

1 **Resource availability and adjustment of social behaviour influence patterns of**
2 **inequality and productivity across societies**

3
4 ***Supplementary material***

5
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Appendix A. Ecology

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Given the life-cycle outline in the main text, the ecological dynamics can be described by a transition matrix (Rodrigues and Gardner 2012) that is given by

$$\mathbf{E} = \begin{pmatrix} p_{R \rightarrow R} & p_{P \rightarrow R} \\ p_{R \rightarrow P} & p_{P \rightarrow P} \end{pmatrix}. \quad (\text{A1})$$

The right-eigenvector of matrix \mathbf{E} gives the fraction of each patch type at ecological equilibrium, which is given by

$$p_R = \frac{1 - p_{P \rightarrow P}}{2 - (p_{R \rightarrow R} + p_{P \rightarrow P})}, \text{ and} \quad (\text{A2})$$

$$p_P = 1 - p_R = \frac{1 - p_{R \rightarrow R}}{2 - (p_{R \rightarrow R} + p_{P \rightarrow P})}, \quad (\text{A3})$$

for resource-rich and resource-poor patches, respectively. If we define a random variable T_t , denoting the state of a focal patch in season t , then the coefficient of correlation between two successive seasons, denoted by τ , is defined as $\tau \equiv \text{cov}(T_t, T_{t+1}) / \sqrt{\text{var}(T_t) \text{var}(T_{t+1})}$. Expanding the right-hand side of this equation, the coefficient of correlation becomes

$$\tau = p_{R \rightarrow R} - (1 - p_{P \rightarrow P}), \quad (\text{A4})$$

where $-1 \leq \tau \leq 1$ (Rodrigues and Gardner 2012).

Appendix B. Reproductive success

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Here I define the expressions for the class-specific reproductive success of breeders, i.e. $w_{\rho\pi\rightarrow\eta\gamma}$. Let us denote the probability that a patch in state π becomes a patch in state γ in the next generation by $p_{\pi\rightarrow\gamma}$. The reproductive success of a mother in condition ρ in a patch of quality π through her offspring that become breeders in condition η in patches of quality γ is then given by

$$w_{\rho\pi\rightarrow\eta\gamma} = f_{\rho\pi}(x_{H\pi}, x_{L\pi}) \left(w_{\pi}^{\phi}(x_{H\pi}, x_{L\pi}) p_{\pi\rightarrow\gamma} + \left(\sum_{\gamma' \in \{R, P\}} p_{\gamma'} p_{\gamma' \rightarrow \gamma} w_{\gamma'}^{\delta}(z_{H\gamma'}, z_{L\gamma'}) \right) \right), \pi \in \{R, P\} \quad (B1)$$

where

$$w_{\pi}^{\phi}(x_{H\pi}, x_{L\pi}) = \frac{1-d}{(\sum_{\rho \in \{H, L\}} f_{\rho\pi}(x_{H\pi}, x_{L\pi}))^{(1-d)} + (\sum_{\gamma \in \{R, P\}} p_{\gamma} \sum_{\rho \in \{H, L\}} f_{\rho\gamma}(z_{H\gamma}, z_{L\gamma}))^{d(1-c)}}, \quad (B2)$$

is the reproductive success of a single philopatric offspring competing for a breeding site in a type- π patch, and

$$w_{\gamma'}^{\delta}(z_{H\gamma'}, z_{L\gamma'}) = \frac{d(1-c)}{(\sum_{\rho \in \{H, L\}} f_{\rho\gamma'}(z_{H\gamma'}, z_{L\gamma'}))^{(1-d)} + (\sum_{\gamma \in \{R, P\}} p_{\gamma} \sum_{\rho \in \{H, L\}} f_{\rho\gamma}(z_{H\gamma}, z_{L\gamma}))^{d(1-c)}}, \quad (B3)$$

is the reproductive success of a single dispersed offspring competing for a breeding site in a type- γ' patch.

