMToolbox in ArcMap 10.2 (Brown, 2014) to inspect a

180   matrix of pairwise Spearman correlation coefficients between twelve-monthly average

181   temperature variables because extreme collinearity between predictor variables in MaxEnt can

182   lead to unreliable results (Brown, 2014). We then removed redundant climate variables with

183   correlation coefficients greater than 0.80, while retaining those that were not highly correlated.

184   The final variables used were temperature in the months of January and July. The default settings

185   for the cross-validate method in MaxEnt were used, except we increased the number of

186   independent models runs from 1 to 20, starting with a random seed, and increased the number of

187   iterations from 500 to 5,000.

188   We constrained analyses to the coastal habitat of the Great Lakes, where C. edentula is

189   restricted due to its obligate association with sandy beaches. We created a raster of habitat

190   suitability across the range of C. edentula from MaxEnt output, which contained the probability

191   of species presence from 0 to 1 for each cell (Phillips et al., 2004; 2006; Elith et al., 2011). We

192   incorporated the entire 555 km extent of the species' latitudinal range; however, we restricted the

193   longitudinal extent of the range to Lakes Michigan and Superior (approximately one half of the

194   species' entire longitudinal range) due to computational constraints of using large geographic

195   areas (Fig. 1D). This process resulted in a total of 876 patches (i.e., raster cells) along the coast

196   where the final size of each individual patch was 36 km^2. Like all distribution models using

197   Maxent (Elith et al., 2006), this approach assumes that the climatic niche of C. edentula can be

198   estimated from its current distribution. We consider this assumption reasonable given that C.

199   edentula's range limits have remained relatively stable in recent history (Rodman, 1973; LaRue

200   et al., 2018) despite its potential for long-distance dispersal by water (Rodman, 1973), and thus it

201   is likely that the species' distribution limits reflect the bounds of its climatic tolerances

202   (Hargreaves et al., 2014).

203   Habitat suitability values were recalculated each year for 25 years of present-day climate

204   and 80 years of projected climate change. Control scenarios assumed present-day habitat

205   suitability values in all patches ranged from 0 – 1 for the entire 105 years. For climate change

206   scenarios, we changed the habitat suitability values across the species' range at nine time points.

207   The values for the first 25 years (2000–2025) were based on the present-day climate map. Over

208   the next 80 years (2025–2095), we generated a new habitat suitability map every 10 years using

209   projected climate change estimates.

210   Habitat suitability values were used to determine the simulated dynamics of the

211   population sizes of local patches and the global population size each year. We chose an average

212 patch population size of 50 individuals, because it is well within the range of observed natural
213 populations in field surveys (LaRue et al., 2018). We constrained the maximum number of
214 individuals living in the range each year to be less than or equal to the product of the average
215 patch population size (50) and the total number of patches with suitability values > 0. This
216 allowed for a possible maximum global population size of 43,800 individuals if all 867 patches
217 had habitat suitability values greater than zero, but the actual size varied each year due to
218 variation in the number of suitable patches available. The maximum number of individuals that
219 could live within each local habitat patch was calculated each year as the product of the habitat
220 suitability value for a given habitat patch and 50 individuals. As seen in our study, the machine
221 learning algorithm of MaxEnt does not always produce a maximum predicted habitat suitability
222 of 1 (e.g. the highest habitat suitability across the entire range equalled 0.6), which could lead to
223 an actual local population size of less than the average of 50 across the range. This would result
224 in a smaller global population size than expected, therefore when this occurred, we scaled the
225 local carrying capacities to reach the expected value of the global population size, but never
226 more than the size of the carrying capacity of the global population each year. This scaling
227 process resulted in local population sizes that ranged from 1 to 120 individuals (e.g., Fig. S1.1)
228 and a mean of 50 individuals. We also incorporated density-independent demographic processes
229 in the population size of patches by randomly sampling a new value of population size for each
230 occupied habitat patch from a normal distribution with a mean equal to the population size
231 within each patch and a standard deviation equal to two.

232   To allow dispersal to evolve, each individual in the model was assigned a unique
233 dispersal kernel and genetic variation within populations in the dispersal distance parameter. To
234 allow for a spatial resolution that spanned the latitudinal extent of the Great Lakes, we combined
235 the wind and water dispersal traits into a single dispersal kernel. This procedure allows for some
236 seeds to successfully disperse long-distances via water dispersal pathways, while allowing for
237 more seeds to successfully disperse shorter distances via wind dispersal pathways, which is in
238 accordance with studies on reproductive success and fitness (Donohue, 1997). Based on this
239 rationale, we used a Weibull distribution to model the fat-tailed dispersal kernel (Nathan et al.,
240 2012) of C. edentula seeds that can disperse locally as well as long distances by water. The
241 Weibull distribution was fitted with two parameters: a fixed shape parameter of 1.0 so that some
242 offspring could be philopatric (i.e., many seeds do not reach the lake, where they would disperse

243 via water), and a scale parameter that varied in units of kilometres to set the dispersal kernel

244 width. For simplicity, we refer to this scale parameter as the dispersal distance, where a larger

245 value indicates a broader dispersal kernel and greater expected dispersal distances than smaller

246 values (e.g., Fig. 1E). We incorporated genetic variation in dispersal distance among individuals

