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1 **Ecological and demographic correlates of cooperation** 2 **from individual to budding dispersal**

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8

9 **Abstract**

10

11 Identifying the ecological and demographic factors that promote the evolution of cooperation
12 is a major challenge for evolutionary biologists. Explanations for the adaptive evolution of
13 cooperation seek to determine which factors make reproduction in cooperative groups more
14 favourable than independent breeding or other selfish strategies. A vast majority of the
15 hypotheses posit that cooperative groups emerge in the context of philopatry, high costs of
16 dispersal, high population density, and environmental stability. This route to cooperation,
17 however, fails to explain a growing body of empirical evidence in which cooperation is not
18 associated with one or more of these predictors. We propose an alternative evolutionary path
19 towards the emergence of cooperation that accounts for the disparities observed in the current
20 literature. We find that when dispersal is mediated by a group mode of dispersal, commonly
21 termed budding dispersal, our mathematical model reveals an association between
22 cooperation and immigration, lower costs of dispersal, low population density, and
23 environmental variability. Furthermore, by studying the continuum from the individual to the
24 partial and full budding mode of dispersal, we can explicitly explain why the correlates of
25 cooperation change under budding. This enables us to outline a general model for the
26 evolution of cooperation that accounts for a substantial amount of empirical evidence. Our
27 results suggest that evolution may have favoured two major contrasting pathways for the
28 evolution of cooperation depending on a set of key ecological and demographic factors.

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Introduction

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Understanding the origin of cooperation poses a problem for evolutionary biologists (Hamilton, 1964, 1996; Maynard Smith & Szathmary, 1996; West *et al.*, 2007). Natural selection favours those individuals who are best adapted to their environment so that, through differential reproduction, their genetic variants become over-represented in the gene pool of future populations (Darwin, 1959; Fisher, 1930; Price, 1970). It is then puzzling why individuals are willing to suffer a reproductive cost to help with the reproduction of their social partners. Hamilton’s inclusive fitness theory provides an answer: natural selection promotes the costly transfer of resources to others whenever donors and beneficiaries are closely related (Hamilton, 1964). When social interactions occur between genetically related individuals, donors still increase their own genetic representation in future generations, albeit indirectly, through copies of their genes that are present in the beneficiaries of their actions (Hamilton, 1964, 1970).

Limited dispersal, whereby individuals tend to remain near their place of birth, provides a simple and general mechanism for generating groups of close relatives. As a result, limited dispersal is often central to theories pertaining to the evolution of cooperative societies (Hamilton, 1964; West *et al.*, 2007). This idea has motivated an extensive literature on the multiple ecological and demographic factors that lead to the evolution of limited dispersal, and ultimately to the evolution of cooperative breeding (e.g. Emlen, 1982, 1991; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2004, 2016). Among these factors, environmental stability, high costs of dispersal, and high density of the population have all been identified as major factors promoting the evolution of limited dispersal and / or cooperation (Komdeur, 1992; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2016). For instance, in the social

59 allodapine bee *Exoneura nigrescens*, the removal of nesting sites leads to higher philopatry
60 (Langer *et al.*, 2004). In the paper wasp *Mischocyttarus mexicanus*, solitary nesting is more
61 common when population density is low, and nest availability and quality is high (Gunnels *et*
62 *al.*, 2008). In the Seychelles warblers, a sudden availability of breeding sites has been shown
63 to disrupt both kin groups and cooperative behaviour (Komdeur, 1992). In African mole-rats,
64 a comparative analysis has shown an association between harsh environments and low food
65 density with the size of social groups (Faulkes *et al.*, 1997). In the Hornbills avian family, a
66 phylogenetic analysis found a positive association between climatic stability and cooperative
67 reproduction (Gonzalez *et al.*, 2013).

68

69 Several authors have attempted to synthesise this wealth of empirical findings to produce a
70 general model of the ecological and demographic factors influencing the evolution of
71 cooperation. For instance, the “habitat saturation” hypothesis, emphasises the role of
72 population density in the evolution of limited dispersal, and how this favours the evolution of
73 cooperation (Selander, 1964; Brown, 1974; Emlen, 1982). The “benefits of philopatry”
74 hypothesis, emphasises the role of the benefits obtained in the natal nest, and how this
75 facilitates cooperation (Stacey & Ligon, 1987, 1991). Notwithstanding the specific emphasis
76 of each model, they all converge on the importance of ecological and demographic
77 constraints for the evolution of delayed or limited dispersal as a primary factor favouring the
78 evolution of cooperative behaviour (Emlen, 1982, 1991; Koenig *et al.*, 1992; Hatchwell &
79 Komdeur, 2000).

80

81 In an increasing number of species, however, the ecological constraints model seems to be at
82 odds with the empirical evidence, which has shown instances where cooperation is not
83 associated with one or more classic predictors of sociality. In several species, cooperation has