Appendix C. Marginal fitness

As we have seen in the main text, the average fitness of a random recipient is given by

$$\frac{d\bar{w}}{dg_{\alpha\sigma}} = \sum_{\pi \in \{R,P\}} \sum_{\rho \in \{H,L\}} u_{\rho\pi} v_{\rho\pi} \frac{dW_{\rho\pi}}{dg_{\alpha\sigma}}. \quad (C1)$$

From equation (3) in the main text, expanding the right-hand side of equation (C1), and because social interactions occur within the local patch only, we get

$$\frac{d\bar{w}}{dg_{\alpha\sigma}} = \sum_{\rho \in \{H,L\}} u_{\rho\pi} \left(\sum_{\gamma \in \{R,P\}} \sum_{\eta \in \{H,L\}} \sum_{\lambda \in \{H,L\}} \frac{\partial w_{\rho\phi \rightarrow \eta\gamma}}{\partial x_{\lambda\sigma}} \frac{dx_{\lambda\sigma}}{dg_{\lambda\sigma}} \frac{dg_{\lambda\sigma}}{dg_{\alpha\sigma}} v_{\eta\gamma} \right), \quad (C2)$$

where: the partial derivatives represent the effect of the phenotype on the class-specific reproductive success; the derivatives of the phenotype with respect to the breeding value, denoted by g , represent the phenotype-to-genotype mapping, which, without loss of generality can be set to one; and the derivatives of breeding values with respect to breeding values represent the coefficient of consanguinity, $g_{\alpha\lambda,\sigma}$, between the actor α and the recipient λ (Bulmer 1994; Rodrigues and Gardner 2016). If we expand the right-hand side of equation (C2) and if we normalise it with respect to the coefficient of consanguinity between the actor and herself, we obtain Hamilton's rule given by equation (6) in the main text.

Appendix D. Stable-class frequencies and reproductive value

From the expressions for the reproductive success of breeding females, as derived above in section B, we define a matrix of expected fitness, which is given by

98
$$\mathbf{w} = \begin{pmatrix} W_{HR \rightarrow HR} & W_{LR \rightarrow HR} & W_{HP \rightarrow HR} & W_{LP \rightarrow HR} \\ W_{HR \rightarrow LR} & W_{LR \rightarrow LR} & W_{HP \rightarrow LR} & W_{LP \rightarrow LR} \\ W_{HR \rightarrow HP} & W_{LR \rightarrow HP} & W_{HP \rightarrow HP} & W_{LP \rightarrow HP} \\ W_{HR \rightarrow LP} & W_{LR \rightarrow LP} & W_{HP \rightarrow LP} & W_{LP \rightarrow LP} \end{pmatrix}. \quad (\text{D1})$$

99

100 The stable-class frequencies (u) are given by the elements of the right-eigenvector
 101 corresponding to the leading eigenvector of this matrix. The reproductive value of a breeding
 102 adult (v) is given by the elements of the left-eigenvector corresponding to the leading
 103 eigenvalue of the fitness matrix \mathbf{w} , where we assume a neutral population (i.e. $x = z$; Fisher
 104 1930; Taylor 1990; Taylor and Frank 1996). Note that the reproductive value of a quality- α
 105 breeder in a type- σ patch, $v_{\alpha\sigma}$, is given by the total number of offspring she has, $f_{\alpha\sigma}$, times the
 106 reproductive value of each offspring, denoted by $V_{\alpha\sigma}$. Therefore, the reproductive value of an
 107 offspring of a quality- α individual in a type- σ patch is simply given by

108

109
$$V_{\alpha\sigma} = \frac{v_{\alpha\sigma}}{f_{\alpha\sigma}}. \quad (\text{D2})$$

110

111 The reproductive success of a focal quality- α breeder in a type- σ patch via offspring that
 112 remain in the native patch is then given by