247 in the first generation by randomly sampling the predetermined mean dispersal distance (varied

248 between parameter sets, Table S1) from a normal distribution with a standard deviation of 0.5

249 km. Reproduction occurred through asexual reproduction of adults each year; while Cakile

250 edentula reproduces sexually, it does so primarily through self-pollination (Donohue, 1997), thus

251 we simplified reproduction to be asexual for computational tractability (Dytham, 2009). Each

252 offspring inherited a slightly modified dispersal distance parameter from their parent, which was

253 created with a random deviate drawn from a normal distribution (mean = parental dispersal

254 distance, standard deviation = 0.1 km) to incorporate genetic and non-genetic sources of

255 phenotypic variation (i.e., mutation and/or environmental variation of a maternally determined

256 dispersal kernel). Dispersal was simulated as the movement of seeds away from the parent plant

257 (Fig. 1D). First, we calculated the Euclidian distance between the parent plants' home habitat

258 patch and all other suitable patches. Next, we used the parental dispersal kernel (assuming that

259 parental traits contribute more to the dispersal kernel than seed traits; Donohue, 1999) to

260 calculate the probabilities that each seed could disperse from its home patch to every other

261 habitat patch in the metapopulation. A longer parental dispersal distance value results in a higher

262 probability for a seed to recruit into other suitable patches (and patches need not be immediately

263 adjacent) versus remaining in the parental patch. Each parent produced 50 seeds, a number

264 consistent with field observations (Donohue, 1998; LaRue et al., 2018). We then proportionately

265 distributed up to 50 offspring per parent across suitable patches based on the dispersal

266 probability values from the parent's dispersal kernel. If the total number of offspring from all

267 parents that dispersed into a habitat patch exceeded the local population size (based on the

268 habitat suitability score), we randomly removed offspring from each patch until the population

269 size in the patch was met. All parents were removed after the dispersal of offspring was

270 completed, consistent with the annual life cycle of Cakile edentula (Rodman, 1973).

271   The effects of geographic variation in dispersal and dispersal distance were evaluated by

272 comparing model outcomes for four different initial patterns of dispersal distance across the

273 species' range: i. uniform-1 km, ii. uniform-5 km, iii. shorter at the range edges than interior

274   (short range-edge dispersal), or iv. longer at the range edges than interior (long range-edge

275   dispersal). The two uniform scenarios had no initial variation in dispersal among populations

276   representing the assumptions of a traditional species' distribution model. The long range-edge

277   scenario represents systems where range-edge populations have higher mean dispersal distances

278   compared to those in the interior (e.g., Abronia umbellate; Darling et al., 2008), while the short

279   range-edge dispersal scenario represents systems where the mean dispersal distance is shorter at

280   the range edges than interior (e.g., C. edentula; LaRue et al., 2018). These spatial patterns were

281   implemented using a quadratic equation (x = latitude, y = dispersal distance; Table S1.1),

282   assuming that the centre of the range was halfway between the southern and northern limits at

283   45.5° N. In these four scenarios, genetic variation in dispersal distance existed within

284   populations to allow for the opportunity of an adaptive evolutionary response to selection to be

285   able to occur. However, we also ran a neutral model for each of the four dispersal scenarios, in

286   which there was no genetic variation in dispersal within populations. Under these conditions,

287   adaptive evolution in dispersal was impossible in the two uniform scenarios, and only occurred

288   in the short and long range-edge scenarios when dispersing offspring successfully colonized any

289   new habitat patch for which that dispersal phenotype did not exist before (e.g., colonization

290   could result in genetic variation being introduced into a population which was previously fixed in

291   its dispersal distance). Finally, we conducted a separate set of analyses that used the same range

292   mean dispersal distance from the short range-edge and long range-edge scenarios, but assumed a

293   uniform distribution across the species range, to ensure that any differences we observed

294   between the uniform and non-uniform dispersal scenarios was due to geographic variation in

295   dispersal distances and not the differences in the grand means. These results confirmed our

296   predictions and are presented in Fig. S1.3.

297   To test how adaptive dispersal evolution and geographic variation of dispersal influence

298   neutral genetic diversity as climate change proceeded, we assigned each individual 50

299   polymorphic microsatellite loci to measure neutral genetic diversity of populations across the

300   range. At the beginning of each model run during initiation (Fig. 1D), each locus had 50 alleles

301   where allele frequencies were specified by the equation:

302    $$A_i = \frac{i}{(Na+1-i)} \cdot \sum_{i=1}^{Na} \frac{i}{(Na+1)-i} \tag{1}$$

303   where Na equalled the total number of alleles and i at equals allele i in the set 1: Na. This

304   equation provides allele frequencies that are typical of neutral allele frequency distributions

305   (adapted from Bernatchez & Duchesne, 2000). Genotypes were created in Hardy-Weinberg

306   Equilibrium for each locus and individuals were assigned multi-locus genotypes by randomly

307   sampling genotypes at each locus with replacement. At the end of the simulated 105 years, we

308   measured the expected heterozygosity and average number of alleles per locus.