84 been found to be associated with immigration, such as in wild western gorillas (*Gorilla*
85 *gorilla*; Bradley *et al.*, 2007), white-winged choughs (*Corcorax melanorhamphos*; Heinsohn
86 *et al.*, 2000), long-tailed tits (*Aegithalos caudatus*; Sharp *et al.*, 2008), or in a ciliate protozoa
87 (*Tetrahymena thermophila*; Schtickzelle *et al.*, 2009; Jacob *et al.*, 2016). Further molecular
88 analysis, in gorillas, white-winged choughs, and long-tailed tits, has shown a high degree of
89 kinship among immigrants (Heinsohn *et al.*, 2000; Bradley *et al.*, 2007; Sharp *et al.*, 2008).
90 These findings are consistent with a group mode of dispersal, commonly termed ‘budding’
91 (e.g. Goodnight, 1992; Gardner & West, 2006), a behaviour also observed in other social
92 species such as in bacteria (*Myxococcus xanthus*, Velicer & Yu, 2003), and banded
93 mongooses (*Mungos mungo*, Cant *et al.*, 2001; Nichols *et al.*, 2012). This empirical evidence
94 suggests an alternative evolutionary path to the emergence of cooperation, in which
95 cooperation is mediated by the budding mode of dispersal, and yet this problem has received
96 surprisingly little attention (for a review see Cote *et al.* 2017). Specifically, how different
97 ecological and demographic factors, such as environmental stability and the cost of dispersal,
98 influence the evolution of budding dispersal and cooperation remains unexplored.

99

100 Here we develop a theoretical model to study how multiple ecological and demographic
101 factors influence the evolution of dispersal under budding and how this, in turn, influences
102 the evolution of cooperation. We describe how temporal variation in resource availability
103 mediates multiple variables such as the genetic relatedness among social partners and the
104 intensity of kin competition. We then study how these variables mediate the evolution of
105 dispersal and how this influences the evolution of cooperative behaviours.

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The Model

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Life-cycle

Here we provide a description of the life cycle of our model organism, a visual depiction of which can be found in Figure 1. We assume a population of asexually-reproducing and haploid individuals subdivided into a very large number of patches (i.e. an infinite island model; Wright, 1931; Hamilton & May, 1977; Rodrigues & Gardner, 2012). A fraction p of these patches is habitable, while a fraction $1-p$ is uninhabitable. Each habitable patch is occupied by n mothers. Uninhabitable patches lack resources to sustain life, and therefore they are “empty”. Each of the n mothers has a very large number of offspring, $F(x_A, y_A)$, which is a function both of the focal mother’s investment in cooperation, x_A , and the focal groups’, including the focal mother, average investment in cooperation, y_A , in a population where the average investment in cooperation is z_A . We discuss the social behaviour in more detail below. After social interactions and reproduction, mothers die. Juveniles become adult females, who form buds. We assume that each bud has n adults. Each bud disperses to a random patch in the population with probability z_D and remains in its natal patch with probability $1-z_D$. Migrant buds are assumed to survive dispersal with probability $1-k$, where k is the cost of dispersal. After dispersal, in the previously occupied patches, there is competition between migrant and native buds for the n available breeding sites, whilst in previously empty patches, competition occurs among immigrant buds only. Only one bud wins, the remainder buds die. After group competition, there is an exchange of adult females between patches, so that adult females remain in their patch with probability $1-m$, and move to another patch with probability m . The exchange of adult females between patches sustains some genetic variation within each group, which would otherwise be clonal (cf. Gardner &

134 West, 2006). We can also interpret migration as a mutation rate, which can be considered as
135 interchangeable in, for example, bacterial populations (e.g. O'Brien *et al.*, 2013). As
136 migration, mutation introduces within-group variation, and in the context of our model is
137 conceptually equivalent. Following movement of adult females, the ecological state of
138 patches may change. With probability α habitable patches produce a surplus of resources so
139 that all offspring born in the patch are viable. However, with probability $1-\alpha$, disturbances
140 (such as wildfires or floods) destroy all the available resources, which leads to the premature
141 death of all of the resident mothers. With probability β , uninhabitable patches do not recover
142 and remain barren, whilst with probability $1-\beta$, uninhabitable patches recover their viability
143 and become habitable again. After these ecological changes, the life-cycle of our model
144 species returns to its starting point.

145

146 **Methods and Analysis**

147

148 We employ the neighbour-modulated approach to kin selection (Taylor & Frank, 1996;
149 Frank, 1998; Rodrigues & Gardner, 2013b) to determine how natural selection acts on the
150 adaptive evolution of dispersal and cooperation. We first analyse the evolution of dispersal,
151 and we then focus on the evolution of cooperation (see Appendix for details).

152

153 Hamilton's Rule: Dispersal

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155 We find that the condition for natural selection to favour the evolution of dispersal, a form of
156 Hamilton's rule (Hamilton, 1964; Charnov, 1977), is given by:

157

$$158 \quad -v_O + (1 - k)(pv_O + (1 - p)v_E) + v_O hR > 0, \quad (1)$$

159

160 where: $v_O = \omega_O \alpha / (\alpha + 1 - \beta)$ is the reproductive value of a juvenile competing for a breeding site
161 in an occupied patch, where $\omega_O = 1 / ((1 - z_D) + z_D p (1 - k))$ is the probability that a focal individual
162 wins a breeding spot, and $\alpha / (\alpha + 1 - \beta)$ is the relative probability that the patch remains
163 habitable; $v_E = \omega_E (1 - \beta) / (\alpha + 1 - \beta)$ is the reproductive value of a juvenile competing for a
164 breeding site in an empty patch, in which $\omega_E = 1 / (z_D p (1 - k))$ is the probability that a focal
165 individual wins a breeding spot, and $(1 - \beta) / (\alpha + 1 - \beta)$ is the relative probability that an empty
166 patch becomes habitable; $h = (1 - z_D) / ((1 - z_D) + z_D p (1 - k))$ is the probability that a random
167 individual, after dispersal, was born in the focal patch; and $R = 1 / (n - (n - 1)(1 - m)^2)$ is the
168 relatedness among group members.