113

114
$$w_{\alpha\sigma \rightarrow \eta\gamma}^{\phi} = f_{\alpha\sigma}(z_{H\sigma}, z_{L\sigma}) w_{\sigma}^{\phi} p_{\sigma \rightarrow \gamma}. \quad (\text{D3})$$

115

116 This is simply the total number of offspring produced by a focal breeder multiplied by the
 117 probability that the offspring obtains a breeding site, which must be also multiplied by the
 118 probability that the patch becomes a type- γ patch. Finally, the philopatric component of a
 119 breeder's reproductive value is given by

120

$$121 \quad v_{\alpha\sigma}^{\phi} = \sum_{\gamma \in \{R,P\}} \sum_{\eta \in \{H,L\}} w_{\alpha\sigma \rightarrow \eta\gamma}^{\phi} v_{\eta\gamma}. \quad (D4)$$

122

123 This is the reproductive success of each breeder times the reproductive value of each
 124 successful offspring according to their class.

125

126 **Appendix E. Relatedness**

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128 To determine the relatedness coefficient between the high- and low-quality individuals I
 129 define recursion equations that describe how the genetic structure of the population change
 130 from one generation to the next (Bulmer 1994; Rodrigues and Gardner 2013a,b). The
 131 probability that a resource-rich patch (or a resource-poor patch) was a resource-rich patch in
 132 the previous generation is $p_{R \rightarrow R}$ (or $p_{P \rightarrow R}$), while the probability that it was a low-quality
 133 patch in the previous generation is $p_{R \rightarrow P}$ (or $p_{P \rightarrow P}$). The probability that two adults sampled at
 134 random are both born in a resource-rich patch (or in a resource-poor patch) is

135

$$136 \quad \varphi_{\sigma} = \left(\frac{(f_{H\sigma} + f_{L\sigma})(1-d)}{(f_{H\sigma} + f_{L\sigma})(1-d) + (p(f_{HR} + f_{LR}) + (1-p)(f_{HP} + f_{LP}))(1-c)} \right)^2. \quad (E1)$$

137

138 The probability that a philopatric juvenile is offspring of the high-quality breeder in a
 139 resource-rich patch (or in a resource-poor patch) is $U_{HR} = f_{HR}/(f_{HR} + f_{LP})$ (or $U_{HP} =$
 140 $f_{HP}/(f_{HP} + f_{LP})$), and the probability that a philopatric juvenile is offspring of the low-quality
 141 breeder in a resource-rich patch (or in a resource-poor patch) is $U_{LR} = f_{LR}/(f_{HR} + f_{LR})$ (or $U_{LP} =$
 142 $f_{LP}/(f_{HP} + f_{LP})$). In resource-rich patches (or in resource-poor patches), with probability U_{HR}^2 (or
 143 U_{HP}^2) and with probability U_{LR}^2 (or U_{LP}^2) two juveniles sampled at random are siblings, in
 144 which case their relatedness is 1. In resource-rich patches (or in resource-poor patches), with

145 probability $2U_{HR}U_{LR}$ (or $2U_{HP}U_{LP}$) two juveniles sampled at random are not siblings, in
 146 which case their relatedness is r_R (or r_P). The recursion equations are the given by

147

$$148 \quad r'_\sigma = \sum_{\gamma \in \{R,P\}} p_{\gamma|\sigma} \varphi_\gamma (U_{H\gamma}^2 + U_{L\gamma}^2 + 2U_{H\gamma}U_{L\gamma}r'_\gamma) \quad , \sigma \in \{R, P\} \quad (E2)$$

149

150 At equilibrium, the relatedness coefficients among breeders will not change between
 151 successive generations, in which case $r'_R = r_R$, and $r'_P = r_P$. We can then solve this system of
 152 equation to find the relatedness coefficients among breeders.

