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Title: Spatio-temporal dynamics of density-dependent dispersal during a population colonisation

Year: 2019

Version: Accepted version (Final draft)

Please cite the original version:

1   **Spatio-temporal dynamics of density-dependent dispersal during a**

2   **population colonisation**

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15   **Running title:** Density-dependent dispersal during a colonisation

16   **Author contributions:** SDB, MB, AEGL, and ALS conceived the study and analyses. SDB

17   and MB performed the analyses, and wrote the manuscript with ALS. DNR and ALS

18   designed and coordinated the guppy introduction experiments. PB coordinated the genetic

19   sampling and the parentage assignments. All authors contributed to the discussion of results

20   and commented on the manuscript.

25   **Article type**: Letters

26   **Number of words in abstract**: 146

27   **Number of words in main text**: 4959

28   **Number of references**: 88

29   **Number of figures, tables and text boxes**: 6

30

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37 **Abstract**

38 Predicting population colonisations requires understanding how spatio-temporal changes in

39 density affect dispersal. Density can inform on fitness prospects, acting as a cue for either

40 habitat quality, or competition over resources. However, when escaping competition, high

41 local density should only increase emigration if lower-density patches are available

42 elsewhere. Few empirical studies on dispersal have considered the effects of density at the

43 local and landscape scale simultaneously. To explore this, we analyze 5 years of individual-

44 based data from an experimental introduction of wild guppies *Poecilia reticulata*. Natal

45 dispersal showed a decrease in local density dependence as density at the landscape level

46 increased. Landscape density did not affect dispersal among adults, but local density-

47 dependent dispersal switched from negative (conspecific attraction) to positive (conspecific

48 avoidance), as the colonisation progressed. This study demonstrates that densities at various

49 scales interact to determine dispersal, and suggests that dispersal trade-offs differ across life

50 stages.

51

Introduction

Dispersal is a fundamental driver of population regulation and distribution across space (Bowler & Benton 2005; Kokko & López-Sepulcre 2006; Clobert *et al.* 2012). The decision to leave a patch can be affected by several factors (Matthysen 2012), and is ultimately the result of balancing fitness costs and benefits. Local competition can be a major driving factor of dispersal, causing individuals to disperse at high local patch densities with decreased per capita resources (positive density-dependent dispersal: Léna *et al.* 1998; Doak 2000; French & Travis 2001; Bitume *et al.* 2013; Weiss-Lehman *et al.* 2017). Alternatively, a high local density may act as a cue to habitat quality, such as low predation risk or optimal environmental conditions, causing individuals to prefer patches with higher densities (negative density-dependent dispersal: Stamps 1988, 1991; Muller *et al.* 1997; Peacor 2003; van Buskirk *et al.* 2011). In some cases, increased conspecific density may itself be a factor conferring fitness advantages, such as dilution of predation risk or favourable social behaviours (Bygott *et al.* 1979; Foster & Treherne 1981; Dehn 1990; Hass & Valenzuela 2002; Bilde *et al.* 2007; McFarland *et al.* 2015). Kinship can further shape dispersal, strengthening positive density-dependent dispersal to avoid kin competition (Hamilton & May 1977). Beyond competition, kinship can also favour dispersal to avoid inbreeding (Wolff *et al.* 1988; Lehmann & Perrin 2003) or discourage it to benefit from cooperation with kin (Lambin *et al.* 2001; Hatchwell 2009).

Dispersal is often costly (Bonte *et al.* 2012). Movement can be energetically demanding, and individuals might fail to find suitable habitats or face mortality during transfer. Ultimately, dispersal will be selected for when the benefits outweigh the costs, and fitness expectations elsewhere exceed those of the current habitat patch. Because of this, the benefit-cost calculation should take into account both the local and the landscape contexts. For example, if resource competition drives dispersal, high local density should only favour dispersal if

77   there are available patches with lower densities. Therefore, dispersal should be driven by the

78   interaction of population density at the local and landscape scales, where landscape density is

79   an indication of habitat saturation. While theoretical studies implicitly consider different

80   spatial scales (e.g. Metz & Gyllenberg 2001; Poethke & Hovestadt 2002), empirical studies

81   rarely consider both scales simultaneously (see Wojan *et al.* 2015 for an exception).

82   Throughout a colonisation, the cost-benefit balance may shift in time, changing the observed

83   patterns of density-dependent dispersal. For example, settlement decisions during the early

84   phases can be facilitated by conspecific attraction because density can be an indicator of

85   habitat quality (Fletcher 2006). As local densities increase further, competition and positive

86   local density-dependent dispersal may become more important, but only insofar as available

87   patches of lower density in the landscape are still available, as argued above. Two other

88   factors can drive trade-off changes in time: ecological succession, and local adaptation.

89   Ecological succession predicts dispersal to increase with patch age, as the probability of

90   extinction through new species colonisations or catastrophic events rises (Ronce *et al.* 2005;

91   Rodrigues 2018). Local adaptation to increasing patch density can also alter the fitness

92   benefits of emigrating. When patch density is high, selection will locally favour life histories

93   that can better cope with competition and resource limitation (Pianka 1970; Mueller *et al.*

94   1991; Bassar *et al.* 2010). As fitness becomes less sensitive to local density (e.g. Bassar *et al.*

95   2013), or even lower at low densities (e.g. Sokolowski *et al.* 1997), the benefit of moving

96   from high to low-density patches may not outweigh the cost of dispersal. Consequently, the

97   incentive to disperse should decrease as individuals adapt to high local densities. The

98   interaction between local adaptation and density-dependent dispersal has been studied in

99   short-term experiments (Meylan *et al.* 2007), but the long-term consequences in natural

100   populations are yet to be evaluated.

101   The study of density-dependent dispersal and its evolution in natural populations is

102   challenging, as it requires a system where samples vary in the degree to which they depart

103   from their equilibrium densities and resource availability. Ideally, one would perturb the

104   densities of populations at equilibrium and monitor the consequences. Alternatively, one can

105   take advantage of natural colonisations or artificial translocations to monitor the spatio-

106   temporal changes in density and dispersal. Such whole-population perturbations have been

107   proposed as powerful systems to study the interaction between ecological and evolutionary

108   processes (Smallegange & Coulson 2013). Here we study changes in density-dependent

109   dispersal following an experimental translocation of guppies *Poecilia reticulata* (Peters,

110   1859) in the Guanapo drainage of the Caribbean island of Trinidad.

111   In their native environment, guppies have repeatedly colonised predator-free reaches,

112   upstream from habitats where predation pressure is high (Alexander *et al.* 2006). The two

113   environments are separated by barrier waterfalls that prevent predators, but not guppies, from

114   dispersing upstream (Reznick *et al.* 2001). When a colonisation event occurs, the release

115   from predation, coupled with a fast life history, causes rapid population growth and high

116   densities (Travis *et al.* 2014). Persistently high population densities trigger the adaptation to

117   resource limitation that favours slower life histories (Reznick *et al.* 2012; Bassar *et al.* 2013).

