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Author(s): De Bona, Sebastiano; Bruneaux, Matthieu; Lee, Alexander; Reznick, David N.; Bentzen, Paul; Lopez Sepulcre, Andres

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31 **Corresponding author:** Sebastiano De Bona

32 Dept. of Biological and Environmental Science, PO Box 35, FI-40014

33 University of Jyväskylä, Finland

34 Email: sebastiano.s.debona@jyu.fi

35 Phone: +393494448025 Fax: +358142601021

36

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

52 **Introduction**

53 Dispersal is a fundamental driver of population regulation and distribution across space
54 (Bowler & Benton 2005; Kokko & López-Sepulcre 2006; Clobert *et al.* 2012). The decision
55 to leave a patch can be affected by several factors (Matthysen 2012), and is ultimately the
56 result of balancing fitness costs and benefits. Local competition can be a major driving factor
57 of dispersal, causing individuals to disperse at high local patch densities with decreased per
58 capita resources (positive density-dependent dispersal: Léna *et al.* 1998; Doak 2000; French
59 & Travis 2001; Bitume *et al.* 2013; Weiss-Lehman *et al.* 2017). Alternatively, a high local
60 density may act as a cue to habitat quality, such as low predation risk or optimal
61 environmental conditions, causing individuals to prefer patches with higher densities
62 (negative density-dependent dispersal: Stamps 1988, 1991; Muller *et al.* 1997; Peacor 2003;
63 van Buskirk *et al.* 2011). In some cases, increased conspecific density may itself be a factor
64 conferring fitness advantages, such as dilution of predation risk or favourable social
65 behaviours (Bygott *et al.* 1979; Foster & Treherne 1981; Dehn 1990; Hass & Valenzuela
66 2002; Bilde *et al.* 2007; McFarland *et al.* 2015). Kinship can further shape dispersal,
67 strengthening positive density-dependent dispersal to avoid kin competition (Hamilton &
68 May 1977). Beyond competition, kinship can also favour dispersal to avoid inbreeding
69 (Wolff *et al.* 1988; Lehmann & Perrin 2003) or discourage it to benefit from cooperation with
70 kin (Lambin *et al.* 2001; Hatchwell 2009).

71 Dispersal is often costly (Bonte *et al.* 2012). Movement can be energetically demanding, and
72 individuals might fail to find suitable habitats or face mortality during transfer. Ultimately,
73 dispersal will be selected for when the benefits outweigh the costs, and fitness expectations
74 elsewhere exceed those of the current habitat patch. Because of this, the benefit-cost
75 calculation should take into account both the local and the landscape contexts. For example,
76 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)

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 ± 1 m. 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.

200 *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).

296 *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 \pm 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

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).

388 Dispersal studies, especially in vertebrates, often focus on natal dispersal (e.g. Matthysen
389 2005; Støen *et al.* 2006; Meylan *et al.* 2007; Wojan *et al.* 2015). Natal dispersal is thought to
390 be predominant and extensive (Greenwood & Harvey 1982), and to have a big impact on
391 fitness and population dynamics (Matthysen 2012), but this observation may reflect the bias
392 towards studies of birds and mammals. We chose to study both adult and natal dispersal and
393 found them to differ profoundly in the way they are shaped by density conditions. Contrary to
394 natal dispersal, we observed no effect of landscape density on adult dispersal, but rather a
395 change in density-dependent dispersal with time that was independent of landscape density
396 (Figure 4b,d). Specifically, adults show a continuous trend from negative to positive density-
397 dependent dispersal (i.e. from lower to higher dispersal at high densities).

398 The initial negative density-dependent dispersal of adults could be reflective of the schooling
399 behaviour characteristic of the high-predation guppies introduced (Seghers 1974).
400 Aggregation is an effective antipredatory strategy in predator-rich communities (Magurran
401 1990; Magurran *et al.* 1993), has a genetic basis (Seghers & Magurran 1991), and is lost
402 when guppies are transplanted from high- to low-predation environments (Magurran *et al.*
403 1992). The initial conspecific attraction could also be due to guppies using density as a cue
404 for habitat quality in an unfamiliar environment (Fletcher 2006). For a high-predation
405 adapted guppy, high conspecific density might be a good indicator of a lack of predators.

