

1 **Spatial sorting and range shifts: consequences for evolutionary potential and genetic**  
2 **signature of a dispersal trait**

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17

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19 **Abstract**

20 Species are shifting their ranges under climate change, with genetic and evolutionary  
21 consequences. As a result, the spatial distribution of genetic diversity in a species' range can  
22 show a signature of range expansion. This genetic signature takes time to decay after the  
23 range stops expanding and it is important to take that lag time into account when interpreting  
24 contemporary spatial patterns of genetic diversity. In addition, the return to spatial  
25 equilibrium on an ecologically relevant timescale will depend on migration of genetic  
26 diversity across the species' range. However, during a range shift alleles may go extinct at the  
27 retracting range margin due to spatial sorting. Here we studied the spatial pattern of genotypes  
28 that differ in dispersal rate across the species range before, during and after a range shift,  
29 assessed the effect of range retraction on this pattern, and quantified the duration of the  
30 ephemeral genetic signature of range expansion for this trait. We performed simulation  
31 experiments with an individual-based metapopulation model under several contemporary  
32 climate change scenarios. The results show an increase of the number of individuals with high  
33 dispersal rate. If the temperature increased long enough the allele coding for low dispersal rate  
34 would go extinct. The duration of the genetic signature of range expansion after stabilisation  
35 of the species' distribution lasted up to 1200 generations after a temperature increase for 60  
36 years at the contemporary rate. This depended on the total displacement of the climate  
37 optimum, as the product of the rate of temperature increase and its duration. So genetic data  
38 collected in the field do not necessarily reflect current selection pressures but can be affected  
39 by historic changes in species distribution, long after the establishment of the current species'  
40 range. Return to equilibrium patterns may be hampered by loss of evolutionary potential  
41 during range shift.

42

43 **Keywords:** Metapopulation; individual-based model; climate change;

## 44 **Introduction**

45 Species are shifting their ranges under climate change (Chen et al., 2011; Parmesan and Yohe,  
46 2003), which has genetic and evolutionary consequences (Excoffier et al., 2009; Kubisch et  
47 al., 2014; Parmesan, 2006). The genetic diversity present at the expanding range margin is  
48 smeared across the landscape on the expansion wave (Excoffier and Ray, 2008). This is the  
49 case for neutral as well as adaptive genetic variation (Cobben et al., 2012a; Cobben et al.,  
50 2011; Edmonds et al., 2004; Hewitt, 1996; Ibrahim et al., 1996; Klopstein et al., 2006; Travis  
51 et al., 2010; Travis et al., 2007). Under these conditions, the genetic configuration of the  
52 newly colonised populations is largely the result of the demographic process under range  
53 expansion, and not of selection (Travis et al., 2007), although some traits are selected for  
54 under range expansion, particularly the ability to disperse and traits related to population  
55 growth rate (Hill et al., 2011; Moreau et al., 2011; Phillips et al., 2010).

56         With regard to the ability to disperse, both theoretical and empirical studies report an  
57 increased dispersal capacity as a result of spatial sorting under range expansions (e.g. Burton  
58 et al., 2010; Phillips et al., 2006; Thomas et al., 2001; Travis and Dytham, 2002; Travis et al.,  
59 2013). Good dispersers gather at the range margin and from there they colonise new territory,  
60 while the poor dispersers lag behind. This eventually leads to a spatial gradient in dispersal  
61 capacity across the species' range, which can be regarded as a genetic signature of range  
62 expansion (Phillips et al., 2010). After the range stops expanding, it takes time for such a  
63 genetic signature of range expansion to decay, especially when the variation for these traits  
64 needs to migrate from the centre of the range or to develop through *de novo* mutations  
65 (Dytham et al., 2014; Phillips et al., 2010). During that time period populations are in spatial  
66 disequilibrium as a result of the past range expansion. In a time when many investigators are  
67 gathering genetic data from natural populations to study selection pressures and micro-  
68 evolution, accounting for different explanations of genetic make-up is crucial (Currat et al.,

69 2006; Ray and Excoffier, 2009). Investigating the genetic signature of range expansion is  
70 therefore of importance for the interpretation of contemporary spatial patterns in genetic  
71 diversity.

72         Particularly for a dispersal trait, it can be expected that the decay of this genetic  
73 signature of range expansion may take a long time: after the range expansion stops the net  
74 effect of selection will be for lower dispersal capacity, yet low dispersal genotypes are by  
75 definition slow dispersers. Kubisch et al. (2010) showed that the establishment of genotypes  
76 with low dispersal rates after range expansion is the result of the migration of variation, and  
77 does not involve the establishment of new, beneficial mutations. In their study we see a slow  
78 return to equilibrium dispersal rate values at the expanding range margin after range  
79 expansion, but this result is not specifically quantified or discussed. In contrast, Henry et al.  
80 (2014) claimed a fast return to equilibrium values after range expansion, resulting from  
81 selection for beneficial mutations. In a mechanistically more realistic model, Dytham et al.  
82 (2014) showed that the state of spatial disequilibrium can last for a substantial time period  
83 after the range expansion. In addition, they observed that the speed of range expansion  
84 depends on selection for existing variation rather than for new variation due to mutations,  
85 even under a high mutation rate (Dytham et al., 2014). This is in line with theory and  
86 empirical data on micro-evolution, in which evolutionary changes that are relevant at  
87 ecological timescales depend on changes in allele frequencies rather than on new mutations.  
88 However, none of the above studies have explicitly discussed or tried to quantify the time  
89 period during which populations are in spatial disequilibrium.