153

154 **Appendix F. Optimal behaviour and convergence stability**

155

156 Here I determine the convergence stability (Christiansen 1991; Eshel 1996; Taylor 1996) of
 157 the optimal competitive effort strategies. To determine if a set of optimal competitive effort
 158 strategies is convergence stable we define the matrix:

159

$$160 \quad \left(\begin{array}{cccc} \frac{\partial(S_{HR}|x=z)}{\partial z_{HR}} & \frac{\partial(S_{HR}|x=z)}{\partial z_{LR}} & \frac{\partial(S_{HR}|x=z)}{\partial z_{HP}} & \frac{\partial(S_{HR}|x=z)}{\partial z_{LP}} \\ \frac{\partial(S_{LR}|x=z)}{\partial z_{HR}} & \frac{\partial(S_{LR}|x=z)}{\partial z_{LR}} & \frac{\partial(S_{LR}|x=z)}{\partial z_{HP}} & \frac{\partial(S_{LR}|x=z)}{\partial z_{LP}} \\ \frac{\partial(S_{HP}|x=z)}{\partial z_{HR}} & \frac{\partial(S_{HP}|x=z)}{\partial z_{LR}} & \frac{\partial(S_{HP}|x=z)}{\partial z_{HP}} & \frac{\partial(S_{HP}|x=z)}{\partial z_{LP}} \\ \frac{\partial(S_{LP}|x=z)}{\partial z_{HR}} & \frac{\partial(S_{LP}|x=z)}{\partial z_{LR}} & \frac{\partial(S_{LP}|x=z)}{\partial z_{HP}} & \frac{\partial(S_{LP}|x=z)}{\partial z_{LP}} \end{array} \right) \Bigg|_{z=z^*} \quad (F1)$$

161

162 where $S_{p\sigma}$ represents the left-hand side of Hamilton's rule for the expression of the behaviour
 163 of each individual depending on its status and patch type. The set of optimal strategies (z_{HR}^* ,
 164 z_{LR}^* , z_{HP}^* , and z_{LP}^*) are convergence stable if the eigenvalues of matrix (F1) have negative real
 165 parts (Otto and Day 2007).

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Appendix G. Fecundity and social interactions

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170 G1. General behavioural function

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172 In general, the fecundity of a focal individual depends on the resources available in the local

173 patch, denoted by μ_σ , on its personal quality, denoted by $q_{\rho\sigma}$, and on social interactions,

174 denoted by $s_{\rho\sigma}$. Thus, the fecundity of a focal class- ρ individual in a type- σ patch is given by

175

$$176 \quad f_{\rho\sigma} = \mu_\sigma (q_{\rho\sigma} + s_{\rho\sigma}). \quad (\text{G1.1})$$

177

178 As described in the main text, I assume that the behavioural function for social interactions

179 depends on a personal component, denoted by Ψ , and on a group component, denoted by Θ .

180 The personal component depends on the phenotype $x_{\rho\sigma}$ of the focal individual, whereas the

181 group component depends on the phenotype of all individuals in the group, which I represent

182 by the vector of phenotypes \mathbf{x}_σ . Thus, the social interactions term take the following

183 functional form:

184

$$185 \quad s_{\rho\sigma} = \Psi(x_{\rho\sigma})\Theta(\mathbf{x}_\sigma). \quad (\text{G1.2})$$

186

187 The fecundity cost of the behaviour is then given by the effect of the focal's phenotype on the

188 personal component of the social interactions. Thus

189

$$190 \quad C_{\rho\sigma} = -\frac{\partial f_{\rho\sigma}}{\partial x_{\rho\sigma}} = -\mu_\sigma \frac{\partial \Psi(x_{\rho\sigma})}{\partial x_{\rho\sigma}} \Theta(\mathbf{x}_\sigma). \quad (\text{G1.3})$$

191

192 The fecundity benefit of the behaviour is given by the effect of the actor's phenotype on the

193 group component of the social interactions. Thus

194

$$195 \quad B_{\rho\sigma} = \frac{\partial f_{\rho\sigma}}{\partial x_{\alpha\sigma}} = \mu_{\sigma} \Psi(z_{\rho\sigma}) \frac{\partial \theta(x_{\sigma})}{\partial x_{\alpha\sigma}}. \quad (G1.4)$$

196

197 In the main text, I consider that the behavioural functions give form to a competitive effort
198 game between group mates. Below, I explore different functional forms for the social
199 interactions among group mates.