406 As the colonisation of the low-predation environment progresses, conspecific attraction
407 disappears and avoidance emerges. When guppies colonise low-predation habitats from areas
408 of high predator-induced mortality, local densities increase rapidly, resulting in resource
409 limitation (Travis *et al.* 2014). Positive density-dependent dispersal can be an effective way
410 to escape local competition (Waser 1985; Bowler & Benton 2005; Ronce 2007), and here we
411 observe its emergence in adults as the population increases. A number of studies corroborate
412 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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450

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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 *	-	-

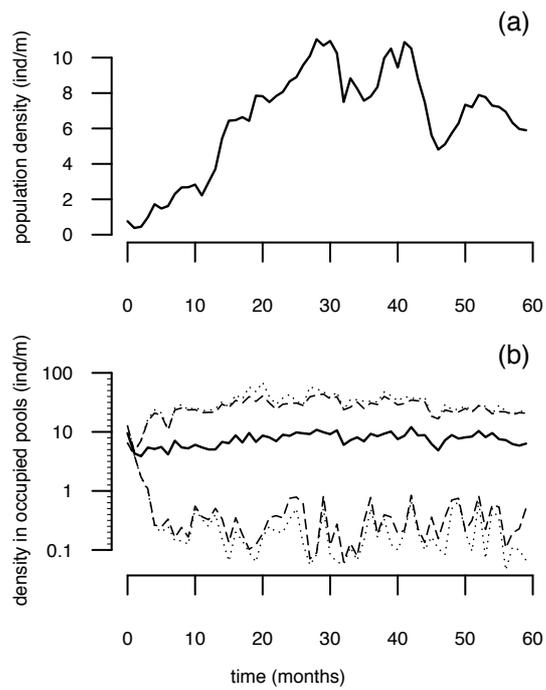
655

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 ***

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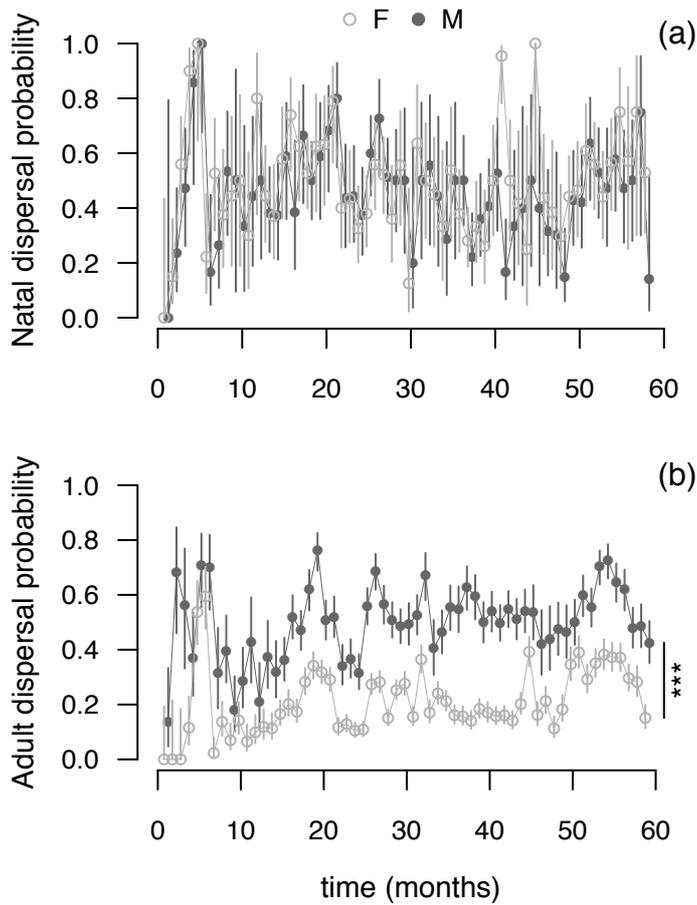
659 **Figure 1.**(a) Landscape population density over time. (b) Range of local densities in occupied
660 pools observed over time, in logarithmic scale. The solid line represents the average local
661 density of occupied pools, the dashed line the 95% upper and lower quantiles, the dotted line
662 the maximum and minimum local density observed.