169

170 The left-hand side (LHS) of inequality (1) readily yields an inclusive fitness interpretation of
171 the behaviour. The first term represents a direct fitness cost of dispersing to a juvenile. A
172 disperser loses a reproductive value v_O , which is the reproductive value she would have won
173 had she decided to stay in her natal patch. The second term represents a direct fitness benefit
174 of dispersing to the focal juvenile. She survives dispersal with probability $1 - k$. With
175 probability p , she arrives at an occupied patch, in which case she obtains a reproductive value
176 v_O , whilst with probability $1 - p$, she arrives at an empty patch, in which case she obtains a
177 reproductive value v_E . Finally, the third term represents an indirect fitness benefit to the focal
178 juvenile. With probability h the benefit goes to a native individual whose relatedness to the
179 focal individual is R , and where the beneficiaries obtain a reproductive value v_O .

180

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184 Hamilton's Rule: Cooperation

185

186 We focus on a social trait in which a mother pays a fecundity cost C to provide a fecundity
187 benefit B to her social partners, including herself. The condition for natural selection to
188 favour the evolution of cooperation is then given by

189

$$190 \quad -Cv + BvR - (B - C)v_P hR > 0, \quad (2)$$

191

192 where v is the reproductive value of an offspring at birth and $v_P = (1 - z_D)v_O$ is the philopatric
193 component of an offspring's reproductive value. That is, an offspring remains in its natal
194 patch with probability $1 - z_D$, in which case it obtains a reproductive value v_O .

195

196 The LHS of inequality (2) readily yields an inclusive fitness interpretation of the behaviour.
197 The first term represents a direct fitness cost to the focal mother. She has C fewer offspring,
198 whose reproductive value would have been v . The second term represents an indirect fitness
199 benefit to the focal mother. Her behaviour improves the fecundity of all group members by a
200 total of B offspring, whose reproductive value is v , a benefit that must be discounted by the
201 relatedness R . Finally, the third term represents an inclusive fitness cost to the focal mother.
202 Her behaviour displaces $B - C$ offspring, who were born in the local patch with probability h .
203 Each displaced offspring represents a cost v_P to the actor, a cost that must be discounted by
204 the relatedness R .

205

206 The cost and benefit of cooperation are given by the slopes of fecundity on the phenotype of
207 individuals (i.e. $-C = \partial F(x_A, y_A) / \partial x_A$, and $B = \partial F(x_A, y_A) / \partial y_A$); see Appendix D for details). We

208 assume that fecundity depends on the relative competitiveness of each mother within each
 209 group, and on the public good available to each group member. Investment in cooperation
 210 (x_A) decreases an individual's relative competitiveness within each group but increases the
 211 amount of the public good available. In order to plot ES cooperation strategies, we assume
 212 that the fecundity of a focal individual is given by $F(x_A, y_A) = ((1-x_A)/(1-y_A))y_A$ (cf. Frank,
 213 1994). Thus, $C(z_A) = z_A/(1-z_A)$, and $B(z_A) = 1/(1-z_A)$. In the appendix, we show that the
 214 specific functional form does not have a qualitative impact on our results.

215

216 Hamilton's rule and inclusive fitness

217

218 Above we have considered a particular partition of Hamilton's rule, in which each additive
 219 term represents a selective pressure and where the costs (C 's) and benefits (B 's) are given in
 220 number of offspring. In the original formulation of Hamilton's rule, however, selection is
 221 partitioned into additive direct and indirect fitness components, and costs and benefits are
 222 given in terms of fitness (Hamilton 1964). This original formulation of Hamilton's rule can
 223 be recovered by re-arranging the LHS's of inequalities (1) and (2) and by considering the
 224 'others-only' coefficient of relatedness, rather than the 'whole-group' coefficient of
 225 relatedness (Pepper 2000). Hamilton's rule for the evolution of dispersal becomes

226

$$227 \quad - \underbrace{\left(v_O - (1-k)(pv_O + (1-p)v_E) - v_O h \frac{1}{n} \right)}_c + \underbrace{v_O h \frac{n-1}{n}}_b r > 0, \quad (3)$$

228

229 where: c is the fitness cost of the behaviour; b is the fitness benefit of the behaviour; and r is
 230 the 'others-only' relatedness between actor and recipients. The direct fitness effect is then
 231 given by $-c$ whereas the indirect fitness effect is given by br . Likewise, Hamilton's rule for
 232 the evolution of cooperation becomes

233

$$234 \quad - \underbrace{\left(Cv - Bv \frac{1}{n} + (B - C)v_P h \frac{1}{n} \right)}_{c'} + \underbrace{\left(Bv \frac{n-1}{n} - (B - C)v_P h \frac{n-1}{n} \right)}_{b'} r > 0. \quad (4)$$

235

236 Evolutionarily Stable Strategies

237

238 Our aim is to find the Evolutionarily Stable (ES) dispersal, denoted by z_D^* , and the ES
 239 investment in cooperation, denoted by z_A^* . An evolutionary singular dispersal (or
 240 cooperative) strategy occurs when natural selection favours neither a slight increase nor a
 241 slight decrease in the probability of dispersal (or in cooperation). This evolutionary
 242 equilibrium occurs when the corresponding LHS of Hamilton's rule is null. A joint
 243 evolutionary singularity strategy (z_D^*, z_A^*) occurs when the LHS of both Hamilton's rules, as
 244 given by inequalities 1 and 2, are simultaneously null. We investigate both the convergence
 245 and evolutionary stability of these joint optimal strategies. To determine the evolutionary
 246 stability of the evolutionary singularities, we construct a genetic model that is equivalent to
 247 our kin selection model (Ajar, 2003; Wild, 2011; Rodrigues & Johnstone, 2014; Appendix
 248 E). We use this genetic model to check the validity of the analytical results derived from our
 249 kin selection model, and to check the convergence stability (Christiansen, 1991; Eshel, 1996),
 250 and the evolutionary stability (Maynard Smith & Price, 1973; Metz & Gyllenberg, 2001;
 251 Ajar, 2003; Rodrigues & Johnstone 2014) of the joint optimal strategies (Appendix E). Our
 252 analysis suggests that all evolutionary singular strategies are both convergence and
 253 evolutionarily stable (Appendix F).