118   Such colonisation dynamics can be replicated by performing artificial translocations from

119   high- to low-predation sites along the same stream (Reznick *et al.* 1990; Travis *et al.* 2014),

120   allowing for a detailed observation of the evolutionary change in action. The adaptation to

121   high density and resource limitation in terms of growth and reproduction is well characterised

122   (Reznick 1982; Reznick & Endler 1982; Reznick & Bryga 1996; Reznick *et al.* 1996), but the

123   consequences on dispersal remain unstudied. The natural pool-riffle structure in montane

124   streams facilitates the investigation of the interaction between the local and landscape scales.

125   Pools, where most guppies occur, are separated by riffles and represent spatial units (patches)

6

126   where competition over resources occurs. Despite a clear increase in landscape density after

127   introduction, pools vary largely in density in time and space (Figure 1). This allows us to

128   disentangle the ecological effect of density from the long-term trend as the population adapts

129   to higher average densities.

130   Our study aims to answer two questions: (1) how does the interaction between local and

131   landscape density shape dispersal?, and (2) do we observe temporal changes in dispersal and

132   its response to density as the colonisation progresses? Because the effects of competition in

133   guppies are age specific (Bassar *et al.* 2013, 2016), we will distinguish between natal (or

134   juvenile) dispersal and adult (or breeding) dispersal. Natal dispersal is classically defined as a

135   movement between the birth site and the location at first reproduction. Adult dispersal occurs

136   between successive reproductive events (Greenwood & Harvey 1982; Matthysen 2012).

137   If dispersal is driven by resource competition, we predict it to be positively affected by local

138   density at low landscape densities, when unsaturated pools are available. If kin competition

139   plays a role, this pattern should be stronger at higher within-pool relatedness. As densities

140   increase across the landscape and resource limitation becomes widespread, the importance of

141   local density-dependent dispersal should decrease, due to the paucity of alternative low-

142   density habitats. This decline should be reflected in a negative interaction between local and

143   landscape density on dispersal. Alternatively, if density acts as a cue to habitat quality, or

144   individual aggregation is beneficial, we expect a decrease of dispersal with local density.

145   Again, kinship could strengthen the pattern if there is kin cooperation.

146   We also expect that these factors will change as the colonisation progresses. In particular, we

147   predict that negative density-dependent dispersal will characterize the beginning of the

148   colonisation for two reasons: conspecific presence may be the most reliable cue for habitat

149   quality in novel environments (Fletcher 2006), and the introduced guppies, adapted to high

150 predation, may have a predisposition to find safety in numbers (Seghers 1974; Huizinga *et al.*

151 2009). As the colonisation progresses, we expect competitive dynamics to become more

152 important (Bassar *et al.* 2012), and positive density dependence to emerge; a pattern that

153 should disappear at high landscape densities (due to habitat saturation), and may be

154 attenuated with time, as populations adapt to higher local densities.

155 **Methods**

156 *Study system*

157 This study takes place in headwater streams of the Northern Mountain Range, in the

158 Caribbean island of Trinidad (Trinidad and Tobago, W.I.). We transplanted guppies from a

159 high-predation site in the Guanapo river to a low-predation site upstream, in a tributary

160 stream known as Lower La Laja, in March 2008. This translocation is part of a wider

161 experiment described elsewhere (Lopez-Sepulcre *et al.* 2013; Travis *et al.* 2014). The

162 destination site was guppy-free, killifish *Anablepsoides hartii* (Boulenger, 1890; syn. *Rivulus*

163 *hartii*) being the only fish present prior to introduction. We introduced 38 females and 38

164 males in a section of the stream delimited by two waterfalls. The upstream waterfall was

165 reinforced to prevent upstream movement. Individuals could move downstream, but never

166 back up the bottom waterfall. We split individuals at equal sex ratios into two pools: one

167 located below the upstream waterfall, and one 37 meters downstream.

168 The study stream is naturally subdivided into riffle-delimited pools, defining clear habitat

169 patches. Guppies are found at much lower densities in riffles, where water flows faster

170 preventing organic deposition. In our study stream, pools represent between 44% and 70% of

171 the total benthic area, and contained on average 90% of the captured individuals (ranging

172 between 67% and 100%). For the purpose of this study, we exclude the few guppies found in

173 riffles. Pools are subdivided into microhabitats, among which guppies move freely: fast

174 moving inflow and outflow, a central area of slow, deep water, with deposition of organic

175 matter, and often a marginal area of sandy, shallow water. These microhabitats are

176 represented in varying proportions in each pool.

177 *Individual-based Data*

178 The introduced population has been monitored monthly since introduction, using a capture-

179 mark-recapture design. Every month, individuals over 14 mm are captured using hand nets,

180 and moved in sex- and location-specific containers to a field laboratory for processing. To

181 record individual location, a tape meter is drawn from the top (0 m) to the bottom barrier

182 waterfall (100 m), using reference landscape marks to ensure a consistent placement over

183 consecutive months. With this standardization, variation in the position assigned to the

184 bottom waterfall is lower than ± 1m. Before each capture session, the stream is divided into

185 fishing units defined as a continuous habitat section based on hydromorphology (pool or

186 riffle) and position along the stream. For each fishing unit, the upstream and downstream

187 meter markers are noted.

188 After capture, new recruits are marked in the field laboratory with a unique combination of

189 subcutaneous visible elastomer implants (Northwest Marine Technology, Inc), to allow

190 identification in future captures. Marking is performed under anesthesia with MS-222. Three

191 scales are sampled for subsequent DNA extraction and parentage assignment. Sex and

192 maturation stage are determined based on colouration and anal fin morphology. Individuals

193 are released back to the precise location of capture.

194 Parentage was determined using 43 microsatellite loci amplified from the DNA extracted

195 from the sampled scales and methods including MEGASAT software as described by Zhan

196 and colleagues (2017). We used a full likelihood method using COLONY V., where all

197 individuals (dead or alive) were included as potential parents. Because parentage assignments

198   are only available from March 2008 to February 2014, our analyses are limited to this time

199   period.

Dispersal traits and density

201   We determined individual position each month as the midpoint of the pool it was caught in

202   (i.e. the average of its upstream and downstream bounds). Due to the small inconsistencies in

203   tape measure placement, and the fact that stream morphology (e.g. pool sizes) changes

204   slightly over time, we considered as a dispersal event any change in position larger than half

205   the total length of the pool of origin. This distance threshold corresponds to the minimum

206   distance to be travelled in order to leave a pool and enter a different habitat patch. To

207   estimate natal dispersal, we compared the position at first capture of a new recruit to its

208   mother's position two months before. Given that new recruits are approximately two months

209   old, the latter should approximate the position at birth. To ensure accurate approximation of

210   the birthplace by accounting for the uncertainty around the time of birth, we considered natal

211   dispersal only for those individuals whose mother was found in the same pool the two months

212   preceding the individual's first capture. As with adult dispersal, we considered as a natal

213   dispersal event only a change in position that exceed half the total length of the pool of birth.