309   We ran the model under the different scenarios for projected climate change, dispersal,

310   and evolutionary potential in dispersal (Table S1.2), and recorded the distribution, abundances,

311   and dispersal distances of all individuals at decadal time points during each simulation. Results

312   of preliminary analyses were not sensitive to variation in the average local population size or the

313   number of offspring per parent (e.g., Fig. S1.2), and therefore we maintained values of 50 for

314   each of these parameters across all subsequent analyses. We recorded the mean dispersal

315   distance, expected heterozygosity at microsatellite loci, local population size in each habitat

316   patch, and the proportion of the landscape occupied every ten years between year 2000 (year

317   zero) and 2105. The results for each variable were calculated as the average value over 40

318   replicate iterations. The model and all data analyses were implemented with R version 3.2.4 (R

319   Core Team, 2018).

320   **Results:**

321   Geographic variation in dispersal without adaptive evolution

322   When dispersal could not evolve, the distribution of individual dispersal distances remained

323   relatively constant across the range over time, regardless of the initial pattern of dispersal

324   variation or the climate change scenario imposed (Fig. 2). We found no evidence for range

325   expansion or contraction under either present-day or low-emission climate change scenarios

326   when the initial patterns of dispersal variation were either uniform-1 km (Fig. 2A-B) or shorter at

327   the range edges than the interior (Fig. 2G-H). When the initial dispersal distances were uniform-

328   5 km or when edge populations started with longer dispersal distances than interior populations

329   (i.e., long range-edge), range limits remained stable under present-day climate scenarios (Fig. 2

330   D, J), while the northern range limit expanded under both low- and high-emission climate change

331   scenarios (Fig. 2E-F, K-L). The southern range limit, by contrast, contracted only under the high-

332   emission climate change scenarios, regardless of the initial pattern of dispersal variation (Fig.

333   2C, F, I, L).

334   Geographic variation in dispersal with adaptive evolution

335   Adaptive evolution interacted with initial geographic patterns in dispersal and dispersal distance

336   to shape dispersal and range dynamics as climate change proceeded. When dispersal was allowed

337   to evolve, the northern range limit remained stable under present-day climatic conditions (Fig.

338   3A, D, G, J) and expanded under low- and high-emission scenarios (Fig. 3B-C, E-F, H-I, K-L),

339   regardless of the initial patterns of dispersal variation across *C. edentula's* range. Under high

340   emission climate change, the uniform-5 km dispersal scenario colonized new habitat in the north

341   (Fig. 3F) one decade faster than the short range-edge (Fig. 3I) and long range-edge dispersal

342   scenarios (Fig. 3L), and two decades faster than the uniform-1 km dispersal scenario (Fig. 3C).

343   Increased dispersal distances evolved at the northern range limit under all climate change

344   scenarios (Fig. 3; Fig. S1.3), and the magnitude of this change increased with growing levels of

345   climate change, the presence of starting geographic variation in dispersal, and initial dispersal

346   distance (Fig. 3). The greatest response to selection at the northern limit (i.e., the difference

347   between the initial and final average dispersal distance) occurred in the short range-edge scenario

348   under high-emission climate change (Fig. 3H-I), with mean dispersal distance at the expanding

349   northern limit evolving from 1 km to 6 km within two decades of the onset of climate change. A

350   relatively weaker response to selection on dispersal was observed in the uniform-1 km scenario

351   (Fig. 3B-C), where the mean dispersal distance at the northern limit evolved from 1 km to only 3

352   km within three decades of the onset of climate change (Fig. 3C). Increased dispersal distances

353   also evolved at the expanding northern edge in the long-edge (Fig. 3K-L) and uniform-5 km

354   scenarios (Fig. 3E-F), with an initial mean dispersal distance of 5 km growing to 6.5 km and 7

355   km, respectively, in the northernmost populations within two decades of the onset of high-

356   emission climate change (Fig. 3F). Like the northern limit, the southern limit remained stable

357   under low-emission and present-day climates (Fig. 3, A-B, D-E, G-H, J-K), and expanded

358   northward (contracting) under the high-emission climate scenario (Fig. 3C, H, I, L). Selection

359   drove the evolution of increased dispersal distance in southern populations under both climate

360   change scenarios, regardless of the initial dispersal parameters applied (Fig. 3C, F, I, L).

361   Impact of adaptive evolution and dispersal variation on neutral genetic diversity

362   Geographic variation in dispersal and adaptive evolution influenced the distribution of neutral

363   genetic diversity across the range. Expected heterozygosity was always lower across the range

364   when dispersal was allowed to evolve (c.f., Fig S1.4; Fig. 4). We found that expected

365   heterozygosity was lower at the range edges compared to the interior under the low- and high-

366   emission climate change scenarios (Fig. 4). We also found that expected heterozygosity was by

367   far the lowest in the northern range-edge populations than elsewhere in *C. edentula's* range

368   under all climate scenarios and was most pronounced when climate change occurred (Fig. 4; Fig.

369   S1.4). Range-wide genetic diversity measured as the average number of alleles per locus was

370   slightly greater in the absence of climate change (NA = 45.1) and low-emission climate scenarios

371   (NA = 45.2) in comparison with the high-emission climate change scenarios (NA = 41.7) (Fig.

372   4).

373   **Discussion:**

374   Even in the absence of dispersal evolution, geographic variation in dispersal distances can play

375   an important role in determining range-wide outcomes for species' responses to climate change.