254

255 **Results**

256

257 Here we describe the evolution of cooperation and dispersal with respect to the cost of
258 dispersal (k), proportion of habitable patches (p), and the temporal stability of the local
259 environment (τ), where $\tau = \alpha - (1 - \beta)$. We explore how the different model parameters
260 influence the ES dispersal rate (z_D^*) and the ES investment in cooperation (z_A^*). We analyse
261 our results in terms of the relative direct ($v_D = (1-k)(pv_O+(1-p)v_E)/v_O$) and relative indirect (ρ_D
262 $= v_O hR/v_O$) benefits of dispersal, and in terms of the relative kin-selected benefits ($v_A = vR/v$),
263 and the relative kin competition costs ($\rho_A = v_P hR/v$) of cooperation (Figures 2 - 4).

264

265 How does the cost of dispersal influence cooperation (Figure 2)? We find that, in general,
266 higher costs of dispersal have a negative impact on the evolution of cooperation (Figure 2
267 (d)). When many dispersers die in transit between patches, fewer immigrants arrive at each
268 patch. This increases kin competition, which disfavours the evolution of cooperation (Figure
269 2 (c)). In addition, higher dispersal costs reduce the benefits of dispersal (Figure 2 (a)), which
270 leads to lower ES dispersal rates. This, in turn, further increases the intensity of kin
271 competition, and the corresponding costs associated with cooperation. Counter to intuition,
272 when the environment is unstable and the cost of dispersal is already high, dispersal tends to
273 rise with increasing cost of dispersal (Figure 2 (b)). This is because higher costs of dispersal
274 increase the competition among close relatives, and therefore it also increases the indirect
275 fitness benefits to dispersers. In other words, even if a disperser is likely to perish in a
276 dispersal event, they will indirectly benefit as their kin left behind will benefit from reduced
277 competition within the patch. How does the cost of dispersal in unstable environments
278 influence the evolution of cooperation? Two opposing factors drive the evolution of
279 cooperation. First, the cost of dispersal leads to less immigration and therefore to higher kin
280 competition for local resources. Second, higher kin competition leads to higher dispersal

281 rates, which in turn erodes kin competition. Overall, the cost of dispersal increases the
282 intensity of kin competition, which disfavours the evolution of cooperation (Figure 2).

283

284 How does habitat occupancy (p) mediate investment in cooperation (Figure 3)? We find that
285 when the local environment is stable (temporal correlation, $\tau \approx 1$), cooperation increases with
286 habitat occupancy. By contrast, when the local environment is unstable ($\tau \ll 1$), cooperation
287 decreases with habitat occupancy (Figure 3 (*c* & *d*)). In stable environments, barren patches
288 rarely become fertile again, and therefore any immigrant that lands in one of these patches is
289 unlikely to reproduce. As a result, higher habitat occupancy decreases the chances that
290 dispersers migrate to a barren patch, which increases the expected direct benefits of dispersal,
291 which leads to higher ES dispersal rates (Figure 3 (*a* & *b*)). Higher dispersal rates from
292 occupied patches reduce the intensity of local kin competition, and therefore cooperation
293 becomes more beneficial (Figure 3 (*d*)).

294

295 When the local environment is unstable ($\tau < 1$), higher habitat occupancy leads to lower
296 direct benefits of dispersal (Figure 3 (*a*)). The value of occupied patches is now greatly
297 reduced because: (i) they have higher competition (as they have philopatric individuals and
298 not only immigrants), and (ii) they may be more likely to become extinct (if $\tau < 0$). When the
299 fraction of poor quality occupied patches increases in the population, dispersal is disfavoured
300 (Figure 3 (*b*)). This is because dispersers are more likely to find themselves in a poorer patch
301 after dispersal. Low dispersal rates increase the intensity of local kin competition, and this
302 disfavours the evolution of cooperation (Figure 3 (*c*)).

303

304 How does temporal correlation (τ) influence the potential for cooperation (Figure 4)? We
305 find that the potential for cooperation decreases as the environment becomes more stable

306 (Figure 4 (c & d)). Stable environments reduce the direct fitness benefit of dispersal (Figure 4
307 (a)), which disfavors the evolution of dispersal (Figure 4 (b)). This leads to an increase in
308 the intensity of kin competition, which disfavors costly investments into cooperative
309 behaviours (Figure 4 (c & d)). In addition, temporal stability increases the value of occupied
310 patches, which also increases the costs associated with kin competition (Figure 4 (c)). This
311 additional factor further disfavors investment into cooperation (Figure 4 (d)).