214   We defined landscape density as the total number of individuals captured in the whole stream

215   in a given month, divided by the total length of the stream (100m), which was constant.

216   Previous capture-mark-recapture analysis shows that the capture probability in pools is high

217   and stable (approximately 90%, unpublished data), justifying the number of captured

218   individuals was a good proxy for population size for the purposes of this study. Local density

219   was calculated monthly for every pool that contained at least one individual, as the number of

220   guppies captured in that pool divided by the length of the pool. Both measures of density

221   were calculate as individuals/m, which is highly correlated with more detailed estimates

222 of individuals per benthic area (unpublished data). The high degree of variation in local pool

223 density, reached early into the colonisation and maintained throughout the rest of the study

224 years (see Results) allowed us to make inferences regarding the change in density-dependent

225 dispersal patterns.

226 *Kinship*

227 We calculated kinship among all captured individuals using the pedigree data. The methods

228 are detailed in the Supplementary Information. For any given individual, we defined local

229 kinship as the average kinship between the focal individual and all individuals sharing the

230 same pool in a given month. To represent the kin-related incentive to disperse or stay, we

231 calculated kinship differential as the difference between local kinship and the average kinship

232 between the focal individual and all other individuals present in the stream that month,

233 excluding those in the same pool. Kinship differential is therefore an individual-based

234 variable that changes monthly. It assumes positive values when more kin are present locally

235 than at the whole-stream level, and negative values otherwise.

236 *Statistical analyses*

237 We analyzed two response traits describing dispersal: natal dispersal probability (for first

238 recruits) and adult dispersal probability (for recaptured individuals). For each of these traits

239 we fitted a generalized linear mixed effect model (GLMM) where dispersal events are

240 assumed to follow a binomial distribution with a logit link. We fitted separate models for

241 males and females. The explanatory variables we included are: local density, landscape

242 density (in individuals/m), time (in months), and all two- and three-way interactions between

243 them, as fixed effects. We also included kinship differential, as well its interaction with local

244 density.

245   To improve convergence, we centered and scaled local and landscape density measures, and

246   only scaled (not centered) time and kinship pressure, to keep the origin at time 0 and a neutral

247   kinship differential, which improves interpretability. Therefore, in each model the intercept

248   refers to the estimate at time zero, null kinship pressure, average local density and average

249   landscape density. We ruled out multicollinearity problems, which can cause underestimation

250   of significance, by evaluating pairwise Pearson's correlation coefficients among all

251   explanatory variables (Zuur *et al.* 2010).

252   We interpret the effect of local density as the strength of density-dependent dispersal, which

253   will be positive if competition drives dispersal. A significant negative interaction between

254   local and landscape density would imply that positive local density-dependent dispersal is

255   modulated by landscape saturation. An interaction between local density and time reflects a

256   long-term change in the strength of local density dependence that is independent of landscape

257   density. Finally, a significant positive interaction between local density and kinship pressure

258   would suggest kin competition.

259   We included sampling month as a random effect to account for changes in environmental

260   effects shared among pools, as well as the interaction between sampling month and local

261   density to account for random variation in the strength of local density dependence. To

262   account for unmeasured spatial variation in habitat quality we included a random effect for

263   stream segment (see Supporting Information for details on segment definition). To account

264   for repeated measures, we also included as random effects individual identity for adult

265   dispersal, and mother identity for natal dispersal. On average, each mother produced 1.31

266   recruits (ranging from 1 to 9), and with the average range in pool density experienced by a

267   mother being a 3.32-fold difference (ranging from 1X to 231X). When analysing adult

268   dispersal we used local density at the pool of origin as a measure of the experienced local

269   competition over resources. For the analyses of natal dispersal we used instead the local

270   density of the estimated birthplace (i.e. the individual's mother's location two months before

271   the first capture of the individual) one month before the individual's first capture. This was

272   done to account for the effects of density one month before the movement was observed,

273   consistently with what done for adult dispersal.

274   We reduced the models by removing any interaction or main effect that was not significant at

275   the 0.10 level, as determined by a Likelihood Ratio Test. Two-way interactions and main

276   effects were removed sequentially in order of significance.

277   To quantify the difference in dispersal propensity between males and females, we fit a

278   GLMMs that included all individuals, sex as the only explanatory factor, and the same

279   random structure specified above.

280   We conducted all analyses in R (version 3.5.1, R Development Core Team, Vienna, Austria)

281   using the package `lme4` (Bates *et al.* 2015) to fit all models.

282   **Results**

283   *Spatiotemporal Variation in Density*

284   The Pearson's correlation coefficient among any two variables was below 0.11 in all cases

285   except between landscape density and time, when it was 0.57 (Figure S1, Supplementary

286   Information).

287   Landscape population density increased from 0.76 to 11.04 individuals/m in the first 2.5

288   years, followed by a decrease in the remaining 30 months to an average 7.91 individuals/m

289   (Figure 1a). This non-linear increase in landscape density means that population density and

290   time are not perfectly correlated, allowing us to tease apart their effects (see above). Local

291   pool densities ranged from 0.05 to 69 individuals/m in occupied pools throughout the five

292   years. A wide range of local densities appeared in occupied pools already within the first year

293 (from 0.13 to 29 individuals/m), while landscape density remained low, reflecting the

294 abundance of unoccupied pools. By month 20 the full range of local densities was

295 represented, and remained so thereafter (Figure 1b).

Natal dispersal

297 The best fit model for female natal dispersal probability included all two- and three-way

298 interactions between local density, landscape density and time, along with their main effects,

299 but did not include kinship nor its interaction with local density (Table 1). The model without

300 the three-way interaction had a significantly lower fit compared to the full model (Table S1,

301 Supporting Information). For males, the best fit model only included local density, landscape

302 density and their interaction (Table S2, Supporting Information). There is no overall effect of

303 time on average dispersal rates in either sex (Table 1, Figure 2a).

304 During the first part of the colonisation, landscape density modulates the effect of local

305 density on natal dispersal probability, as suggested by the significant negative interaction

306 between local and landscape density (Table 1). In particular, when landscape density is low,

307 high local densities increase the probability of dispersal (positive local density dependence).