376   In our analysis of C. edentula's geographic range, individuals that had longer (5 km) dispersal

377   distances, either uniformly across the species' range or only in edge patches, could colonize

378   novel habitats more quickly, enabling the species' northern range edge to keep pace with

379   changing environmental conditions (Fig. 2). When individuals had uniformly short dispersal

380   distances across the species' range, or when range-edge populations had relatively short dispersal

381   distances, the northern limit could not keep pace with changing climatic conditions because

382   patches that became suitable north of the range limit were not colonized. To date, remarkably

383   few studies have rigorously quantified the extent and distribution of intraspecific variation in

384   dispersal (Saastamoinen et al., 2018; Johnson et al., 2019). Our results highlight that the

385   incorporation of empirical estimates of key dispersal parameters could substantially alter

386   predictions of species' range dynamics in response to climate change.

387   The interaction between geographic variation in dispersal and dispersal evolution results

388   in complex outcomes that are not always intuitive. For example, a C. edentula range

389   characterized by short range-edge dispersal ultimately evolved longer dispersal distances and

390   colonized habitat more quickly at range limits than a range with a uniform initial dispersal

391   distance of 1 km (cf., Fig. 3I, B). This result occurred because gene flow from the interior portion

392   of the range increased the genetic variation in dispersal distances at the range edge more quickly

393   than mutation, allowing a faster response to selection. In all four dispersal scenarios, longer

394   dispersal distances evolved than were present in any habitat patch at the start of the simulations,

395   which is consistent with other individual-based models that investigated how dispersal evolves in

396   response to climate change (e.g., Boeye et al., 2013; Henry et al., 2013; Dytham et al., 2014;

397   Hargreaves et al., 2015; Hillaert et al., 2015). This result suggests that even if metapopulations

398   are at equilibrium with respect to dispersal distances prior to the onset of climate change, they

399   are unlikely to remain at equilibrium as climate change progresses. Spatial sorting has the

400   potential to substantially increase dispersal distance at an expanding range front without

401   dispersal evolving (Shine et al., 2011). However, we found the distribution of dispersal distances

402   across the species' range through time remained relatively constant when dispersal was not

403   allowed to evolve (Fig. 2), suggesting that spatial sorting alone does not explain the increases in

404   dispersal distances that developed at expanding northern limits when dispersal evolved (e.g., Fig.

405   2C; Fig. 3C), at least at the spatial scale evaluated in our model. Finally, our model suggests that,

406   when dispersal is heritable, longer dispersal distances will evolve at southern range limits in

407   response to climate change. Previous studies have shown that there can be both selection for

408   (Hillaert et al., 2015) or against long-distance dispersal at contracting range edges (Boeye et al.,

409   2013; Henry et al., 2013); our result can be explained by the short-term increases in individual

410   fitness that are gained by dispersing away from the contracting southern range limit where

411   habitat quality is declining. However, because our model only included the evolution of dispersal

412   distance and not direction (as expected for many passively dispersing organisms, but not

413   necessarily active dispersers), consistent with spatial sorting (Hastings, 1983), the descendants of

414   highly dispersing parents continued to occupy the southern-most habitat patches. This

415   phenomenon was observed in both the low and high-emission scenarios but was more commonly

416   observed with an initial short range-edge than with the long range-edge dispersal pattern.

417   The overall ability for a species to colonize new habitat over short timescales (e.g., years

418   to decades) may depend upon both the initial dispersal potential of the species and the pattern of

419   geographic variation in dispersal. When the initial mean dispersal distance in northern edge

420   populations are relatively small, as in the uniform-1 km and short range-edge scenarios, dispersal

421 evolution was required for range expansion to occur under climate change (Fig. 2B-C, H-I; 3B-

422 C, H-I). However, dispersal evolution was not required for range expansion when northern

423 populations had relatively high dispersal potential prior to the onset of climate change, as in the

424 uniform-5 km and long range-edge scenarios (Fig. 2E-F, K-L). Collectively, these results

425 indicate that even though dispersal is likely to evolve under all climate change scenarios,

426 successful range expansion is highly dependent on dispersal evolution when the populations at

427 the expanding edge have limited dispersal potential. Furthermore, geographic variation in

428 dispersal influenced range expansion even in the presence of long dispersal distances; the long

429 and short range-edge dispersal scenarios could not colonize habitat as quickly (one decade

430 slower) as the scenario with the longest uniform dispersal distance.

431 In this model, we assumed that the dispersal patterns of the offspring were determined by

432 the parental plant, as is the case for C. edentula (Donohue, 1999), such that the parental plants

433 not only dictate the dispersal characteristics of the seeds, but also contribute directly to dispersal

434 via characteristics such as plant height. Maternal dispersal traits are particularly likely to

435 influence the dispersal kernel of offspring in plants compared to that in animals (Starrfelt &

436 Kokko, 2010). These differences highlight the importance of creating species' distribution

437 models that include taxa-specific dispersal characteristics, such as the parental contribution to the

438 dispersal kernel. When the phenotypic characteristics that determine the dispersal kernel for a

439 species are known, data on variation in those traits can be paired with models that evaluate how

440 variation in these traits influence predicted range shifts under environmental change (e.g.,

441 Dytham et al., 2014). To incorporate evolutionary changes in traits, it is also useful to know their

442 underlying genetic architecture (e.g., numbers of loci, dominance, epistasis) and heritability

443 under varying environmental conditions (Saastamoinen et al., 2018).