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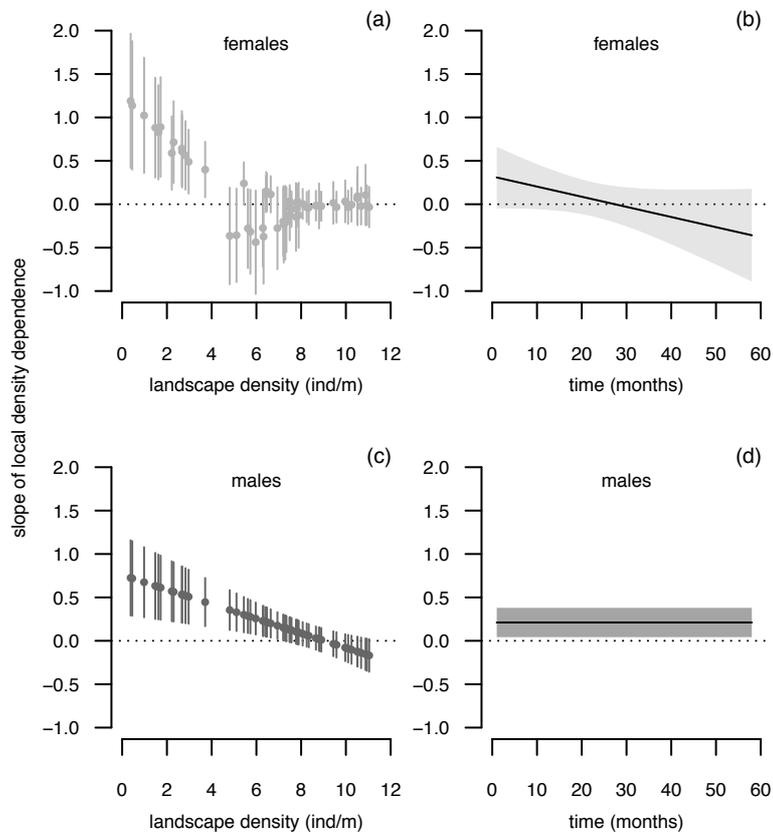
665 **Figure 2.** (a) Natal and (b) adult dispersal propensity over time. The connected circles and
666 bars represent the observed dispersal probability at each month, +/- standard error. Empty
667 circles corresponds to females, filled circles to males.



668

669

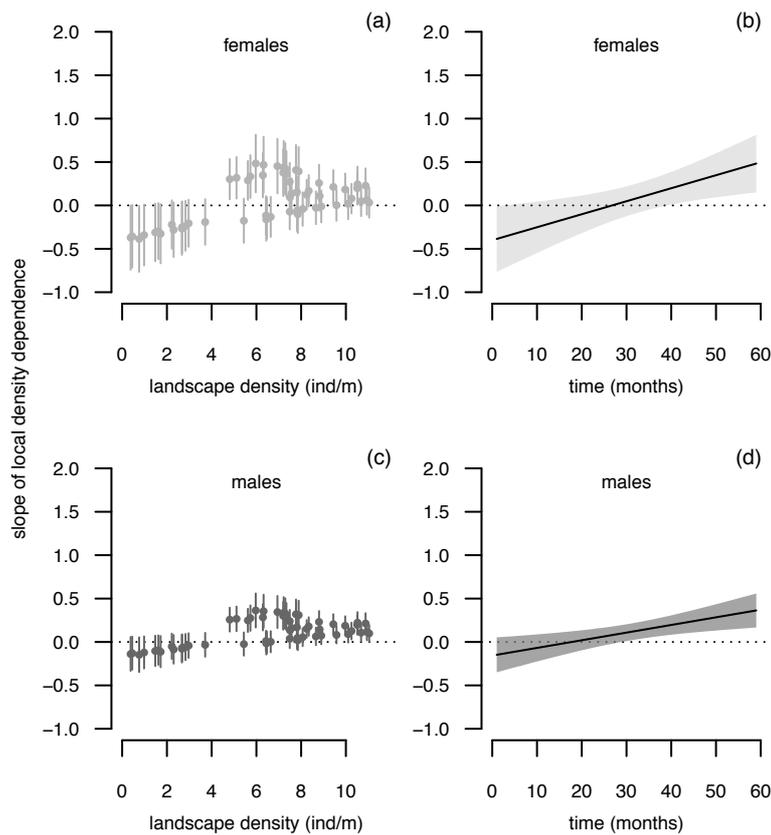
670 **Figure 3.** Determinants of the strength of local density-dependence for natal dispersal,
 671 calculated as the slope of the logit relationship between natal dispersal probability and local
 672 density. (a, c) Strength of density-dependence against landscape density for females and
 673 males. 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