90         Under a climate change scenario with continued temperature increase, many species'  
91 ranges are expected to retract at the margin with the deteriorating thermal conditions,  
92 resulting in a range shift rather than a range expansion (Gillings et al., 2015; Thomas et al.,  
93 2006). This means that slow dispersers might be lost as a result of spatial sorting and

94 subsequent extinction of populations at the retracting margin (Cobben et al., 2012a; Cobben et  
95 al., 2011), while return to equilibrium values after range expansion likely depends on such  
96 existing genetic diversity as argued above (Dytham et al., 2014; Kubisch et al., 2010). Many  
97 studies have reported increased dispersal under range expansion (e.g. Burton et al., 2010;  
98 Phillips et al., 2006; Thomas et al., 2001; Travis and Dytham, 2002; Travis et al., 2013), but  
99 little attention has been given to the consequences of a retracting range margin for dispersal  
100 traits (but see Henry et al., 2014).

101         In this paper we investigated how range shifts affect the distribution of different  
102 genotypes coding for low, medium and high rates of dispersal across the species range. In  
103 addition, we studied the duration of the ephemeral genetic signature of range expansion. For  
104 both, we used a mechanistically realistic model of a range shifting species under climate  
105 change. We simulated a period of temperature increase in several scenarios, during and after  
106 which we registered the distribution of the different dispersal rate genotypes in the landscape  
107 up until 5000 years after model initialisation. To warrant sufficient variation in the existing  
108 genetic diversity under stationary conditions, we employed diploid inheritance, fragmented  
109 habitat and temperature variability. The genetic architecture was designed to get a clear  
110 signature of spatial sorting as well as distinct differences between phenotypes.

111

## 112 **Methods**

113 We used a spatially explicit, individual-based simulation model of a sexually reproducing  
114 species with overlapping generations. The model is called METAPHOR (Verboom et al.,  
115 2001; Vos et al., 2001) and has previously been extended to allow for stochastic temperature  
116 increase (Schippers et al., 2011) and with a genetic module for neutral (Cobben et al., 2012b;  
117 Cobben et al., 2011) and adaptive traits (Cobben et al., 2012a). It was parameterised based on  
118 empirical data for the middle spotted woodpecker (*Dendrocopus medius*), a woodland bird

119 (Hagemeijer and Blair, 1997; Kosenko and Kaigorodova, 2001; Kosinski and Ksit, 2006;  
120 Kosinski et al., 2004; Michalek and Winkler, 2001; Pasinelli, 2000; Pettersson, 1985). Table 1  
121 gives an overview of the parameters used. For the current study we allowed the dispersal rate  
122 to be adaptive and investigated the spatial distribution of the allele frequencies at the dispersal  
123 gene during and after range shift.

124

### 125 Landscape

126 The landscape was 15 km wide (horizontal axis) by 2000 km long (vertical axis). In  
127 horizontal direction the borders were merged, creating a (vertical) tube. The landscape  
128 contained 3000 randomly distributed habitat patches, equalling a total of 5% habitat area. In  
129 vertical direction, a Gaussian temperature curve was shifting across the landscape at various  
130 speeds, and with a standard deviation of 140 km (see Appendix A). This temperature was  
131 used to determine the local habitat quality and each row in the landscape was as such  
132 characterised by a time-specific habitat quality  $q$  [0..1], being 1 at the peak of the distribution  
133 and 0 outside the curve area. We used three temperature increase scenarios, based on work by  
134 the IPCC (2013), of a respective temperature increase of 1°C, 2°C and 4°C by the year 2100,  
135 resulting in equivalent isocline shift rates of 2, 4 and 8 km per year, respectively (see  
136 Appendix A).

137

### 138 Population demography

139 The patches in the landscape were inhabited by individuals that were characterised by their  
140 sex, and their dispersal alleles (see below under Genetics). The yearly life cycle consisted of  
141 recruitment, dispersal, and survival, in this order. Per patch, in each year, the number of  
142 offspring per unique pair of individuals of opposite sex was dependent on local habitat quality  
143  $q$  and population density  $d$ , following:

$$144 \quad R = R_{d0q1} * \left( 1 - \left( 1 - \frac{R_{d0q0}}{R_{d0q1}} \right) * (1 - q) \right) * \left( 1 - \left( 1 - \frac{R_{d1q1}}{R_{d0q1}} \right) * d \right)$$

145 with  $R_{d0q1}$  is the number of offspring at  $d = 0$  and  $q = 1$ , and similar for  $R_{d0q0}$  and  $R_{d1q1}$ .

146 The individual dispersal rate depended on its diploid genotype and can be low (zero), medium  
 147 (0.1) or high (0.2), indicating its yearly dispersal probability. Upon dispersal, individuals  
 148 could leave their patch in every direction in a straight line, and were then assigned to the first  
 149 patch they encountered within their maximum dispersal distance of 15 km. The individual  
 150 survival probability depended on population density  $d$  and habitat quality  $q$ .

$$151 \quad s = s_{d0q1} * \left( 1 - \left( 1 - \frac{s_{d0q0}}{s_{d0q1}} \right) * q \right) * \left( 1 - \left( 1 - \frac{s_{d1q1}}{s_{d0q1}} \right) * (1 - d) \right)$$

152 with  $s_{d0q1}$  is survival rate at  $d = 0$  and  $q = 1$ , and similar for  $s_{d0q0}$  and  $s_{d1q1}$ .