308 For example, six months after introduction, and with a landscape density of 1.62

309 individuals/m, the estimated slope of local density dependence for females (see Supporting

310 Information for details on its calculation) was 0.83 [0.28 – 1.37] (Figure 3a). This means that

311 a fourfold increase in local density (from 5 to 20 individuals/m) causes the estimated natal

312 dispersal propensity to more than double, on average (from 29% to 63%). As landscape

313 density increases, the strength of local density dependence decreases and natal dispersal

314 probability ceases to be affected by local density when the habitat is saturated. For observed

315 values of landscape density higher than 4.81 individuals/m for females and 7.29

316 individuals/m for males, the predicted estimated slope of local density dependence is not

317 significantly different from 0 (Figure 3a,c). In addition, the positive and significant three-way

318 interaction between local density, landscape density and time in females indicates a decrease

319 in the negative effect of landscape density on local density-dependent dispersal. Overall, the

320 effect of landscape density on the strength of density dependence implies that: (1) the

321 strength of local density dependence is positive and strong when landscape density is low and

322 there are available alternatives to disperse to (Figure 3). (2) The strength of local density

323 dependence decreases as landscape density increases and habitats get saturated (Figure 3). (3)

324 For females, but not males, the effect of landscape density over local density dependence

325 decreases with time (Figure 3b).

326 *Adult dispersal*

327 Overall, males are on average more likely to disperse than females (GLMM effect size = 1.59

328 ± 0.04, p-value < 0.001; Figure 2b). Otherwise, the results on the factors affecting adult

329 dispersal were consistent between the two sexes, so we will discuss them together.

330 For both sexes, the best fit model for the probability of adult dispersal included the main

331 effects of local density, time and kinship, as well as the interactions between local density

332 and time, and between local density and kinship (Table 2; Table S3-S4, Supporting

333 Information). Contrary to natal dispersal, these results present no evidence for an effect of

334 landscape density on dispersal probability nor its sensitivity to the strength of local density

335 (Figure 4). Overall estimates of adult dispersal probability at average values of local density

336 show no time effect (Figure 2b), but the strength of local density dependence does. At the

337 time of introduction, adult females were less likely to disperse away from pools with high

338 local densities (negative density dependence, Figure 3d), as suggested by the negative

339 marginally significant effect of local density in the model (Table 2). Males show a similar yet

340 non-significant trend (Table 2, Figure 4d).

341 A significant positive interaction between local density and time (in both females and males)

342 indicates that the initially negative density-dependent dispersal shifted towards positive

343 density-dependent dispersal as the colonisation progresses. For the first half of the study

344 period, adults were more likely to disperse away from low-density pools; while in the second

345 half, adults were more likely to disperse if pool density was high. At the time of introduction

346 the slope of local density dependence estimated by the model (see Supporting Information), is

347 -0.39 [-0.77 – -0.01] for females (Figure 4b). This means that an increase in local density

348 from 5 to 25 individuals/m causes the estimated probability of female dispersal to drop by

349 half, on average (from 35% to 18%). In contrast, after 5 years, the same increase in density

350 causes the expected dispersal probability to double (from 26% to 53%), with a slope of 0.48

351 [0.15 – 0.82] (Figure 4b). Males show a similar pattern. Their dispersal probability also

352 becomes positively density-dependent by the end of the study period, with a slope of 0.36

353 [0.17 – 0.56] (Figure 4d). These results indicate that guppies have shifted their behaviour

354 from conspecific attraction to avoidance of crowded conditions.

355 Contrary to expectation, kinship differential has a negative effect on dispersal probability and

356 a negative interaction with local density, in both males and females. This is inconsistent with

357 theories of kin avoidance and kin competition, and may indicate some kind of kin facilitation.

358 Notwithstanding, kinship effects are substantially smaller than density effects (especially in

359 females), suggesting that the role of kinship is secondary to density.

360 **Discussion**

361 Our results show clear differences in the way density shapes natal versus adult dispersal in

362 the studied population. Natal dispersal is strongly influenced by density, both at the local and

363 landscape level, indicating that juvenile guppies are susceptible to competition over limiting

364 resources. For adults we found no effects of landscape density, but rather a change in local

16

365 density-dependent dispersal throughout the colonisation, from negative to positive, which can

366 have important effects on the spatial ecology of the population.

367 The pattern shown by natal dispersal is consistent with the competition avoidance hypothesis.

368 When landscape density is low, and availability of alternative pools is high, juvenile guppies

369 are more likely to disperse away from crowded pools: i.e. positive density-dependent

370 dispersal is stronger (Figure 3a,c). Competition might be particularly important in juveniles

371 for several factors. First, juvenile fish have high energetic requirements due to their fast

372 growth, and likely require a higher quality diet than adults. Gut content analyses show that

373 smaller (and therefore younger) guppies consume more invertebrates and algae, and less

374 detritus compared to larger ones (Zandonà *et al.* 2011, 2015). Moreover, jaw development

375 can constrain diet and limit the competitive performance of newborn fish (Dial *et al.* 2017).

376 Second, juveniles may be susceptible to cannibalistic behaviour by adults (Loekle *et al.* 1982;

377 Magurran & Seghers 1990; Magurran 2005), which can become important in resource-

378 limited, crowded environments. The occurrence of cannibalistic behaviour is yet to be

379 confirmed in the wild, but is well documented in the laboratory (Magurran & Seghers 1990).

380 As landscape density increases and habitats get saturated, the effect of local density on natal

381 dispersal decreases. At peak landscape density the estimated slope of local density

382 dependence approaches zero, making dispersal density-independent (Figure 3a,c). This

383 finding is in accordance with our initial predictions: dispersal can be an advantageous

384 strategy to escape resource limitation (Ronce 2007), but this is only true when lower density

385 patches are available elsewhere, and fitness prospects increase. Our finding stresses the

386 importance of accounting for different spatial scales, which seldom happens in dispersal

387 studies (cf. Wojan *et al.* 2015).

Dispersal studies, especially in vertebrates, often focus on natal dispersal (e.g. Matthysen 2005; Støen *et al.* 2006; Meylan *et al.* 2007; Wojan *et al.* 2015). Natal dispersal is thought to be predominant and extensive (Greenwood & Harvey 1982), and to have a big impact on fitness and population dynamics (Matthysen 2012), but this observation may reflect the bias towards studies of birds and mammals. We chose to study both adult and natal dispersal and found them to differ profoundly in the way they are shaped by density conditions. Contrary to natal dispersal, we observed no effect of landscape density on adult dispersal, but rather a change in density-dependent dispersal with time that was independent of landscape density (Figure 4b,d). Specifically, adults show a continuous trend from negative to positive density-dependent dispersal (i.e. from lower to higher dispersal at high densities).