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

Sebastiano De Bona
Matthieu Bruneaux
Alex E. G. Lee
Paul Bentzen
David Reznick
Andrés López-Sepulcre

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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:

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

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

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

where:

$$A = \alpha + \beta_{LD} \cdot LD + \beta_t \cdot t + \beta_k \cdot k + \beta_{LD:t} \cdot LD \cdot t \quad (\text{Eq. 1.3})$$

is the intercept of local density dependence and

$$B = \beta_{ld} + \beta_{ld:LD} \cdot LD + \beta_{ld:t} \cdot t + \beta_{ld:k} \cdot k + \beta_{ld:LD:t} \cdot LD \cdot t \quad (\text{Eq. 1.4})$$

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 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.

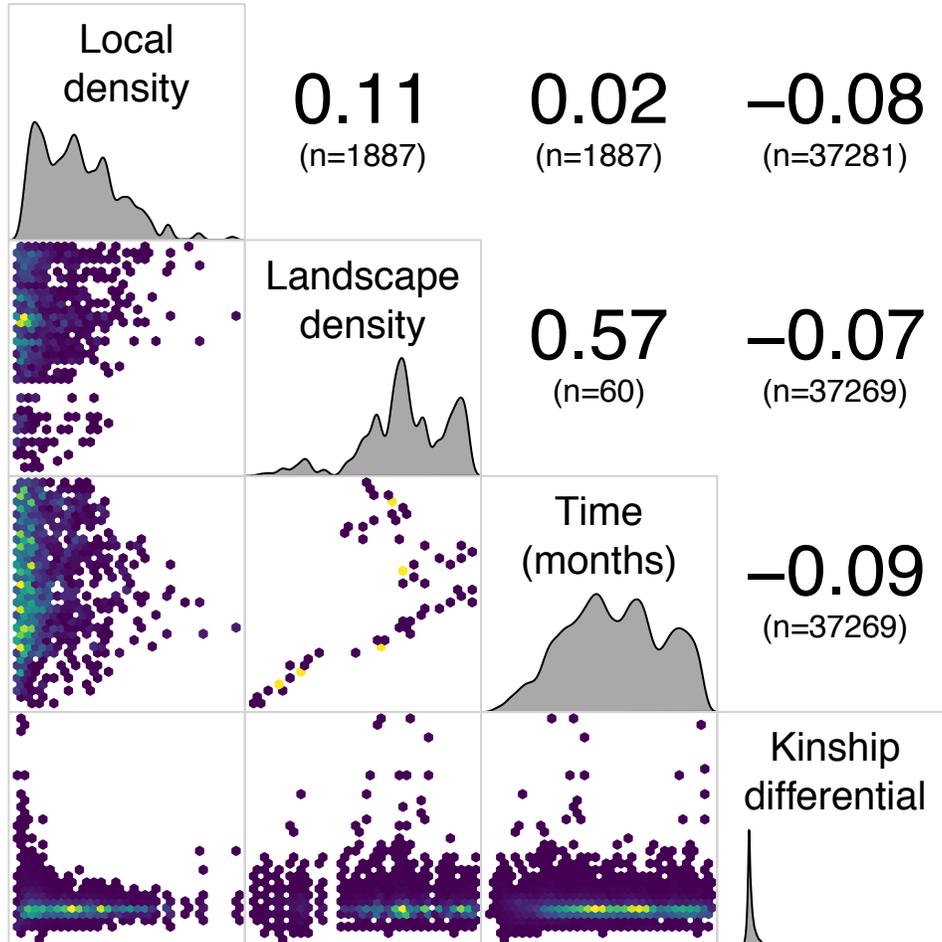


Figure S1: Covariates correlogram

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.

References:

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