153

#### 154 Genetics

155 There were two alleles at the dispersal locus. Allele A signified zero dispersal rate and allele  
 156 B coded for 0.2 dispersal rate (i.e. there was a 20 percent chance that an individual left the  
 157 habitat patch in which it was born). The individuals were diploid and the alleles codominant.  
 158 The actual probability of dispersal was calculated as the arithmetic mean of the alleles that  
 159 they had randomly inherited from each parent: genotype AA is a dispersal rate of 0, AB is 0.1  
 160 dispersal rate and BB is a dispersal rate of 0.2. Pilot runs included additional alleles 1. with  
 161 higher dispersal rates, but these were never maintained beyond model initiation, and 2. with  
 162 finer-scaled rates, many of which were lost in more or less random patterns, and thus blurring  
 163 the signal of spatial sorting. Each allele could mutate at a rate of  $10^{-6}$  (Nachman and Crowell,  
 164 2000) to the other allele. Evolution in this genetic model thus depended mostly on standing  
 165 genetic variation, but had clear differences between phenotypes, while the codominance  
 166 allowed the spread of the A allele in AB individuals (Bell and Aguirre, 2013; Schluter and  
 167 Conte, 2009; Van Belleghem et al., 2014).

168

169 Simulation experiments

170 At initialisation of the model, all habitat patches were filled with 10 adult individuals,  
171 equalling half the carrying capacity  $K$ . Each individual was randomly given two dispersal  
172 alleles. The temperature optimum  $Y_{opt}$  was initialised at 400 km from the southern landscape  
173 edge. After initialisation the model was run for 500 generations, equalling 500 years, to  
174 establish equilibrium population demography and dispersal rate values. After this burn-in  
175 period we applied the stochastic temperature increase for 500 years at three isocline speeds of  
176 2 km yr<sup>-1</sup>, 4 km yr<sup>-1</sup> and 8 km yr<sup>-1</sup>. In a second experiment we used the same three different  
177 isocline shift rates, but combined with three time periods of temperature increase each, and  
178 monitored the population establishment and the distribution of genotypes for 5000 years  
179 afterwards (see Table 2). We performed 10 replicate simulations for both experiments.  
180 Additional control simulations included different standard deviations of the mean speed of the  
181 temperature curve of zero and 280 kilometres, and a different mutation rate of  $10^{-6}$ .

182

183 Analysis

184 We summed the average number of genotypes over 10 replicate simulations in landscape  
185 blocks of 50 km in vertical direction. The equilibrium genotype distribution was defined as  
186 the average number of individuals of each genotype in each 50 km-block across all replicates  
187 of all simulations in year 500 (the year in which we start the temperature increase, so after the  
188 burn-in phase and prior to any disturbances). To quantify the deviation from the equilibrium  
189 range size and location after the stabilisation of the temperature (*Deviation I*), we calculated  
190 in each year and each 50 km-block the sum of the absolute differences in total number of  
191 individuals, corrected for the location of the climate optimum (which is moving during the  
192 period of temperature increase). Similarly, to quantify the deviation from the equilibrium



193 genotype distribution after the stabilisation of the temperature, we calculated in each year and  
 194 each 50 km-block the sum of the absolute differences in individual numbers of each of the  
 195 different genotypes, corrected for the location of the climate optimum (*Deviation II*).

$$196 \text{ Deviation I, } t = \sum_{i=1}^{15} (|\sum_{X=1}^3 (Nx_{i,t=0}) - \sum_{X=1}^3 (Nx_{i,t})|)$$

$$197 \text{ Deviation II, } t = \sum_{X=1}^3 (\sum_{i=1}^{15} (|Nx_{i,t=0} - Nx_{i,t}|))$$

198 with number of individuals  $N$  of genotype  $X$  (AA, AB or BB) in range block  $i$  north of the  
 199 climate optimum, with the location of the climate optimum dependent on time and simulation  
 200 scenario.

201 By comparing these two deviations for all years after the stabilisation of the  
 202 temperature, we could see the difference between the moment that the full species range is re-  
 203 established after climate change stops and the moment that the equilibrium genotype  
 204 distribution is re-established. This difference in time was the period in which the observed  
 205 genotype distribution in the species range is the consequence of past range expansion, the so-  
 206 called ephemeral signature of range expansion, and it was not indicative of current and local  
 207 selection pressures.

208

## 209 **Results**

### 210 Loss of the A allele at the trailing edge

211 At the end of the burn-in phase, so under equilibrium conditions, the metapopulation  
 212 consisted of individuals with dispersal rates of 0, 0.1 and 0.2 (genotypes AA, AB and BB  
 213 respectively; Figure 1 year 0). All three genotypes were present in the total range but the  
 214 individuals with 0 dispersal rate (AA) dominated the centre of the range, while the 0.2  
 215 individuals (BB) had the highest frequency in the margins, where habitat quality and  
 216 population densities were lower. The 0.1 individuals (AB) took an intermediate position. The  
 217 control simulations showed a comparative increase in numbers of dispersive genotypes with

218 increasing standard deviations of the mean speed of the temperature curve, but overall  
219 decreasing population numbers (Figure S1 in Appendix B).

220         The original distribution of the populations and the genotypes within the  
221 metapopulation changed under the range shift that was induced by the temperature increase in  
222 the first experiment (Figure 1). The range shifted, but not as fast as the climate optimum  
223 moved, and this lag resulted in a decline in the metapopulation size in time. The decline was  
224 faster with increasing speed of the climate optimum and an increasing standard deviation of  
225 this mean speed across years (Figure S1 in Appendix B). In addition, there was an increase of  
226 the proportion of 0.2 dispersal rate individuals and the relative size of the area where they  
227 lived, at the expanding edge of the metapopulation. The number of lower dispersal rate  
228 individuals decreased and eventually the A allele went extinct as the habitat quality in the  
229 southern populations fell below the threshold value (Figure 1 yr 500). This pattern occurred in  
230 all simulations in which the metapopulation persisted sufficiently long (e.g. Figure S1 in  
231 Appendix B).