200

201 G2. Investment in a public good

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203 Let us consider the evolution of investment in a public good. I assume that investment in a
204 public good is costly to the actor, but increases the pool of publically available resources. The
205 pool of available resources is assumed to be fairly distributed among all social partners,
206 including the contributor. Investment in the public good is costly, in the sense that the actor's
207 ability to access the pool of publically available resources is impaired by the expression of
208 the behaviour. Given these assumptions, the behavioural function of the social interactions
209 takes the form

210

$$211 \quad s_{\rho\sigma} = (1 - x_{\rho\sigma}) \frac{1}{n_{\sigma}} \sum_{\eta \in \{H,L\}} x_{\eta\sigma}, \quad (G2.1)$$

212

213 where: $\Psi(x_{\rho\sigma}) = (1 - x_{\rho\sigma})$; $\theta(x_{\sigma}) = \frac{1}{n_{\sigma}} \sum_{\eta \in \{H,L\}} x_{\eta\sigma}$; and $n_{\sigma} = 2$ is the number of

214 individuals in the patch. From equations (G1.3) and (G2.1), the cost of the investment in the
215 public good is given by

216

$$217 \quad C_{\rho,\sigma} = \frac{1}{n_{\sigma}} \sum_{\eta \in \{H,L\}} x_{\eta,\sigma}, \quad (G2.2)$$

218

219 which means that the cost paid by the actor is given by the amount of public good available
220 to the focal recipient. From equations (G1.4) and (G2.1), we find that the benefit provided by
221 the focal individual to social partners is given by

222

$$223 \quad B_{\rho\eta,\sigma} = (1 - x_{\eta,\sigma}) \frac{1}{n_{\sigma}}. \quad (G2.3)$$

224

225 In Fig. G2.1 and Fig. G2.2 I present the results for this behavioural function. We find that the
226 results are qualitatively similar to those obtained in the main text for a different behavioural
227 function. In particular, we find a patch productivity and inequality are negatively correlated.