The initial negative density-dependent dispersal of adults could be reflective of the schooling behaviour characteristic of the high-predation guppies introduced (Seghers 1974). Aggregation is an effective antipredatory strategy in predator-rich communities (Magurran 1990; Magurran *et al.* 1993), has a genetic basis (Seghers & Magurran 1991), and is lost when guppies are transplanted from high- to low-predation environments (Magurran *et al.* 1992). The initial conspecific attraction could also be due to guppies using density as a cue for habitat quality in an unfamiliar environment (Fletcher 2006). For a high-predation adapted guppy, high conspecific density might be a good indicator of a lack of predators.

As the colonisation of the low-predation environment progresses, conspecific attraction disappears and avoidance emerges. When guppies colonise low-predation habitats from areas of high predator-induced mortality, local densities increase rapidly, resulting in resource limitation (Travis *et al.* 2014). Positive density-dependent dispersal can be an effective way to escape local competition (Waser 1985; Bowler & Benton 2005; Ronce 2007), and here we observe its emergence in adults as the population increases. A number of studies corroborate the prevalence of density-dependent dispersal in a variety of species (Fonseca & Hart 1996;

413   Léna *et al.* 1998; Støen *et al.* 2006; Meylan *et al.* 2007; De Meester & Bonte 2010; Bitume *et*

414   *al.* 2013; Fronhofer *et al.* 2015; Wojan *et al.* 2015), and its rapid evolution in experimental

415   setups (Fronhofer & Altermatt 2015; Weiss-Lehman *et al.* 2017).

416   An unexpected result in our study was the negative effect of kinship on adult dispersal.

417   Guppies were less likely to leave pools shared with a high number of kin: the opposite is

418   predicted by inbreeding or kin competition avoidance (Hamilton & May 1977; Comins *et al.*

419   1980; Taylor 1988; Motro 1991). It is unclear whether this result is a mere consequence of

420   individuals in successful patches being unlikely to disperse and, therefore, more likely to be

421   highly related; or if it indicates some benefit of living with kin. We found no effect of kinship

422   on natal dispersal.

423   Both adult and natal dispersal showed changes in their patterns with time. Models of

424   ecological succession predict dispersal to increase with patch age regardless of density, due to

425   increased extinction risk from disturbance and interspecific competition (Ronce *et al.* 2005;

426   Rodrigues 2018). Given the short time scale of the experiment and the fact that low-predation

427   streams in Trinidad have very few species of fish, this is unlikely to be the case. Instead, the

428   pattern observed is consistent with density being a changing indicator of fitness prospects, be

429   it patch quality or resource competition, depending on the stage of colonisation. Whether the

430   changes in dispersal represent an evolutionary change or a plastic response remains to be

431   evaluated, and will require common garden experiments.

432   Individual movement is a key trait determining the spatial arrangement of populations

433   (Bowler & Benton 2005; Kokko & López-Sepulcre 2006; Clobert *et al.* 2012). Therefore, the

434   study of dispersal and its evolution is crucial to understand and predict range expansions

435   (Burton *et al.* 2010; Fronhofer & Altermatt 2015; Kubisch *et al.* 2016; Weiss-Lehman *et al.*

436   2017) and the spread of invasives (Kot *et al.* 1996; Travis & Dytham 2002; Arim *et al.* 2006;

437 Phillips *et al.* 2006, 2008; Starrfelt & Kokko 2008). This study suggests that dispersal can

438 change rapidly and substantially as organisms adapt to novel conditions. This result

439 highlights the importance of considering contemporary adaptation in our understanding of

440 species range shifts in the face of environmental change (Kokko & López-Sepulcre 2006).

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652

653 **Table 1**. GLMM for natal dispersal probability. Residual variance and the percentage of variance

654 explained by the random effects were calculated according to Nakagawa & Schielzeth (2010).

|	Females (N = 1352)		Males (N = 1150)	
Random effects	**Variance (%)**	**N Group**	**Variance (%)**	**N Group**
Mother ID	0.48 (11%)	658	0.38 (8%)	599
Sampling (intercept)	0.49 (11%)	58	0.18 (4%)	58
Sampling (Local density)	0.03 (1%)		0.00 (0%)	
Section	0.16 (4%)	23	0.84 (18%)	25
Residual	3.29 (73%)		3.29 (70%)	
Fixed effects	**Estimate (SE)**	**p–value**	**Estimate (SE)**	**p–value**
(Intercept)	- 0.098 (0.425)	0.818	- 0.176 (0.260)	0.499
Local density	0.309 (0.182)	0.090 .	0.211 (0.085)	0.013 *
Landscape density	0.477 (0.323)	0.140	0.386 (0.145)	0.008 **
Time	0.345 (0.401)	0.389	-	-
Local density × Landscape density	- 0.431 (0.180)	0.017 *	- 0.251 (0.079)	0.001 **
Local density × Time	-0.402 (0.244)	0.100	-	-
Landscape density × Time	-0.575 (0.490)	0.240	-	-
Local density × Landscape density × Time	0.524 (0.248)	0.032 *	-	-

655

656   **Table 2**. GLMM for adult dispersal probability. Residual variance and the percentage of variance

657   explained by the random effects were calculated according to Nakagawa & Schielzeth (2010).

|	Females	(N = 18754)	Males	(N = 7588)
Random effects	**Variance (%)**	**N Group**	**Variance (%)**	**N Group**
Individual	0.80 (11%)	2728	0.37 (8%)	2256
Sampling (intercept)	0.60 (11%)	59	0.31 (7%)	59
Sampling (Local density)	0.34 (1%)		0.05 (1%)	
Section	0.49 (4%)	31	0.44 (10%)	30
Residual	3.29 (73%)		3.29 (74%)	
Fixed effects	**Estimate (SE)**	**p–value**	**Estimate (SE)**	**p-value**
(Intercept)	- 0.727 (0.279)	0.009 **	0.812 (0.236)	< 0.001 ***
Local density	- 0.386 (0.194)	0.046 *	- 0.148 (0.102)	0.150
Time	- 0.103 (0.251)	0.683	- 0.112 (0.198)	0.573
Kinship	- 0.095 (0.026)	< 0.001 ***	- 0.204 (0.041)	< 0.001 ***
Local density × Time	0.551 (0.202)	0.006 **	0.324 (0.112)	0.004 **
Local density × Kinship	-0.073 (0.024)	0.003 **	- 0.174 (0.035)	< 0.001 ***

658

659   **Figure 1.**(a) Landscape population density over time. (b) Range of local densities in occupied

660   pools observed over time, in logarithmic scale. The solid line represents the average local

661   density of occupied pools, the dashed line the 95% upper and lower quantiles, the dotted line