232

### 233 The genetic signature of range shift

234 In experiment 2, once the temperature stabilised, the distribution of the genotypes re-  
235 established their equilibrium, but only after a certain amount of time (Figure 2). This amount  
236 of time depended on the total displacement of the temperature optimum, so the speed of the  
237 isotherm shift multiplied by the number of years of temperature increase. This displacement  
238 also determined the shape of the deviation curve (deviation II being the measure for how far  
239 the metapopulation was from spatial equilibrium with regard to the distribution of the  
240 different genotypes), with a typical initial increase in the genotype distribution deviation for  
241 large displacements (Figure 3c). The genotype distribution deviation was always larger than  
242 the range deviation (Figure 3), but for small displacements the lines ran in parallel (Figure

243 3a). For intermediate displacements, both deviations converged towards equilibrium values,  
244 with the range deviation levelling off first (Figure 3b). This means that when the range  
245 reached its equilibrium size, the spatial pattern of the different dispersal genotypes was not  
246 yet in the equilibrium situation.

247

## 248 **Discussion**

249 We have investigated how range shifts affect the distribution of genotypes of different  
250 dispersal rates across the species range. The combination of spatial sorting and range  
251 retraction could lead to the extinction of the A allele, coding for low dispersal rate. When the  
252 temperature stabilised before the extinction of the A allele, the equilibrium spatial distribution  
253 of genotypes was able to recover. This, however, took an extensive amount of time,  
254 dependent on the total displacement of the temperature optimum for the investigated range of  
255 temperature increase rates. We expected that for low rates of temperature increase the  
256 genotype distribution would differ less from the equilibrium distribution under range shift,  
257 because then the selection pressures hardly change compared to a stable range. It is thus  
258 important to note that for the investigated system any realistic scenario of the rate of  
259 temperature increase under climate change had an effect on the spatial distribution of the  
260 genotypes. As such, recovery time here did not depend on the rate of temperature increase per  
261 se, but on the final total displacement of the temperature optimum. After the range shift was  
262 completed and the species' range had reached its equilibrium size, it took up to 20 times the  
263 duration of the temperature increase period before the spatial distribution of genotypes was at  
264 equilibrium. Although the genetic signature of range expansion is ephemeral, it can affect the  
265 spatial distribution of genotypes in the landscape for a long time period after the range stops  
266 expanding. This is important for the interpretation of genetic field data, since signatures of

267 adaptive evolution in genetic data can mimic signatures of range expansion (Currat et al.,  
268 2006; Ray and Excoffier, 2009).

269         The metapopulation in equilibrium consisted of individuals with 0, 0.1, and 0.2  
270 dispersal probability. The observed gradient of increasing dispersal rate from the core of the  
271 metapopulation to the range margins at equilibrium was as anticipated, as dispersal is  
272 essential at the margin due to the variable habitat quality, but only occasionally beneficial in  
273 the range core as a result of the high densities there (Clobert et al., 2004; Ronce, 2007). This  
274 led to a frequency-dependent selection, with a large proportion of non-dispersers and lower  
275 proportions of dispersive individuals in the core of the range. Control simulations initialised  
276 with additional alleles coding for higher dispersal rates, showed that the relative costs of  
277 dispersal were too high anywhere across the range for their persistence in the metapopulation  
278 at equilibrium. During the range shift the relative number of individuals with 0.2 dispersal  
279 rate increased as a result of spatial sorting (Shine et al., 2011). Again, in control simulations  
280 allowing for mutations with higher dispersal rates, we observed that such mutations could  
281 arise, but they never managed to establish themselves in the population during range shift.

282         While most studies focus on the evolution of dispersal traits under range expansion  
283 (Excoffier et al., 2009; Kubisch et al., 2011; Shine et al., 2011; Thomas et al., 2001; Travis  
284 and Dytham, 2002), we have here used a range shift scenario. We showed that in the  
285 retracting part of the range the genetic variation coding for lower dispersal rates may go  
286 extinct (Figure 1). As soon as the lower dispersal individuals were confined to populations  
287 near the southern range margin where local selection favours higher dispersal, there was no  
288 chance of recovery for the A allele. This happened even though the metapopulation under  
289 equilibrium conditions consisted for more than two thirds of individuals carrying an A allele,  
290 so with 0 and 0.1 dispersal rates (Figure 1). Such loss of genetic variation at the trailing edge  
291 of a shifting metapopulation is a so far non-described consequence of spatial sorting (Shine et

292 al., 2011; Travis and Dytham, 2002). While spatial sorting is usually referred to as the  
293 phenomenon that dispersive genotypes gather at the expanding range margin (Phillips et al.,  
294 2010; Shine et al., 2011), our results indicate that this concept may be broadened to include  
295 the confinement and possible extinction of poor disperser alleles at the retracting range  
296 margin under range shift. This may cause a range-wide loss of adaptive genetic variation  
297 (Cobben et al., 2012a; Henry et al., 2014). Whether such a phenomenon can be or has been  
298 observed in the field we do not know. While the importance of rear edge populations for the  
299 conservation of species genetic diversity has been noted (Hampe and Petit, 2005), this  
300 concerned populations that are older than the populations in the core and leading range  
301 margin and have persisted in an ice age refugium. In addition, loss of genetic diversity in  
302 small and isolated populations as a result of genetic drift is a well-established theory and has  
303 been observed in empirical studies as well (Pearson et al., 2009). However, observing the loss  
304 of genetic diversity as a result of spatial sorting would require a well-advanced range  
305 retraction, while the first retractions have only been observed recently (Gillings et al., 2015;  
306 Thomas et al., 2006). Historical and ongoing range contractions are plentiful (Channell and  
307 Lomolino, 2000; Laliberte and Ripple, 2004; Rodríguez, 2002), but are not necessarily  
308 associated with a range shift, and information about the adaptive genetic composition of such  
309 species' ranges is not available at the moment (but for neutral diversity see Koen et al., 2014).