312

313 Finally, what is the relationship between dispersal and cooperation? For a large range of
314 parameter values, we find a positive correlation between dispersal and cooperation when we
315 vary a model parameter (Figure 5). Exceptions occur when the cost of dispersal is high and
316 the environment is unstable (Figure 5 (a, b & d)). In this case, the ES dispersal rate of
317 juveniles increases with the cost of dispersal. Higher dispersal rates directly oppose higher
318 costs of dispersal, with the former acting to alleviate kin competition and the latter increasing
319 kin competition. This latter effect is stronger than the former and, as a result of higher net kin
320 competition, investment into cooperation decreases with increasing dispersal rates. At
321 intermediate levels of environmental stability, we also find a negative correlation between the
322 dispersal rate of juveniles and investment in cooperation as patch occupancy increases
323 (Figure 5 (f)). In some areas of parameter space the model is biologically unrealistic
324 (represented by grey shaded areas on Figure 5). Here, there isn't a realistic combination of
325 parameter values (α and β) that gives values of τ and p that could occur in nature (e.g. if $\tau = -$
326 1, and $p = 1/4$, then α is negative ($-1/2$)).

327

328 Individual, partial and complete budding dispersal

329

330 Above, we have explored how budding dispersal influences general patterns of cooperation
331 as a function of the different model parameters. Here, we explore these results in three main
332 directions. First, we investigate cases where the migration rate is set to zero. Next, we explore
333 cases where the size of each bud is allowed to vary in relation to patch size. Finally, we
334 explore a clonal expansion scenario, whereby each patch is colonised by a single individual
335 who then produces offspring that fill up all of the available breeding sites.

336

337 *Migration rate* -- In the previous sections, we have assumed that there is an exchange of
338 individuals between groups after the dispersal stage, which sustains some within-group
339 genetic variation. Here we explore some of the consequences of having no exchange of
340 individuals between groups ($m \rightarrow 0$). Under this scenario, if we assume a saturated
341 population (i.e. $p = 1$), we recover Taylor's (1992) result for the evolution of cooperation
342 when there is a single breeder per patch, in which case Taylor's condition for the evolution of
343 cooperation becomes $B > C$. In this case, individuals invest all of their resources into
344 cooperation (i.e. $z_A^* = 1$), irrespective of the dispersal rate. Similarly, we also recover
345 Hamilton & May's (1977) result for the evolution of dispersal, where the ES dispersal rate is
346 $z_D^* = 1/(1+k)$. In other words, we find that clonal groups behave as if they were individuals,
347 and we recover the classic results of Taylor (1992) and Hamilton & May (1977).

348

349 *Bud size* -- Above, we showed that for a wide range of the parameter space we discover an
350 unexpected positive correlation between dispersal and cooperation when individuals disperse
351 in groups, where the size of each dispersing group, denoted by n_B , was assumed to exactly
352 match patch size (i.e. $n_B = n$; Figure 5). Here, we relax this assumption and explore this result
353 further by taking into account the size of the bud (n_B) relative to the number of available
354 breeding sites (n). In particular, we assume that the size of each bud (n_B) can be less than, or

355 greater than, the number of available breeding sites, with $n_B \in \{1, 2, \dots, n, n+1, \dots\}$. Thus,
356 when $n_B = 1$, we have a pure individual mode of dispersal; when $1 < n_B < n$, we have a partial
357 budding dispersal mode; and when $n_B \geq n$, we have a complete budding mode of dispersal. In
358 the main model, we also assumed that all individuals had exactly the same fecundity. Here,
359 we relax this assumption and we consider that a single dominant individual has higher
360 fecundity than the $n - 1$ subordinate individuals. Thus, $F_H \geq F_L$, where F_H is the fecundity of the
361 dominant individual and F_L is the fecundity of a subordinate individual (see Appendix G for
362 details).

363

364 As shown in Figure 6, we find that both dispersal and cooperation increase with bud size,
365 irrespective of patch size. In particular, we find that in the limit case, under the individual
366 mode of dispersal (i.e. $n_B = 1$), the optimal levels of dispersal and cooperation are relatively
367 low. As bud size increases, both dispersal and cooperation gradually rise until bud size
368 becomes equal to, or greater than, the number of breeding spots (i.e. $n_B \geq n$ and all breeding
369 spots are filled by individuals from the same bud), at which point both dispersal and
370 cooperation stabilise at their highest values.

371

372 The effect of temporal stability, i.e. τ , on the optimal level of cooperation strongly depends
373 on the mode of dispersal. Under the individual mode of dispersal (i.e. $n_B = 1$), temporal
374 stability and cooperation are positively correlated. Stable environments select against
375 dispersal, which increases relatedness, and higher relatedness, in turn, favours cooperation.
376 Unstable environments select for dispersal, which decreases relatedness. Lower relatedness,
377 in turn, selects against cooperation. This pattern gradually changes as bud size increases and
378 beyond a threshold bud size the coefficient of temporal stability and cooperation become
379 negatively correlated. As under the individual mode of dispersal, stable environments are

380 associated with philopatry and unstable environments with dispersal when bud size increases.
381 However, the effects of philopatry and dispersal on cooperation differ when bud size
382 increases beyond the set threshold. Under such scenario, philopatry becomes associated with
383 strong kin competition, which leads to the evolution of lower levels of cooperation. Dispersal
384 becomes associated with weak kin competition, which leads to the evolution of higher levels
385 of cooperation.