444 Neutral genetic diversity within populations across a species' range is an important

445 consideration in conservation and should be incorporated into species' distribution models that

446 strive to predict the response of species to climate change (i.e., Edmonds et al., 2004; Klopfstein

447 et al., 2006). While the interactive effects of geographic variation in dispersal and dispersal

448 evolution may ultimately dictate if new patches are colonized, the neutral effects associated with

449 colonization, such as population bottlenecks, can have large effects on remaining genetic

450 diversity. In our analysis, adaptive evolution always reduced neutral genetic diversity across the

451 species' range (Fig 4; Fig. S1.4); furthermore, dispersal evolution allowed for increased
452 colonization of new habitat, further reducing the amount of neutral genetic diversity in all newly
453 colonized populations due founder effects (Edmonds et al., 2004; Klopfstein et al., 2006). These
454 effects unfolded irrespective of climate change regime or the initial pattern of geographic
455 variation in dispersal. The genome-wide reduction in genetic diversity associated with increased
456 colonization may be substantial, as loci that are putatively neutral with respect to climate change,
457 may be required for future adaptive responses to other environmental changes (e.g., infectious
458 disease, habitat alterations) (Bridle & Vines, 2007; Eckert et al., 2008; Gaston, 2009).

459 Even though the interaction between geographic variation and adaptive evolution in
460 dispersal is complex, accounting for these multifaceted interactions can substantially improve
461 our potential to design conservation strategies that successfully manage populations, species, and
462 communities threatened by climate change. Here, we found that incorporating dispersal variation
463 and adaptive evolution into species distributions models had large effects on the range dynamics
464 that are predicted for one species, and we hypothesize that predictions for other species would
465 change as well. According to our study, dispersal measured at one point in a species' range will
466 potentially lead to significant errors in predicted range shifts with climate change if dispersal
467 distances vary across the species' range. Overall, our results emphasize that more detailed
468 experimental and observational studies of dispersal variation for individual taxa are required to
469 better predict the eco-evolutionary responses of different species to ongoing and future
470 environmental change.

471

472 **Acknowledgements**:

478 **References**

479 Bateman, B. L., H. T. Murphy, A. E. Reside, K. Mokany, & J. VanDerWal. (2013)

480   Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact

481   modelling. Diversity and Distributions 19:1224-1234.

482 Bell, G. & A. Gonzalez. (2011) Adaptation and Evolutionary Rescue in Metapopulations

483   Experiencing Environmental Deterioration. Science 332:1327-1330.

484 Boeye, J., J. M. J. Travis, R. Stoks, & D. Bonte. (2013) More rapid climate change promotes

485   evolutionary rescue through selection for increased dispersal distance. Evolutionary

486   Applications 6:353-364.

487 Bosse, M., L. G. Spurgin, V. N. Laine, E. F. Cole, J. A. Firth, P. Gienapp, et al. (2017) Recent

488   natural selection causes adaptive evolution of an avian polygenic trait. Science 358:365-368.

489 Bridle, J. R. & T. H. Vines. (2007) Limits to evolution at range margins: when and why does

490   adaptation fail? Trends in Ecology and Evolution 22:140-147.

491 Brown, J. L. (2014) SDMtoolbox: a python-based GIS toolkit for landscape genetic,

492   biogeographic and species distribution model analyses. Methods in Ecology and Evolution

493   5:694-700.

494 Christie, M. R. & K. L. Searle. (2017) Evolutionary rescue in a host–pathogen system results in

495   coexistence not clearance, Evolutionary Applications 11: 681-693.

496 Darling, E., K. E. Samis, & C. G. Eckert. (2008) Increased seed dispersal potential towards

497   geographic range limits in a Pacific coast dune plant. New Phytologist 178:424-435.

498 Donohue, K. (1997) Seed dispersal in Cakile edentula var. lacustris: Decoupling the

499   fitness effects of density and distance from the home site. Oecologia 110: 520-

500   527.

501 Donohue, K. (1999) Seed dispersal as a maternally influenced character: Mechanistic basis of

502   maternal effects and selection on maternal characters in an annual plant. American

503   Naturalist 154:674-689.

504 Dytham, C., J. M. J. Travis, K. Mustin, & T. G. Benton. (2014) Changes in species' distributions

505   during and after environmental change: which eco-evolutionary processes matter more?

506   Ecography 37:1210-1217.

507   Eckert, C. G., K. E. Samis, & S. C. Lougheed. (2008) Genetic variation across species'

508   geographical ranges: the central-marginal hypothesis and beyond. Molecular Ecology

509   17:1170-1188.

510   Edmonds, C. A., A. S. Lillie, & L. L. Cavalli-Sforza. (2004) Mutations arising in the wave front

511   of an expanding population. Proceedings of the Royal Society B 101:975-979.

512   Elith, J., S. J. Phillips, T. Hastie, M. Dudik, Y. E. Chee, & C. J. Yates. (2011) A statistical

513   explanation of MaxEnt for ecologists. Diversity and Distributions 17:43-57.

514   Garnier, J. and M. A. Lewis. (2016) Expansion Under Climate Change: The Genetic

515   Consequences. Bulletin of Mathematical Biology 78:2165-2185.

516   Gaston, K. J. (2009) Geographic range limits of species. Proceedings of the Royal Society B

517   276:1391-1393.