310         The disequilibrium distribution of genotypes after the range stops expanding, and its  
311 long duration may reduce the species' fitness (Cobben et al., 2012a; Dytham et al., 2014) as it  
312 represents a form of maladaptation. Here we showed in an ecologically realistic model that if  
313 the variation for a specific trait needs to migrate or develop by *de novo* mutations, and the  
314 trait itself is related to a reduced tendency to disperse, this period of disequilibrium may last  
315 for hundreds or even thousands of years. Control simulations with an increased mutation rate  
316 of  $10^{-4}$  seldom showed the establishment of a low dispersive mutation which then increased

317 the return rate to equilibrium. Similar studies report a lengthy phase of spatial disequilibrium  
318 and a dependency on existing genetic diversity rather than of new mutations (Dytham et al.,  
319 2014; Kubisch et al., 2010). In contrast, Henry et al. (2014) mention a fast return to  
320 equilibrium distributions of dispersal rates after range expansion due to the establishment of  
321 beneficial mutations. They however used a high mutation rate of  $10^{-3}$ , a larger model  
322 population, and haploid inheritance. Under diploid inheritance, the phenotypic effect of a  
323 beneficial mutation is diluted in heterozygotes. As long as the allele frequency is low the  
324 allele will exist almost completely within heterozygotes. In diploids the return to spatial  
325 equilibrium will therefore depend on the migration of existing (standing) genetic variation  
326 (Schluter and Conte, 2009; Van Belleghem et al., 2014) rather than on mutations.

327         Burton et al. (2010) showed in a modelling study that the presence of a competing  
328 species in the region to be colonised can greatly reduce the extent to which dispersal traits are  
329 selected for in populations at the leading edge. Additionally, in a large metapopulation as the  
330 one we modelled, you may expect adaptation to local environmental conditions, although for  
331 small subpopulations such adaptation is less common (Leimu and Fischer, 2008). Bourne et  
332 al. (2014) showed that the spread of a genotype that is beneficial under climate change only  
333 facilitates population rescue when there is no strong local selection against non-specialists.  
334 Such local adaptation could therefore be of consequence (Kubisch et al., 2013), especially  
335 when there is genetic linkage between the underlying genes or it essentially involves the same  
336 traits (Brown et al., 2007).

337         With continuously changing environmental conditions and land use patterns we can  
338 safely assume that many species (or species traits) are permanently in disequilibrium. In  
339 Europe, even now, some species are still expanding their ranges after the last glacial  
340 maximum. This means that observed phenotypes in the field cannot be assumed to perfectly  
341 reflect the local and current selection pressures (Currat et al., 2006; Edmonds et al., 2004;

342 Klopstein et al., 2006; Lindström et al., 2013; Ray and Excoffier, 2009). However, field  
343 studies investigating changing local population composition in the period after colonisation  
344 have shown that less dispersive phenotypes can be found within years (Lindström et al., 2013)  
345 to decades (Thomas et al., 2001) after initial colonisation. This could be the result of the  
346 genetic architecture and heritability of the dispersal trait, or of trade-offs with other traits. For  
347 the cane toads e.g. (in Lindström et al., 2013) the dispersal capacity is the result of a  
348 combination of many different traits (Phillips et al., 2010), which are combined during spatial  
349 sorting (Shine et al., 2011). The individuals that have replaced the fast dispersers within eight  
350 years after initial colonisation had about half of the dispersal distance of the pioneer toads  
351 (Lindström et al., 2013), and there was a continuous strong selection against fast dispersal in  
352 these toads (Brown et al., 2007). Dispersal traits are very diverse, and it is no exception that  
353 they are polygenic, although heritability is mostly greater than 0.3 (Ronce, 2007). Conditional  
354 dispersal has been observed (Clobert et al., 2004; Donohue, 1999; Imbert and Ronce, 2001),  
355 but often the relative role of genetic changes and plasticity in changes of dispersal phenotypes  
356 is unclear (Ronce, 2007). We have modelled dispersal as a single gene trait and completely  
357 heritable, in line with particular empirical evidence (Haag et al., 2005; Roff, 1986; Van  
358 Belleghem et al., 2014), to quantify the duration of the genetic signature of range expansion  
359 for a trait for which the variation either needs to migrate or mutate. Control simulations  
360 including more alleles showed qualitatively similar (yet less distinct) patterns and equal  
361 recovery times. If the low dispersive A allele was recessive (Roff, 1986), the AB and BB  
362 genotypes would have the same phenotype of 0.2 dispersal rate. Additionally, the AB  
363 genotype was then expected to be present at low frequencies at the range margin under stable  
364 conditions (Wright, 1969). This may be sufficient to prevent the colonisation lag for the A  
365 allele and in any case likely shortens the period of spatial disequilibrium. Increasing  
366 complexity of genetic architecture to include multiple loci or regulator genes, or including

367 multiple traits might further influence spatial disequilibrium patterns and evolutionary  
368 potential and remains an interesting field of future investigation. The current study shows that  
369 co-dominant heritable genetic variation for low dispersal rates on a single gene can cause a  
370 long period of spatial disequilibrium and loss of evolutionary potential under range shifts due  
371 to spatial sorting.