662   the maximum and minimum local density observed.
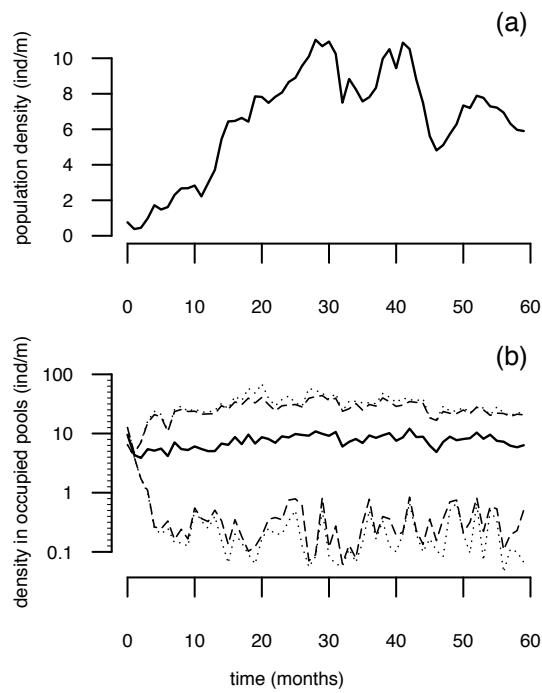

663

664

665   **Figure 2**. (a) Natal and (b) adult dispersal propensity over time. The connected circles and

666   bars represent the observed dispersal probability at each month, +/- standard error. Empty

667   circles correpons to females, filled circles to males.
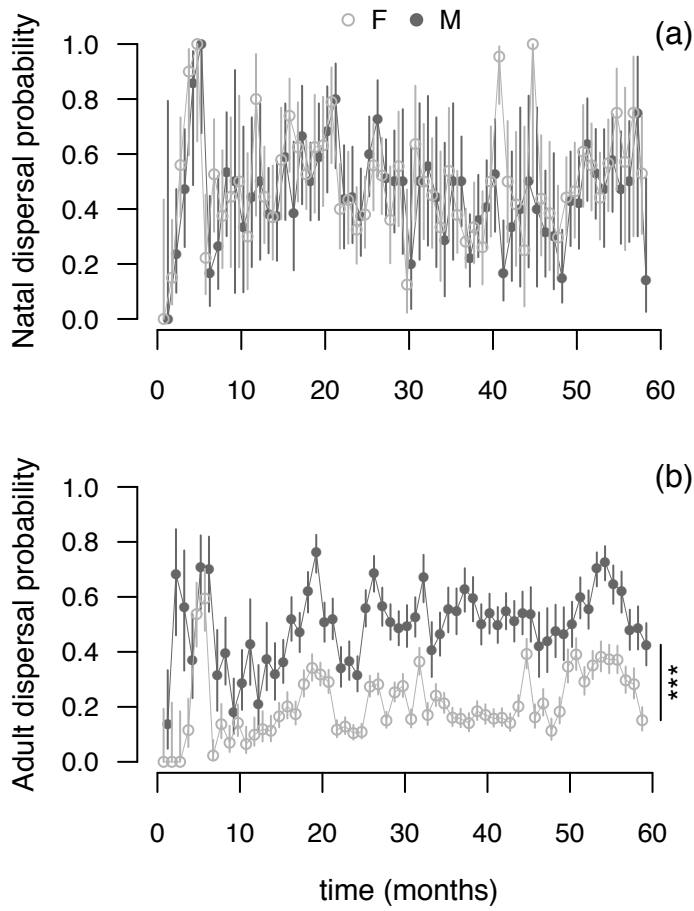

668

669

670 **Figure 3**. Determinants of the strength of local density-dependence for natal dispersal,

671 calculated as the slope of the logit relationship between natal dispersal probability and local

672 density. (a, c) Strength of density-dependence against landscape density for females and

673 males. Dots indicate the estimated slope (i.e. strength) of local density dependence at

674 observed combinations of landscape density and time. Bars indicate the 95% Monte Carlo

675 prediction intervals. (b, d) Change in the strength of natal density-dependent dispersal with

676 time, in females and males. The black line represents the slope of density dependence at fixed

677 landscape density of 6.51 individuals/m, corresponding to the average landscape density

678 during the five years. In males (d) the slope of local density dependence is independent of

679 time (see Results). Grey shaded areas represent 95% prediction intervals generated with a

680 Monte Carlo simulation.

681

682

34
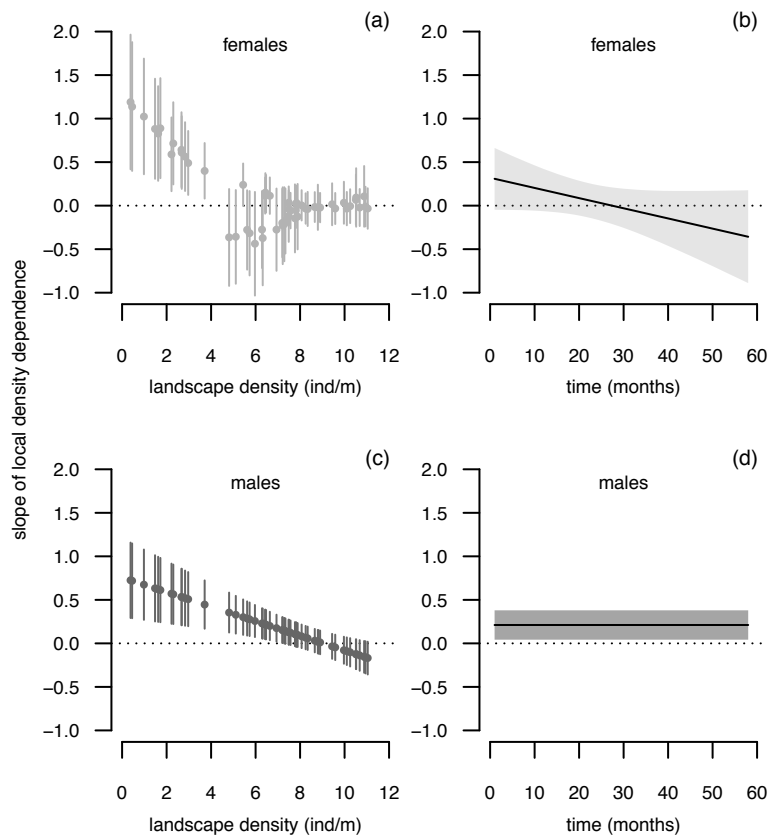
683 **Figure 4**. Determinants of the strength of local density-dependence for adult dispersal,

684 calculated as the slope of the logit relationship between adult dispersal probability and local

685 density. (a, c) Strength of density dependence against landscape density for females and

686 males. Dots indicate the estimated slope (i.e. strength) of local density dependence at

687 observed combinations of landscape density and time. Bars indicate the 95% Monte Carlo

688 prediction intervals. Change in the strength of adult density-dependent dispersal with time, in

689 females (b) and males (d). The black line represents the predicted slope of density

690 dependence (see Results). Grey shaded areas represent 95% prediction intervals generated