386

387 *Clonal expansion* -- Akin to full budding dispersal is clonal colonisation. To consider this
388 scenario, we modify the model of the previous section. In particular, we consider that a single
389 individual colonises a patch with multiple available breeding spots that remain open. The
390 coloniser takes up the dominant position, and then reproduces clonally, with the offspring
391 taking up all other available breeding spots and adopting the role of subordinates (see
392 Appendix I for details). Under these conditions, we find that the dynamics of dispersal and
393 cooperation are similar to those observed under full budding dispersal. In particular, we find
394 that high levels of cooperation evolve irrespective of temporal stability and of patch size (see
395 Figure I in Appendix I).

396

397

Discussion

398

399 Identifying the ecological and demographic factors that shape the evolution of cooperation
400 has been a long-standing problem for evolutionary ecologists (Koenig & Dickinson, 2004,
401 2016; West *et al.*, 2007). The “habitat saturation” hypothesis, for instance, suggests that high
402 population density tends to disfavour immigration, and as a result favours the evolution of
403 cooperation (Salender, 1964; Brown, 1974; Emlen, 1982). The “benefits of philopatry”
404 hypothesis emphasises the benefits obtained in the natal patch as a force driving philopatry,

405 which in turn promotes cooperative behaviour (Stacey & Ligon, 1987, 1991). Independently
406 of the specific viewpoint of each different hypothesis, the common idea is that cooperation
407 evolves in the context of environments with strong ecological and demographic constraints
408 on dispersal and independent breeding, of which environmental stability, high costs of
409 dispersal, and high population density are usually regarded as the primary constraining
410 factors (Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2016).

411

412 Recent observational and experimental studies, however, have uncovered variation in
413 cooperation that is not explained by these models. A common thread across these studies is
414 the existence of budding or some form of group dispersal (e.g. Heinsohn *et al.*, 2000;
415 Williams & Rabenold, 2005; Bradley *et al.*, 2007; Sharp *et al.*, 2008; Jacob *et al.*, 2016). This
416 observation has led us to advance the central hypothesis of our study where we propose that
417 budding may mediate a shift in the ecological and demographic variables shaping the
418 evolution of cooperation. To test this hypothesis, we developed a kin-selection theoretical
419 model in which we varied key factors to study their effect on the evolution of dispersal and
420 ultimately on the evolution of cooperation. Our model supports our initial hypothesis, as we
421 found that under budding dispersal, cooperation becomes associated with environmental
422 instability, immigration, low costs of dispersal, and low population density. These results
423 provide a foundation for a general model for the evolution of cooperation in which its
424 correlates are in contrast with the ecological and demographic correlates proposed by the
425 hypotheses based on ecological constraints.

426

427 Support for our findings comes from different lines of research. For instance, white-winged
428 coughts are cooperative breeders who live in groups of relatives that show some degree of
429 reproductive skew. Social groups can last for several generations, but ecological

430 perturbations can lead to their demise. In one of such instances, severe droughts resulted in
431 high mortality and group fragmentation (Heinsohn *et al.*, 2000). New groups were readily
432 established, each comprised of sub-groups of close kin and individuals of different origins.
433 After the establishment of new groups, reproductive skew was immediately developed, and
434 researchers found a positive correlation between reproductive success and the number of
435 relatives present in the new groups (Heinsohn *et al.*, 2000). Long-tailed tits are also
436 cooperative breeders that show relatively high levels of dispersal, in which dispersers often
437 fail to establish independent breeding. Sharp *et al.* (2008) has shown that around 40% of the
438 failed breeders become helpers at an established nest, with over 30% joining the nest of a
439 close relative. These cases illustrate situations where there is an association between
440 relatively high immigration, high relatedness and cooperation, and in the case of white-
441 winged choughs high environmental instability, as outlined in our model.

442

443 In our model, and in white-winged choughs, dispersal is partially driven by ecological
444 disturbances. We can expect, however, that in some cases, dispersal may be caused by other
445 factors that vary over time. For instance, sex-biased dispersal is common in sexually
446 reproducing species, a behaviour that is often driven by the costs of inbreeding. In lions,
447 males are the dispersing sex, while females are philopatric. Dispersal by males is particularly
448 important when their own daughters become adult group members, in which case the costs of
449 inbreeding rapidly escalate. Males may disperse solitarily but also in groups of different
450 sizes, and they are more likely to associate in groups when close kin are available. Groups of
451 males are more likely to take over a pride, and therefore improve their reproductive success
452 (Packer *et al.*, 1991). In brown jays, males are also the dispersing sex. Immigration is often
453 made in groups, and not random, as males are more likely to disperse to a group where other

454 close relatives are already present (Williams & Rabenold, 2005). This suggests that kin
455 selection and cooperation is associated with both budding and dispersal.

456

457 We also uncover the result that bud size relative to number of available breeding spots drives
458 both the potential for cooperation and dispersal, especially under more unstable
459 environments. This analysis provides a continuum between the individual mode of dispersal
460 to complete budding dispersal. Cooperative breeders such as the western bluebird (*Sialia*
461 *Mexicana*) and the superb fairy-wren (*Malurus cyaneus*), will often delay dispersal when
462 food is scarce and competition for quality patches is high. Here, quality patches do not often
463 become available, so a kin group is established and cooperative behaviours persist. However,
464 when quality patches become available helpers will prefer to disperse individually and breed
465 (Dickinson *et al.*, 2014; Pruett-Jones & Lewis, 1990). As such, cooperation is established
466 when patches are stable even under individual dispersal, however, when new patches become
467 available relatedness will decline as groups disperse and cooperation is unlikely to be
468 maintained.