518   Gormally, C. L., J. L. Hamrick, & L. A. Donovan. (2011) Genetic structure of a widely dispersed

519   beach annual, Cakile edentula (Brassicaceae). American Journal of Botany 98:1657-1662.

520   Hargreaves, A. L. & C. G. Eckert. (2014) Evolution of dispersal and mating systems along

521   geographic gradients: implications for shifting ranges. Functional Ecology 28:5-21.

522   Hargreaves, A. L., K. E. Samis, & C. G. Eckert. (2014) Are species' range limits simply niche

523   limits writ large? A review of transplant experiments beyond the range. The American

524   Naturalist 183: 157-173.

525   Hargreaves, A. L., S. F. Bailey, & R. A. Laird. (2015) Fitness declines towards range limits and

526   local adaptation to climate affect dispersal evolution during climate-induced range shifts.

527   Journal of Evolutionary Biology 28:1489-1501.

528   Hasting, A. (1983) Can spatial variation alone lead to selection for dispersal? Theoretical

529   Population Biology 24: 244-251.

530   Henry, R. C., G. Bocedi, C. Dytham, and J. M. J. Travis. (2014) Inter-annual variability

531   influences the eco-evolutionary dynamics of range-shifting. Peerj 2.

532   Hillaert, J., J. Boeye, R. Stoks, & D. Bonte. (2015) The evolution of thermal performance can

533   constrain dispersal during range shifting. Journal of Biological Dynamics 9:317-335.

534   Johnson, J.S., R.S. Cantrell, C. Cosner, F. Hartig, A. Hastings, H.S. Rogers, E.W. Schupp, K.

535   Shea, B.J. Teller, X. Yu, D. Zurell, G. Pufal. (2019) Rapid changes in seed dispersal traits

536   modify plant responses to global change. AOB Plants plz020:

537   https://doi.org/10.1093/aobpla/plz020

538   Klopfstein, S., M. Currat, & L. Excoffier. (2006) The fate of mutations surfing on the wave of a

539   range expansion. Molecular Biology and Evolution 23:482-490.

540   Kubisch, A., R. D. Holt, H. J. Poethke, & E. A. Fronhofer. (2014) Where am I and why?

541   Synthesizing range biology and the eco-evolutionary dynamics of dispersal. Oikos 123:5-22.

542   Kubisch, A., T. Degen, T. Hovestadt, & H. J. Poethke. (2013) Predicting range shifts under

543   global change: the balance between local adaptation and dispersal. Ecography 36:873-882.

544   Lane, M. (2008) Data citation in the electronic environment, a white paper commissioned by

545   GBIF. Copenhagen, Global Biodiversity Information Facility.

546   LaRue, E. A., J. D. Holland, & N. C. Emery. (2018) Environmental predictors of dispersal traits

547   across a species geographic range. Ecology 99: 1857-1865.

548   Nathan, R., E. Klein, J. J. Robledo-Arnuncio, & E. Revilla. (2012) Dispersal kernels: review.

549   Dispersal Ecology and Evolution:187-210.

550   Palkovacs, E. P., M. T. Kinnison, C. Correa, C. M. Dalton, & A. P. Hendry. (2012) Fates beyond

551   traits: ecological consequences of human-induced trait change. Evolutionary Applications

552   5:183-191.

553   Phillips, B. L., G. P. Brown, J. K. Webb, & R. Shine. (2006) Invasion and the evolution of speed

554   in toads. Nature 439:803-803.

555   Phillips, S. J., M. Dudik, & R. E. Schapire. (2004) A maximum entropy approach to species

556   distribution modelling. Proceedings of the 21st Learning Conference on Machine

557   Learning:655-662.

558   Phillips, S. J., R. P. Anderson, & R. E. Schapire. (2006) Maximum entropy modeling of species

559   geographic distributions. Ecological Modelling 190:231-259.

560   Prudhomme, C., N. Reynard, & S. Crooks. (2002) Downscaling of global climate models for

561   flood frequency analysis: Where are we now? Hydrological Processes 16:1137–1150.

562   Razgour, O., J. Juste, C. Ibanez, A. Kiefer, H. Rebelo, S. J. Puechmaille, et al. (2013) The

563   shaping of genetic variation in edge-of-range populations under past and future climate

564   change. Ecology Letters 16:1258-1266.

565   Riba, M., M. Mayol, B. E. Giles, O. Ronce, E. Imbert, M. van der Velde, et al. (2009) Darwin's

566   wind hypothesis: does it work for plant dispersal in fragmented habitats? New Phytologist

567   183:667-677.