372

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- 553

554 **Tables**

555

556 Table 1. Model parameters and variables used.

<b>description</b>	<b>value</b>	<b>unit</b>	<b>symbol</b>
recruitment at density = 0 and quality = 1	2.4	offspring/female	$R_{d0q1}$
recruitment at density = 1 and quality = 1	1	offspring/female	$R_{d1q1}$
recruitment at density = 0 and quality = 0	0	offspring/female	$R_{d0q0}$
maximum dispersal distance	15	km	
dispersal probability genotype AA	0.0	year <sup>-1</sup>	
dispersal probability genotype AB	0.1	year <sup>-1</sup>	
dispersal probability genotype BB	0.2	year <sup>-1</sup>	
survival probability at density = 1 and quality = 1	0.6	year <sup>-1</sup>	$S_{d1q1}$
survival probability at density = 0 and quality = 1	0.8	year <sup>-1</sup>	$S_{d0q1}$
survival probability at density = 1 and quality = 0	0.35	year <sup>-1</sup>	$S_{d1q0}$
survival standard deviation	0.15	year <sup>-1</sup>	
mutation rate	10 <sup>-6</sup>	generation <sup>-1</sup>	
number of patches	3000		
patch carrying capacity	20	individuals	$K$
temperature isocline speed	2, 4, 8	km year <sup>-1</sup>	$T$
weather variability	140	km	$\sigma_d$
initial temperature optimum location	400	km from the south edge	$Y_{opt,0}$

557

558



559 Table 2. Model simulations in both experiments, with rates of isocline shift and the periods  
 560 for which they were simulated. For experiment II the total displacements of the climate  
 561 optimum after the period of temperature increase are given.

	<i>experiment I</i>		<i>experiment II</i>
<b>rate of isocline shift</b>	<b>stopped after</b>	<b>stopped after</b>	<b>optimum displacements</b>
2 km year <sup>-1</sup>	500 yrs	50, 100, 200 yrs	100, 200, 400 km
4 km year <sup>-1</sup>	500 yrs	30, 60, 120 yrs	120, 240, 480 km
8 km year <sup>-1</sup>	500 yrs	10, 20, 60 yrs	80, 160, 480 km

562

563

564 **Figure legends**

565

566 Figure 1. The distributions of the 0 (light grey), 0.1 (medium grey), and 0.2 (dark grey)  
567 dispersal rate individuals in time in the landscape under the range shift caused by the  
568 temperature isocline shift rate of  $2 \text{ km year}^{-1}$ , stopped after 500 years. The bold black bars  
569 indicate the spatial locations of the average temperature optimum in the specific years.

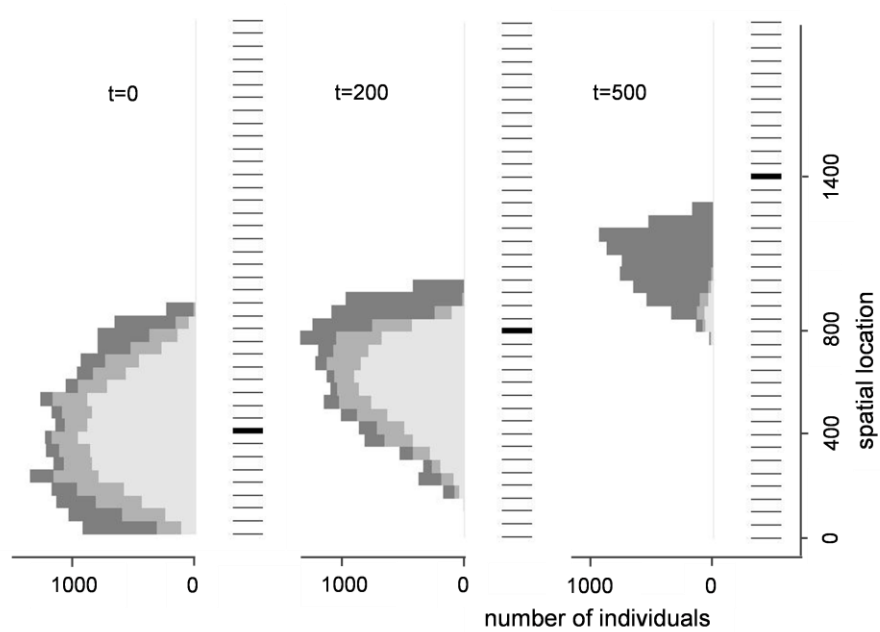
570

571 Figure 2. The distributions of the 0 (light grey), 0.1 (medium grey), and 0.2 (dark grey)  
572 dispersal rate individuals in time in the landscape under the range shift caused by the  
573 temperature isocline shift rate of  $8 \text{ km year}^{-1}$ , stopped after 60 years. The bold black bars  
574 indicate the spatial locations of the average temperature optimum in the specific years.