691 with a Monte Carlo simulation.
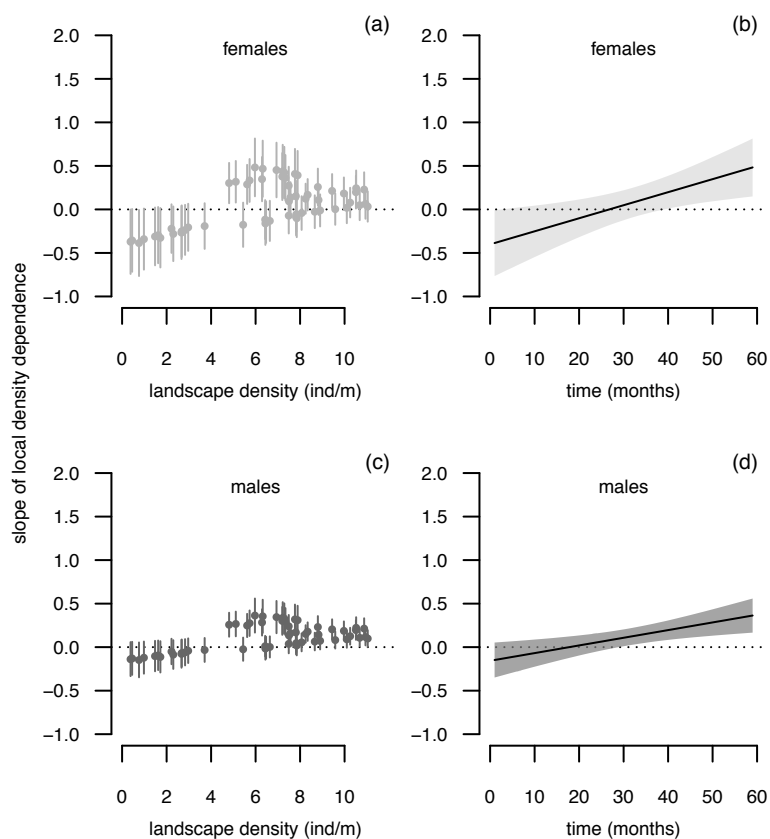
692

Supplementary Information

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Contents

APPENDIX 1

Calculation of the Slope of Density Dependence

We calculated the strength (slope) of local density dependence for a given dispersal trait from the fixed effect parameter estimates, of the final GLMM model fit. For a full model including the main effect of local density ld, landscape density LD and time t, and all two and three way interactions on a trait y, the predicted value of y is:

$$E(y) = \alpha + \beta_{ld} \cdot ld + \beta_{LD} \cdot LD + \beta_t \cdot t + \beta_k \cdot k + \beta_{ld:LD} \cdot ld \cdot LD +$$
$$\beta_{ld:t} \cdot ld \cdot t + \beta_{ld:k} \cdot ld \cdot k + \beta_{LD:t} \cdot LD \cdot t + \beta_{ld:LD:t} \cdot ld \cdot LD \cdot t \tag{Eq. 1.1}$$

where β_i represents the estimated effect of the covariate i, $\beta_{i:j}$ represents the estimated effect of the interaction between i and j, and α represents the intercept.

This equation can be reorganised as:

$$E(y) = (\alpha + \beta_{LD} \cdot LD + \beta_t \cdot t + \beta_k \cdot k + \beta_{LD:t} \cdot LD \cdot t) +$$
$$(\beta_{ld} + \beta_{ld:LD} \cdot LD + \beta_{ld:t} \cdot t + \beta_{ld:k} \cdot k + \beta_{ld:LD:t} \cdot LD \cdot t) \cdot ld$$

or

$$E(y) = A + B \cdot ld \tag{Eq. 1.2}$$

where:

$$A = \alpha + \beta_{LD} \cdot LD + \beta_t \cdot t + \beta_k \cdot k + \beta_{LD:t} \cdot LD \cdot t \tag{Eq. 1.3}$$

is the intercept of local density dependence and

$$B = \beta_{ld} + \beta_{ld:LD} \cdot LD + \beta_{ld:t} \cdot t + \beta_{ld:k} \cdot k + \beta_{ld:LD:t} \cdot LD \cdot t \tag{Eq. 1.4}$$

is the slope of local density dependence. If the final fitted model is not the full model, the betas corresponding to parameters which are not estimated are set to 0. To estimate an error around the slope of density dependence we used Monte Carlo simulations. We drew 100,000 sets of values for all β from a multivariate normal distribution with the point estimates as mean values for each beta and the variance-covariance matrix extracted from the model. We then calculated 100,000 slopes using the equation 1.4, and calculated the 95% central quantiles. This corresponds to the 95% prediction intervals drawn in Figure 3 and 4 as bars (a,c) and shaded areas (b,d).

APPENDIX 2

Determination of Stream Segments

Given the constant natural restructuring of the stream morphology, it is challenging to track a pool through time, since this appears more or less modified at at each monthly observation. Pools can change slightly in size and location due to hydrological and debris dynamics; new small pools can be formed, others dry out or transform into riffles; two separate pools can merge together or be created by the split of a larger pool (e.g. as a consequence of a treefall in the stream bed). In order to account for habitat quality in a way which would be consistent through the observation time, we tracked each pool through time by assigning to it a unique identifier. We established the following rules to determine whether a pool maintained the same identifier from one month to the next:

- A pool maintained the same identifier if it shifted upstream, downstream or changed in length by maintaining at least an overlap adding up to half the original length of the pool.
- Two pools were given the same identifier if they originated from a larger pool that had been split or if they merged into a larger pool at any later point during our observation time.
- A newly originated pool, which had no obvious precursor during previous month, received a new identifier.

APPENDIX 3

Model Selection Tables

The following tables summarise the likelihood ratio tests (LRT) used for the selection of the best model. The χ^2 and p-values refer to the LRT performed between a model and the previous, containing one more term. LD = Landscape density, ld = local density, t = time, kin = kinship. Crosses indicate the presence of that term in the model.