469

470 At the other end of the spectrum are eusocial insects who need a cooperative group to
471 establish a new nest site. When a colony of honey bees (*Apis mellifera*) divide, the old queen
472 will swarm with several thousand workers to find a new patch, leaving remaining resources
473 to colony members and a new queen (Camazine *et al.*, 1999). Here, the quality and quantity
474 of resources in a patch will determine dispersal rate, and cooperation will remain high during
475 dispersal through budding.

476

477 Dispersal in other eusocial insects, such as the drywood termite (*Cryptotermes secundus*)
478 where patch resources are limited, is dependent on ecological factors such as food

479 availability. When food becomes scarce in the nest, there is an increase in maturation of
480 individuals into dispersing sexuals that go on to colonise new nests as a single monogamous
481 queen (clonal colonisation in our model) (Korb and Schmidinger, 2004). Here, patch quality
482 determines dispersal rate, and although individual dispersal is established, clonal colonisation
483 of empty patches ensures high relatedness and maintains selection for dispersal. These
484 examples demonstrate the vital role ecological determinants play in the evolution of dispersal
485 and how the dispersal strategy can act to disrupt or maintain cooperative behaviours during
486 dispersal events, depending on whether dispersal is budding or individual.

487

488 In many cases, testing theoretical predictions linked to dispersal and cooperation is not
489 experimentally tractable in vertebrates and higher organisms. However, experimental
490 approaches using single cellular organisms highlights the critical role of dispersal strategy in
491 maintaining cooperative groups during dispersal events. These studies reveal budding as a
492 key factor for resolving conflicting selective pressures between cooperation and kin
493 competition (Kümmerli *et al.*, 2009; Taylor *et al.*, 2013; Jacob *et al.*, 2016). For example,
494 using a ciliated protozoan model system (*Tetrahymena thermophile*) Jacob *et al.* (2016)
495 found that the aggregative behaviour of the strain (determined by their genotype) altered the
496 plastic reaction norms of dispersal behaviour. Specifically, cooperation and dispersal are
497 maintained via the avoidance of kin-competition through long distance dispersal, and the
498 maintenance of kin structure through group dispersal.

499

500 Reflecting on the results gained in this study, it is interesting to consider the parallels that
501 may be important for vector-borne diseases, such as malaria. Malaria often exists within a
502 host as a mixed-genotype infection, i.e. they are frequently dispersing to occupied patches
503 (Read *et al.*, 2002). But kinship patterns observed within an infected host suggest that

504 relatedness within the mosquito vector (i.e. during dispersal) is high (Nkhoma *et al.*, 2012).
505 Moreover, it seems that parasites can discriminate between related and non-related malaria
506 parasites (Reece *et al.*, 2008), suggesting kin structure to be important to the success of the
507 parasitic lifecycle. If relatedness within the vector is high, then relatedness is not destroyed
508 by dispersal, and a type of budding dispersal is established. Besides, theoretical work has
509 shown that both high competition within a mixed-genotype infection (Read *et al.*, 2002) and
510 long distance transmission mechanisms (such as those that are vector-borne; Boots & Sasaki,
511 1999) will select for more virulent pathogens. The consequence of this higher virulence are
512 more unstable patch dynamics (because the host dies more quickly), and our work predicts
513 this will also select for a higher dispersal rate. In support of this theory, a recent study found
514 that passaging the parasitic nematode, *Heterorhabditis floridensis*, under conditions that
515 resulted in low relatedness within new hosts led to reduced growth and lower virulence. In
516 contrast, passaging under conditions that led to high relatedness within the new host led to
517 higher growth and more virulent strains (Shapiro-Ilan & Raymond, 2016). This empirical
518 result matches the predictions made above; nematodes that disperse to a new host while
519 maintaining kin structure will have increased growth, resulting in decreased patch stability
520 (as host mortality increases). These specific examples illustrate how a budding group remains
521 competitive when entering a colonised patch, however, what remains to be experimentally
522 tested is the longer term evolutionary consequences. Does intense within patch competition
523 reduce patch stability and subsequently select for higher dispersal?

524

525 Our results suggest that the role of the demographic and ecological correlates of cooperation
526 strongly depend on group size. Despite this, group size has been relatively neglected in the
527 classic hypotheses for the evolution of cooperation (Selander, 1964; Brown, 1974; Emlen,
528 1982; Stacey & Ligon, 1987, 1991), which have largely focused on identifying the ecological

529 and environmental factors that lead to group formation and sociality. Our results suggest a
530 more complex picture for the evolution of cooperation, where group size plays a pivotal role.
531 For instance, when group size is small, the effect of environmental stability of cooperation
532 significantly depends on the mode of dispersal. When individuals disperse independently, the
533 degree of environmental stability has a large impact on cooperation. By contrast, when
534 individuals disperse in a group, the degree of environmental stability has little impact on
535 cooperation. This pattern, however, is reversed when individuals live in large social groups.
536
537 Our results contrast with the idea that dispersal and cooperation should in general be
538 negatively correlated, as proposed by classic hypotheses, such as the “habitat saturation”
539 (Selander, 1964; Brown, 1974; Emlen, 1982) or the “benefits of philopatry” hypothesis
540 (Stacey & Ligon, 1987, 1991). Another exception to the classic literature is the study of Le
541 Galliard et al. (2005) that also found a positive correlation between dispersal and cooperation.
542 However, the reasons underlying the positive correlation are diverse. In Le Galliard et al., an
543 elevated cost of mobility leads to an increase in both dispersal and cooperation. In our study,
544 by contrast, increased cost of dispersal leads to a decrease in both dispersal and cooperation.
545 In Le Galliard et al., increased dispersal and cooperation occurs because the cost of mobility
546 raises the levels of local aggregation. In our study, decreased dispersal occurs because of the
547 direct effect of the cost of dispersal. As such, decreased cooperation occurs because costly
548 dispersal decreases dispersal rates, and lower dispersal rates raises kin competition, which
549 ultimately leads to decreased cooperation.
550
551 Understanding the evolutionary consequences of the complex interactions between dispersal
552 and cooperation is a non-trivial task. Species will differ in many respects regarding their life-
553 cycle, breeding system, and genetics. Extending our model to take into account species-