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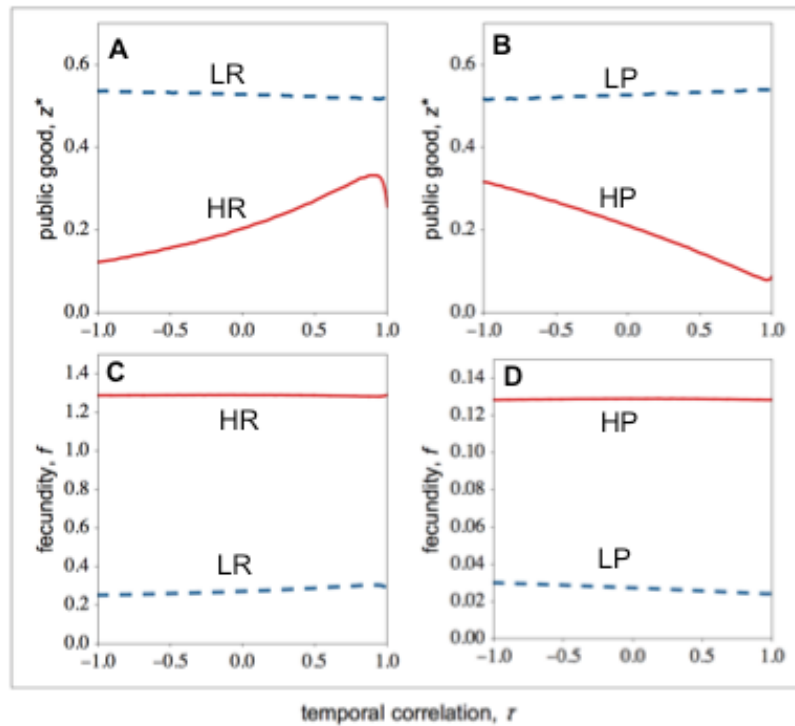
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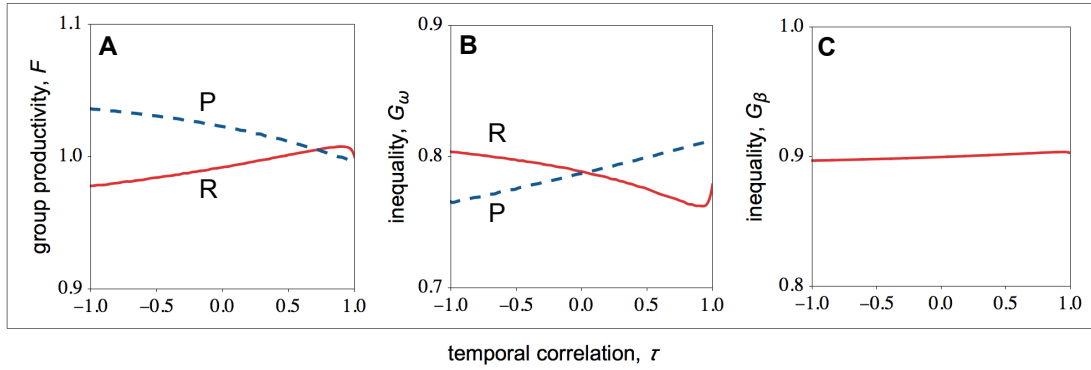


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245 *Figure G2.1.* Optimal investment in public good (z^*) and fecundity (f) of high- (solid lines)
 246 and low-quality (dashed lines) individuals as a function of the temporal correlation (τ). [A,C]
 247 In resource-rich patches, average investment in the public good increases as the environment
 248 becomes more stable. [B,D] In resource-poor patches, average investment in the public good
 249 decreases as the environment become more stable. Environmental stability leads to higher
 250 average fecundity in resource-rich patches, while it leads to lower average fecundity in
 251 resource-poor patches. Parameter values: $c = 0.9$, $d = 0.1$, $p = 0.5$, $q_{HR} = q_{HP} = 1.0$, $q_{LR} = q_{LP}$
 252 $= 0.1$, $\mu_R = 1.0$, $\mu_P = 0.1$.

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256 *Figure G2.2.* Relative group productivity (F), within-group inequality (G_ω), and between-
 257 group inequality (G_β) as a function of the temporal correlation (τ). Group productivity is
 258 plotted relative to the baseline group productivity in each patch. Baseline group productivity
 259 is given by group productivity in a stable environment (i.e. $F_0 = F(\tau = 1)$). Thus, $F = F(\tau)/F_0$.

260 [A] Environmental stability in resource-availability leads to higher productivity in resource-
 261 rich patches, but to lower productivity in resource-poor patches. [B] In resource-rich patches,
 262 inequality decreases as the environment becomes more stable. In resource-poor patches,
 263 inequality increases as the environment becomes more stable. [C] Productivity in resource-
 264 rich patches increases, relative to that of resource-poor patches, as the environment becomes
 265 more stable. Parameter values: $c = 0.9$, $d = 0.1$, $p = 0.5$, $q_{HR} = q_{HP} = 1.0$, $q_{LR} = q_{LP} = 0.1$, $\mu_R =$
 266 1.0 , $\mu_P = 0.1$.