568 Rodman, J. E. (1973) Systematics and evolution of the genus Cakile (Cruciferae). Contributions
569   from the Gray Herbarium of Harvard University:3-146.
570 Saastamoinen, M., G. Bocedi, J. Cote, D. Legrand, F. Guillaume, C. W. Wheat, et al. (2018)
571   Genetics of dispersal. Biological Reviews of the Cambridge Philosophical Society 93: 574 –
572   599.
573 Savage, A. E. & K. R. Zamudio. (2016) Adaptive tolerance to a pathogenic fungus drives major
574   histocompatibility complex evolution in natural amphibian populations. Proceedings of the
575   Royal Society B 283: 20153115.
576 Siepielski, A. M., M. B. Morrissey, M. Buoro, S. M. Carlson, C. M. Caruso, S. M. Clegg, T, et
577   al. (2017) Precipitation drives global variation in natural selection. Science 355:959-962.
578 Starrfelt, J., H. Kokko. 2010. Parent-offspring conflict and the evolution of dispersal distance.
579   American Naturalist 175: 38-49.
580 Talavera, M., M. Arista, & P. L. Ortiz. (2012) Evolution of dispersal traits in a biogeographical
581   context: a study using the heterocarpic Rumex bucephalophorus as a model. Journal of
582   Ecology 100:1194-1203.
583 Taylor K. E., R. J. Stouffer, & G. A. Meehl. (2012) An overview of CMIP5 and the experiment
584   design. Bulletin of the American Meteorological Society, 93, 485-498.
585 Weiss-Lehman, C., R. A. Hufbauer, & B. A. Melbourne. (2017) Rapid trait evolution drives
586   increased speed and variance in experimental range expansions. Nature Communications
587   8:14303.
588 Willmott, C. J. & K. Matsuura (2001) Terrestrial Air Temperature and Precipitation: Monthly
589   and Annual Time Series (1950 -1999),
590   http://climate.geog.udel.edu/~climate/html_pages/README.ghcn_ts2.html.
591

592 **Biosketch**:

593 The goal of this research team is to further the understanding of how rapid evolution influences
594 range dynamics under environmental change through the combination of modelling and
595 empirical approaches. The team focuses on critical drivers underlying species distributions such
596 as dispersal, habitat specialization, and the evolution of domestication or invasion. This study
597 was the product of a doctoral dissertation project conducted at Purdue University by E.A.L.
598 Author contributions: E.A.L, N.C.E, and M.R.C. conceived the study idea; L.B. created the

599   climate data; E.A.L. and M.R.C. developed the individual-based model; E.A.L. collected the

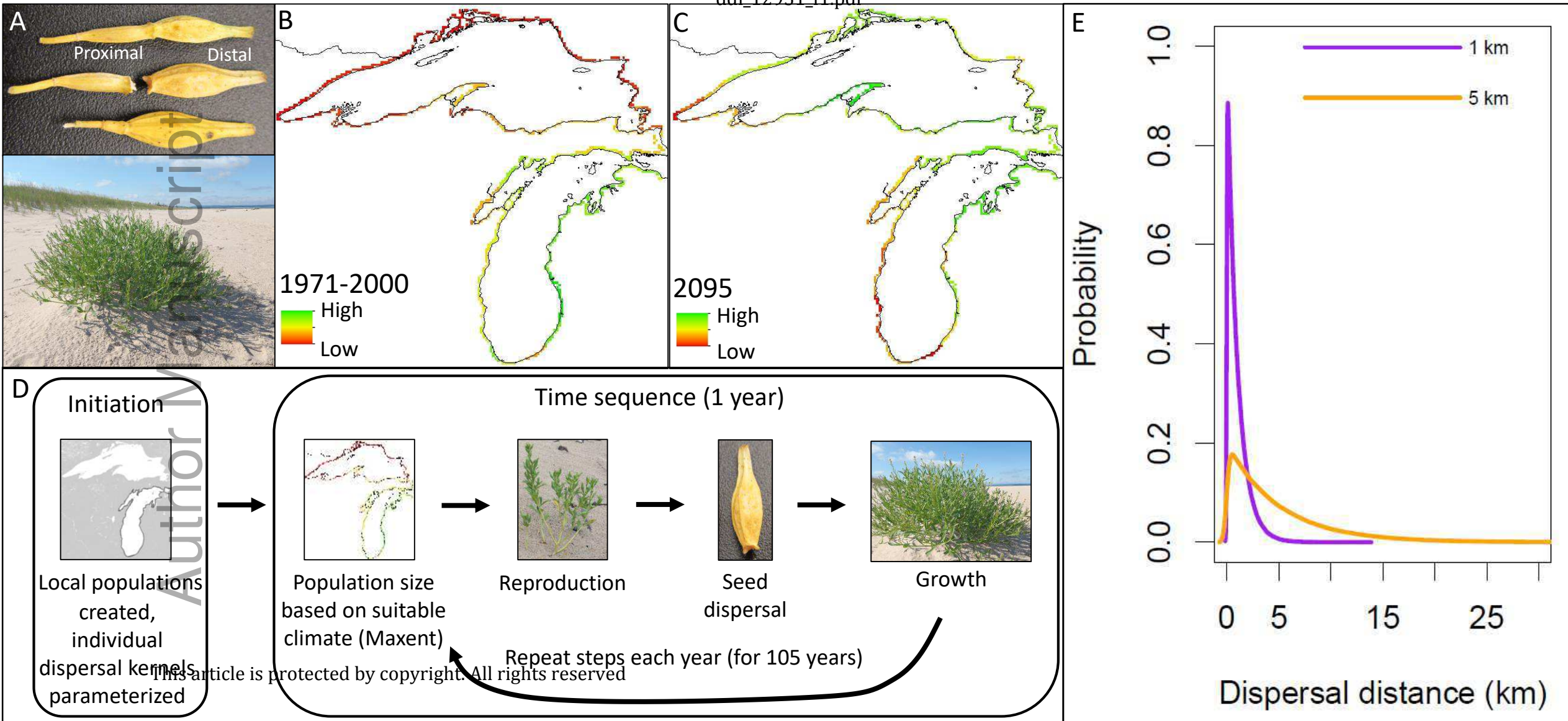600   data, analysed the data, and led the writing; all authors edited the manuscript.