554 specific biological factors presents an exciting and promising line of future research. For
555 example, we might consider populations in which group size varies (e.g. Rodrigues &
556 Gardner, 2013a) or cases in which group members differ in their quality (e.g. Rodrigues &
557 Gardner, 2013b). Furthermore, one may also consider situations in which, alongside the
558 evolution of dispersal, budding itself is also an evolving trait rather than a fixed parameter.
559 Our analysis here provides a general framework to build and extend upon, so we might
560 understand how budding influences the joint evolution of dispersal and cooperation within
561 the context of a complex biological system.

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Tables

781

782 **Table 1** | Defined list of parameters used in model

Parameter	Definition
α	Probability that a patch will remain habitable
β	Probability that a patch will remain inhabitable
k	Cost of dispersal
m	Probability that an adult female moves to a new patch (facilitating genetic exchange)
n	Number of mothers within a patch
p	Proportion of habitable patches
τ	Temporal patch stability
x_A	Focal mother's investment in cooperation
y_A	Focal group's average investment in cooperation
z_A	Population's average investment in cooperation

	Probability of dispersing
z_D	

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Figures Legends

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Figure 1 | Lifecycle described by the model. Groups of mothers (n) exist within habitable

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patches (white), also present are non-habitable patches (grey). Individuals within the focal

794

patch will produce $F(x_A, y_A)$ offspring, yield is determined as a function of the focal mother's

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investment in cooperation, x_A , and the focal group's average investment in cooperation, y_A .

796

Mature adult buds will disperse to all patches (z_D) or remain in their natal patch ($1 - z_D$) and

797

compete for patch occupancy; migration between patches facilitates genetic exchange

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between buds (m). Patch quality has the potential to change after bud dispersal and

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competition, a patch may remain habitable (α), become inhabitable ($1 - \alpha$), remain

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inhabitable (β), or become habitable ($1 - \beta$). Buds within inhabitable patches will perish; the

801

cycle begins again.

802

803

Figure 2 | [a] The direct (v_D ; solid lines) and indirect (ρ_D ; dashed lines) benefit of dispersal

804

as a function of the cost of dispersal (k). [c] The kin selected benefit (v_A ; solid lines) and the

805

kin competition cost (ρ_A ; dashed lines) as a function of the cost of dispersal (k). [b,d] The ES

- 806 dispersal rates (z_D^*) and the ES investment in cooperation (z_A^*) as a function of the cost of
- 807 dispersal (k). Parameter values: $[a-d] m = 0.01, n = 5, p = 0.5, [a,c] z_D = 0.5$.

808 **Figure 3** | [a] The direct (v_D ; solid lines) and indirect (ρ_D ; dashed lines) benefit of dispersal
809 as a function of patch occupancy (p). [c] The kin selected benefit (v_A ; solid lines) and the kin
810 competition cost (ρ_A ; dashed lines) as a function of patch occupancy (p). [b,d] The ES
811 dispersal rates (z_D^*) and the ES investment in cooperation (z_A^*) as a function of patch
812 occupancy (p). Parameter values: [a-d] $m = 0.01, n = 5, k = 0.5$, [a,c] $z_D = 0.5$.

813

814 **Figure 4** | [a] The direct (v_D ; solid lines) and indirect (ρ_D ; dashed lines) benefit of dispersal
815 as a function of the temporal correlation (τ). [c] The kin selected benefit (v_A ; solid lines) and
816 the kin competition cost (ρ_A ; dashed lines) as a function of the temporal correlation (τ). [b,d]
817 The ES dispersal rates (z_D^*) and the ES investment in cooperation (z_A^*) as a function of the
818 temporal correlation (τ). Parameter values: [a-d] $m = 0.01, n = 5, p = 0.5$, [a,c] $z_D = 0.5$.

819

820 **Figure 5 | Sign of the correlation between dispersal and cooperation;** as the cost of
821 dispersal changes [panels a-d], as the patch occupancy changes [panels e-g], and as the
822 temporal correlation changes [panel h], as a function of model parameters. The grey regions
823 are not mathematically tractable. The sign is given by the partial derivatives of the ES
824 strategies with respect to ∂ variable (either k, p , or τ) for each combination of parameter
825 values. Parameter values: [a-h] $m = 0.01, n = 5$. [a,e] $\tau = 0.0$ [b,f] $\tau = 0.5$. [c,g] $\tau = 1.0$. [d,h] p
826 $= 0.5$.

827

828 **Figure 6 | ES dispersal and cooperation strategies under individual dispersal, and**
829 **partial and complete budding dispersal.** Bud size (n_B) changes relative to patch size (n)
830 under variable temporal instability (τ) ranging from -1.0 to 1.0 (see legend). Parameter
831 values: $k = 0.5, p = 0.5, F_L = F_H/10, m = 0.01$.

832