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276 G3. Simple competitive effort

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278 In the main text, I considered a competitive effort behavioural function. In this section, I
279 consider a variation of this behavioural function. More specifically, I consider a case in
280 which the fraction of resources obtained by the focal individual is not relative to the average
281 competitive effort in the local group, as in the main text (cf Frank 1994). Thus, I assume that
282 competitive effort, denoted by $x_{\rho\sigma}$, directly increases the fraction of resources obtained by
283 the focal individual, but it reduces the focal's contribution to the common pool of resources.
284 The fecundity of a focal individual through social interactions is then given by

285

286
$$s_{\rho\sigma} = x_{\rho\sigma} \left(1 - \frac{1}{n_\sigma} \sum_{\eta \in \{H,L\}} x_{\eta\sigma} \right). \quad (G3.1)$$

287

288 where: $\Psi(x_{\rho\sigma}) = x_{\rho\sigma}$ and $\Theta(x_\sigma) = \left(1 - \frac{1}{n_\sigma} \sum_{\eta \in \{H,L\}} x_{\eta\sigma} \right)$. From equations (G1.3) and
289 (G3.1), the cost of competitive effort becomes

290

291
$$C_{\rho\sigma} = - \left(1 - \frac{1}{n_\sigma} \sum_{\eta \in \Omega_\sigma} x_{\eta\sigma} \right). \quad (G3.2)$$

292

293 Note that the cost is negative. That is the investment in competitive effort confers a direct
294 benefit to the recipient that is proportional to the pool of resources available to the recipient.
295 From equations (G1.4) and (G3.1), the benefit provided by the focal actor to a group mate is
296 given by

297

298
$$B_{\alpha\rho,\sigma} = -z_{\rho,\sigma} \frac{1}{n_\sigma}. \quad (G3.3)$$

299

300 Note that the benefit is negative. That is an additional investment in competitive effort
301 reduces the amount of resources publically available to each of the social partners. In Fig.
302 G3.1 and Fig. G3.2, I present the results for this behavioural function. We find that the results
303 are qualitatively similar to those obtained in the main text for a different behavioural
304 function. In particular, we find a patch productivity and inequality are negatively correlated.

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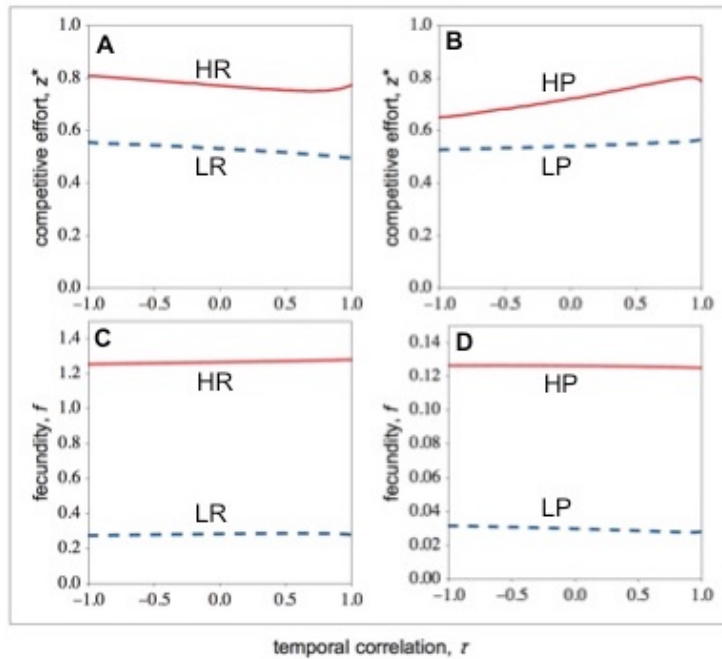
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321 *Figure G3.1.* Competitive effort (z) and fecundity (f) of high- (solid lines) and low-quality
 322 (dashed lines) individuals as a function of the temporal correlation (τ). [A,C] In resource-rich
 323 patches, temporal stability in resource-availability decreases average investment in
 324 competitive effort. [C,D] In resource-poor patches, temporal stability in resource-availability
 325 increases average investment in competitive effort. Temporal stability leads to higher average
 326 fecundity in resource-rich patches, while it leads to lower average fecundity in resource-poor
 327 patches. Parameter values: $c = 0.9$, $d = 0.1$, $p = 0.5$, $q_{HR} = q_{HP} = 1.0$, $q_{LR} = q_{LP} = 0.1$, $\mu_R = 1.0$,
 328 $\mu_P = 0.1$.