601   **Figure Legends**

602   **Figure 1.** The dispersal strategy of Cakile edentula, example maps of predicted habitat

603   suitability across its geographic range in the Great Lakes, model steps, and range of dispersal

604   kernel shapes. A) The home-site (proximal) and water-dispersing (distal) fruits of C. edentula

605   (top) and the typical growth form of the plant on a Great Lakes beach (bottom). B) The predicted

606   distribution of habitat suitability under present day climate (1971–2000) and C) under projected

607   high emissions climate change in year 2095, where green represents high habitat suitability,

608   yellow represents intermediate habitat suitability, and red represents low habitat suitability. D)

609   General overview of steps in our hybrid species distribution model that combined climatic niche

610   modelling with an individual-based model. First, the population genetic and demographic

611   characteristics of populations across the range are initiated at the beginning of the simulation.

612   The remaining steps occur each year in order including: the determination of the metapopulation

613   and local carrying capacities based on climatic habitat suitability values, asexual reproduction,

614   dispersal of the offspring based on the maternal dispersal kernel, seed establishment, death of

615   parental plants, and plant growth for seed production in the next year.

616   **Figure 2.** Changes in the dispersal kernel over 105 generations for dispersal scenarios with no

617   adaptive evolution. A) present-day climate and uniform-1 km dispersal, B) low-emission and

618   uniform-1 km dispersal, C) high-emission and uniform-1 km dispersal, D) present-day climate

619   and uniform-5 km dispersal, E) low-emission and uniform-5 km dispersal, F) high-emission and

620   uniform-5 km dispersal, G) present-day climate and short range-edge dispersal, H) low-emission

621   and short range-edge dispersal, I) high-emission and short range-edge dispersal, J) present-day

622   climate and long range-edge dispersal, K) low-emission and long range-edge dispersal, and L)

623   high-emission and long range-edge dispersal. Insets (far left) illustrate the dispersal distance

624   across the latitudinal range at the beginning of the simulation and colour scale (far right)

625   illustrate the average dispersal distance ranging from short (purple) to long (red). Grey squares

626   indicate a 0.5 degree area of latitude in the range that contained no individuals.

627   **Figure 3.** Changes in the dispersal kernel over 105 generations for scenarios when dispersal

628   kernels were allowed to evolve in response to climate-induced changes to habitat quality over the

629   course of the simulation. A) present-day climate and uniform-1 km dispersal, B) low-emission

630   and uniform-1 km dispersal, C) high-emission and uniform-1 km dispersal, D) present-day

631   climate and uniform-5 km dispersal, E) low-emission and uniform-5 km dispersal, F) high-

632   emission and uniform-5 km dispersal, G) present-day climate and short range-edge dispersal, H)

633   low-emission and short range-edge dispersal, I) high-emission and short range-edge dispersal, J)

634   present-day climate and long range-edge dispersal, K) low-emission and long range-edge

635   dispersal, and L) high-emission and long range-edge dispersal. Insets (far left) illustrate the

636   dispersal distance across the latitudinal range at the beginning of the simulation and colour scale

637   (far right) illustrate the average dispersal distance ranging from short (purple) to long (red). Grey

638   squares indicate a 0.5 degree area of latitude in the range that contained no individuals.

639   **Figure 4.** Effects of geographic variation in dispersal distance and adaptive evolution of

640   dispersal distance on the spatial distribution of expected heterozygosity (left y-axis) and average

641   number of alleles per locus for 50 microsatellites across the species' range (right y-axis). Panels

642   are as follows: A) present-day climate and uniform-1 km dispersal, B) low-emission and

643   uniform-1 km dispersal, C) high-emission and uniform-1 km dispersal, D) present-day climate

644   and short range-edge dispersal, E) low-emission and short range-edge dispersal, F) high-

645   emission and short range-edge dispersal, G) no climate change and long range-edge dispersal, H)

646   low-emission and long range-edge dispersal, and I) high-emission and long range-edge dispersal,

647   J) present-day climate and uniform-5 km dispersal, K) low emission and uniform-5 km dispersal,

648   and L) high emission and uniform-5 km dispersal. Expected heterozygosity was calculated for

649   each locus and then averaged across loci within a patch. The filled blue circles represent the

650   mean expected heterozygosity over 0.5 degrees of latitude at year 2105 (left y-axis), the grey

651   shading is the standard deviation of the mean, and the light blue open circles are the estimates for

652   individual populations. The orange horizontal line represents the average number of alleles per

653   locus across the range in year 105 (right y-axis). The black vertical line at latitude = 47.9 marks

654   the northern range limit from year 0–25 during present-day climate.

A — Proximal / Distal

B — 1971-2000 — High / Low

C — 2095 — High / Low

D — Initiation — Time sequence (1 year)

Local populations created, individual dispersal kernels parameterized → Population size based on suitable climate (Maxent) → Reproduction → Seed dispersal → Growth

Repeat steps each year (for 105 years)

E — Probability vs Dispersal distance (km); 1 km, 5 km