Table S1: Natal dispersal probability (females)

ld	LD	t	kin	ld:LD	ld:t	LD:t	ld:kin	ld:LD:t	Df	logLik	AIC	χ^2	p-value
+	+	+	+	+	+	+	+	+	15	-897.66	1825.33		
+	+	+	+	+	+	+		+	14	-898.15	1824.31	0.981	0.322
+	+	+		+	+	+		+	13	-898.19	1822.39	0.077	0.781

Table S2: Natal dispersal probability (males)

ld	LD	t	kin	ld:LD	ld:t	LD:t	ld:kin	ld:LD:t	Df	logLik	AIC	χ^2	p-value
+	+	+	+	+	+	+	+	+	15	-757.76	1545.52		
+	+	+	+	+	+	+	+		14	-757.81	1543.62	0.095	0.758
+	+	+	+	+	+		+		13	-757.81	1541.62	0.008	0.931
+	+	+	+	+	+				12	-757.84	1539.69	0.065	0.799
+	+	+	+	+					11	-758.06	1538.12	0.433	0.51
+	+	+		+					10	-758.51	1537.03	0.903	0.342
+	+			+					9	-759.15	1536.29	1.266	0.261

Table S3: Adult dispersal probability (females)

ld	LD	t	kin	ld:LD	ld:t	LD:t	ld:kin	ld:LD:t	Df	logLik	AIC	χ^2	p-value
+	+	+	+	+	+	+	+	+	15	-8520.49	17070.98		
+	+	+	+	+	+	+	+		14	-8520.69	17069.37	0.397	0.528
+	+	+	+	+	+		+		13	-8520.7	17067.4	0.025	0.874
+	+	+	+		+		+		12	-8520.73	17065.47	0.071	0.79
+		+	+		+		+		11	-8520.77	17063.54	0.069	0.793

Table S4: Adult dispersal probability (males)

ld	LD	t	kin	ld:LD	ld:t	LD:t	ld:kin	ld:LD:t	Df	logLik	AIC	χ^2	p-value
+	+	+	+	+	+	+	+	+	15	-4757.51	9545.02		
+	+	+	+	+	+	+	+		14	-4757.52	9543.04	0.021	0.886
+	+	+	+		+	+	+		13	-4758.37	9542.75	1.705	0.192
+	+	+	+		+		+		12	-4758.88	9541.75	1.002	0.317
+		+	+		+		+		11	-4759.2	9540.39	0.643	0.422

APPENDIX 4

Correlation among covariates

To ensure our results were not affected by multicollinearity, we checked Pearson's correlation coefficients among the variables used as covariates.
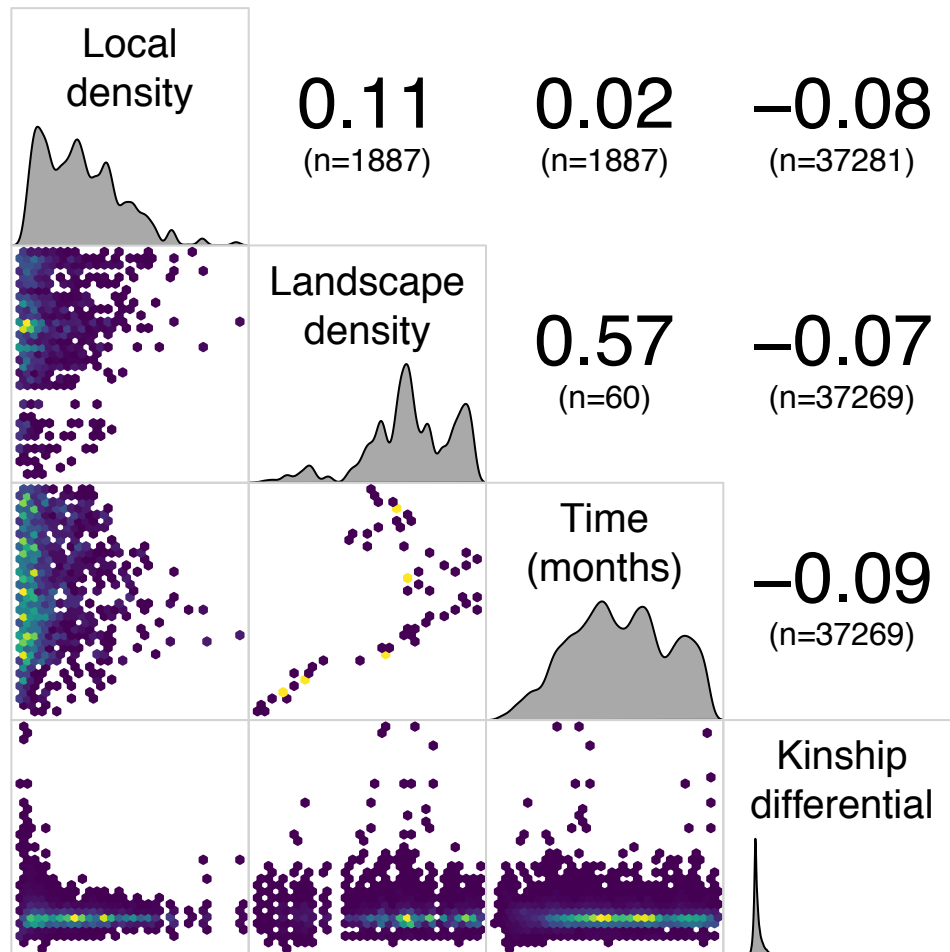

Figure S1: Covariates correlogram

APPENDIX 5

Kinship matrix calculation

The kinship matrix coefficients $\phi_{i,j}$ were calculated iteratively for each cohort, from the first to the last month of sampling. Cohort assignment for any given individual was based on the first sampling month for this individual.

Assuming that individual j is from an earlier cohort than individual i or at most that individuals i and j are from the same cohort, the coefficients $\phi_{i,j}$ were calculated according to the following rules, in order of priority:

- 0 if individuals i and j are both founders
- $\frac{1}{2}$ if $i = j$ and individual i is a founder
- $\frac{1}{2} \times (\phi_{mother_i,j} + \phi_{father_i,j})$ if individuals i and j are distinct
- $\frac{1}{2} \times (1 + \phi_{mother_i,father_i})$ if $i = j$

In our pedigree data, all individuals introduced on the first month are considered as founders. For all other individuals, mother and father assignment was based on the pedigree reconstruction. In some cases, it was not possible to assign a mother, a father, or both to a given individual. However, since in such cases the unknown parents of an individual i had to be part of the earlier cohorts of the studied population, we imputed the parental kinship coefficients $\phi_{mother_i,j}$ (resp. $\phi_{father_i,j}$) with any other individual j of the same or earlier cohort than individual i by averaging with equal weights the kinship coefficients of all potential mothers (resp. fathers) of individual i with individual j (Henderson 1988, Lynch and Walsh 1998). The potential mothers (resp. fathers) were selected by taking all females (resp. males) present in the earlier cohorts up to one year before the first capture of individual i (i.e. in cohorts $month_{i-1}$ to $month_{i-12}$). We used a 12-month interval as the threshold for going back in time to select putative parents as this is intermediate between the average life expectancy of mothers or fathers and the mid-point of the observed life spans of mothers and fathers. To explore the sensitivity of our kinship estimates to different values of this threshold, we also calculated kinship coefficients using 3, 6, and 24 months threshold. The distribution of kinship coefficients across the entire sampling period and the temporal evolution of average landscape kinship show very little differences between the threshold values used.

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