575

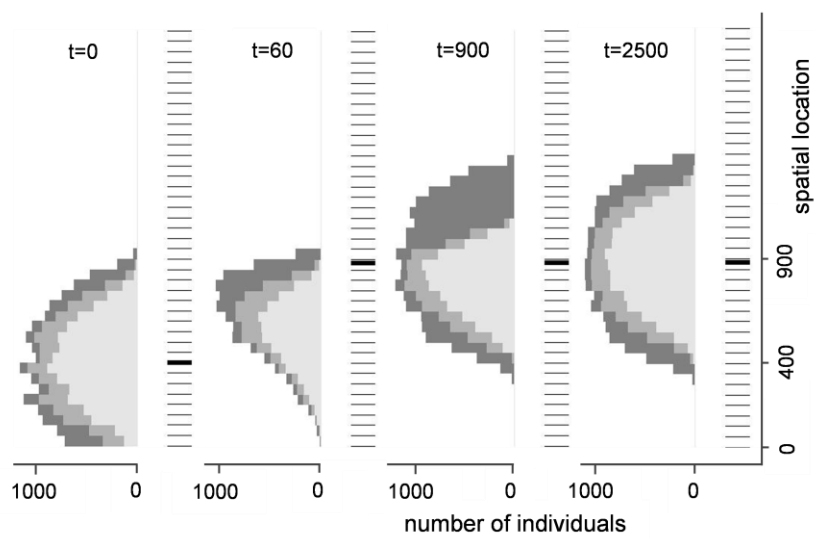
576 Figure 3. The range size deviation of total numbers of individuals in time (deviation I, -●-) and the genotype distribution deviation (deviation II, -○-) in time since the year of  
577 temperature stabilisation for every scenario. The deviations are calculated as the sum of the  
578 absolute differences in numbers of individuals between the equilibrium distribution and the  
579 distribution in each year, per 50 km-block. a. Scenario of  $2 \text{ km year}^{-1}$  isocline shift for 50  
580 years, b. Scenario of  $4 \text{ km year}^{-1}$  isocline shift for 60 years, c. Scenario of  $8 \text{ km year}^{-1}$  isocline  
581 shift for 60 years.  
582

583



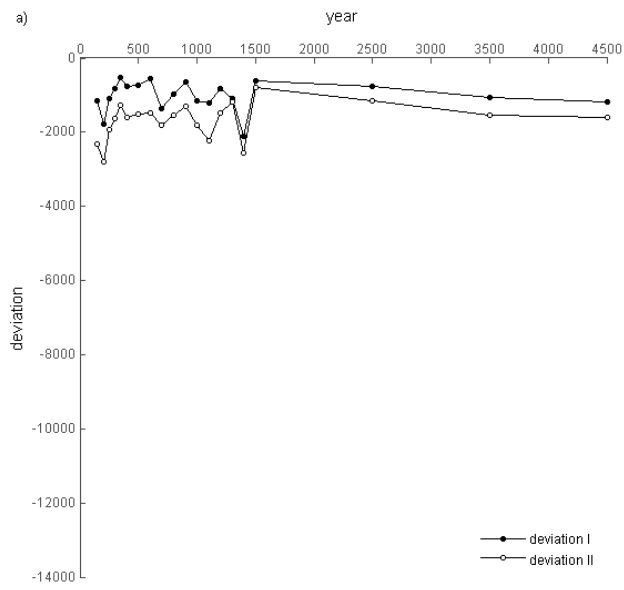
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585 Figure 1



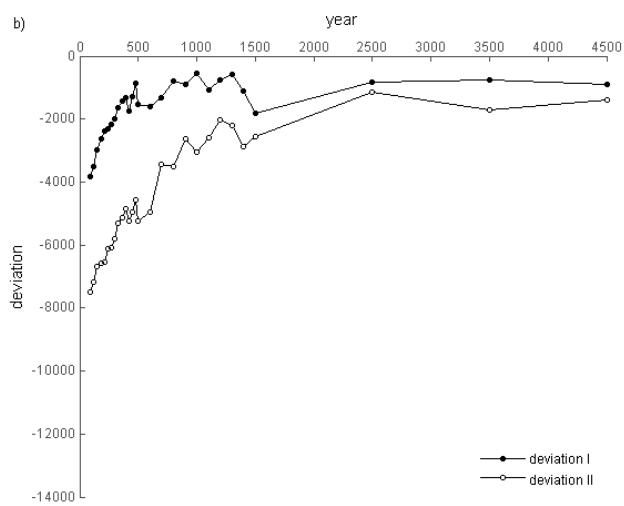
586

587 Figure 2



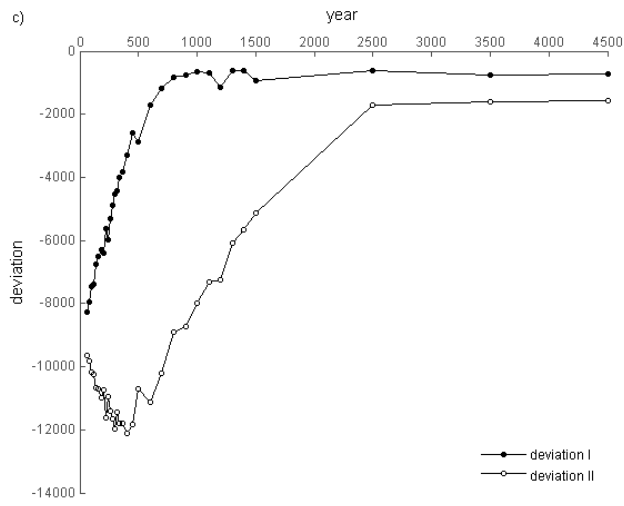
588

589 Figure 3a



590

591 Figure 3b



592

593 Figure 3c

594 **Appendix A**

595

596 We used three temperature increase scenarios, based on work by the (IPCC, 2013), of a  
 597 respective temperature increase  $I$  of 1°C, 2°C and 4°C by the year 2100. When translating  
 598 these scenarios to temperature isocline shift rates, we assumed that the simulated  
 599 metapopulation was situated along the European Atlantic coast. The Hadley Centre (2003)  
 600 predicts no regional differences in change of temperature within this stretch of coast for the  
 601 year 2080. We therefore assumed a similar rate of temperature increase across the simulated  
 602 landscape. Unaffected by mountain ranges, this coast line has a temperature gradient  $G$  of  
 603 0.0042 °C per km (Schippers et al., 2011). The current average standard deviation of the  
 604 average temperature  $\sigma_t$  in this region is 0.59 °C (Schippers et al., 2011). We used the  
 605 temperature gradient to convert the explored temperature increase rates and the yearly  
 606 temperature variability, in °C per year and °C respectively, to geographical distances.  
 607 This leads to the speed with which temperature isoclines travel north ( $T$  km yr<sup>-1</sup>) and the  
 608 yearly fluctuation of these lines ( $\sigma_d$  km), by using:

609 
$$T = I / G, \text{ and}$$

610 
$$\sigma_d = \sigma_t / G$$

611 Following from these, the three temperature increase scenarios resulted in equivalent isocline  
 612 shift rates  $T$  of 2 km yr<sup>-1</sup>, 4 km yr<sup>-1</sup> and 8 km yr<sup>-1</sup> respectively, with a standard deviation of the  
 613 temperature optimum  $\sigma_d$  of 140 km. We then calculate the location of the optimal temperature  
 614 in north-south direction ( $Y_{opt}$ ) in a given year  $t$  as:

615 
$$Y_{opt,t} = Y_{opt,0} + T * t + \sigma_d * N_t$$

616 with  $N_t$  is the yearly random number drawn from a standard normal distribution and  $Y_{opt,0}$  is  
 617 the location of the optimal temperature at  $t = 0$ .

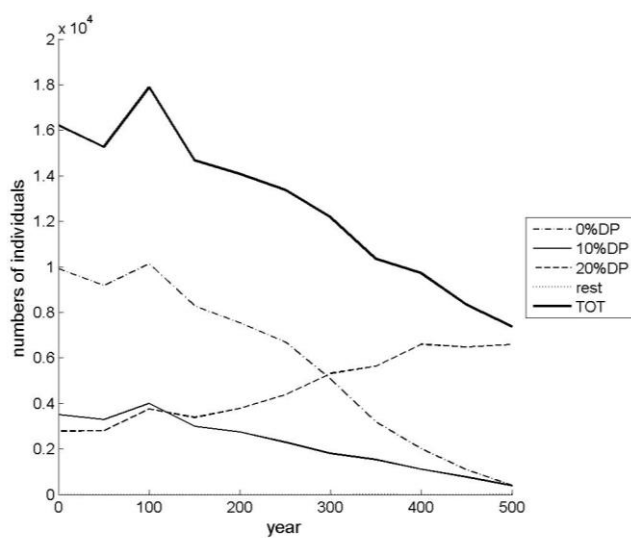
618

## 619 Appendix B

620

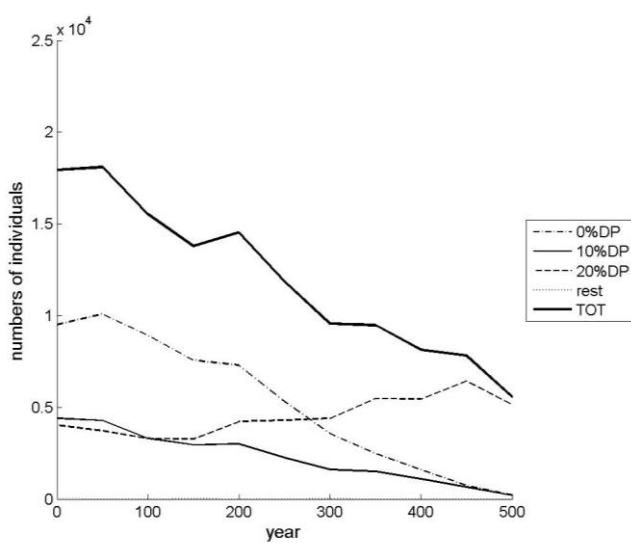
621 Figure S1. The number of individuals with dispersal probabilities of 0 (*0%DP*), 0.1 (*10%DP*),  
 622 and 0.2 (*20%DP*) and the other ( $>0.2$  dispersal rate) individuals (*rest*) and their sum (*TOT*) in  
 623 time under the temperature increase scenario of 2 km/year for standard deviations of the mean  
 624 speed of the shift of the temperature curve of 0 km (a), 140 km (b) and 280 km (c).

625 a)



626

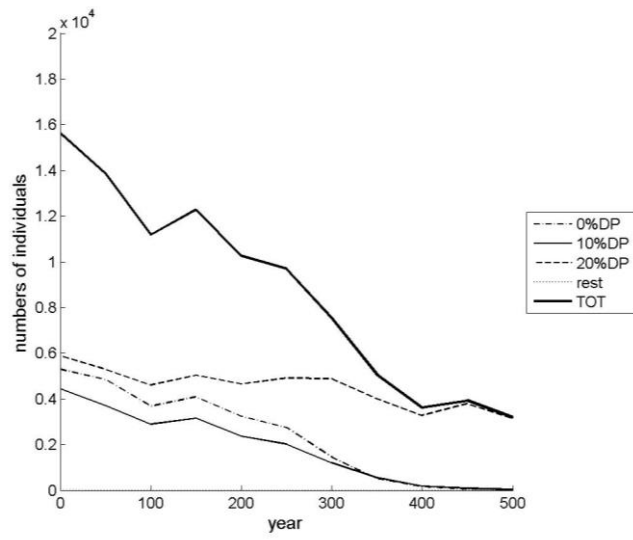
627 b)



628

629

630 c)



631