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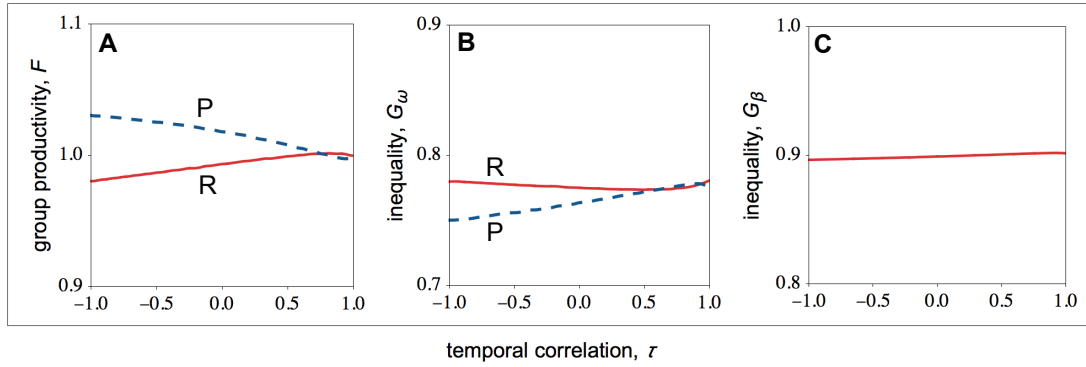
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338 *Figure G3.2.* Relative group productivity (F), within-group inequality (G_ω), and between-
 339 group inequality (G_β) as a function of the temporal correlation (τ). Group productivity is
 340 plotted relative to the baseline group productivity for each patch. Baseline group productivity
 341 is given by group productivity in a stable environment (i.e. $F_0 = F(\tau = 1)$). Thus, $F = F(\tau)/F_0$.

342 [A] Temporal stability in resource-availability leads to lower productivity in resource-rich
 343 patches, while it leads to higher productivity in resource-poor patches. [B] In resource-rich
 344 patches, inequality decreases as the environment becomes more stable. In resource-poor
 345 patches, inequality increases as the environment becomes more stable. [C] Productivity in
 346 resource-rich patches increases, relative to that of resource-poor patches, as the environment
 347 becomes more stable such that inequality between patch types increases. Parameter values: c
 348 $= 0.9$, $d = 0.1$, $p = 0.5$, $q_{HR} = q_{HP} = 1.0$, $q_{LR} = q_{LP} = 0.1$, $\mu_R = 1.0$, $\mu_P = 0.1$.

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358 **Appendix H. Early-life acquisition of individual quality**

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360 Reproductive success and reproductive value

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362 We assume that mothers produce a fraction Q of high-quality offspring, and a fraction $1 - Q$
 363 of low-quality offspring, irrespective of a mother's quality. As a result, the total proportion of
 364 high-quality offspring competing for breeding sites in any focal patch is given by Q while the
 365 proportion of low-quality offspring competing for breeding sites is given by $1 - Q$. Thus, the
 366 probability that the focal patch becomes a type- $\kappa\lambda$ patch is given by

367

368
$$p_{\kappa\lambda} = \binom{n}{m} Q^m (1 - Q)^{n-m}, \quad (\text{H1})$$

369

370 where κ and λ are the quality of each breeder, m is the number of high-quality breeders in the
 371 patch, and n is the patch size, which we set to 2.

372

373 Given the state of the patch, we can now define the number of breeding spots for each type of
 374 offspring quality. Let us denote the number of quality- i breeding spots in a type- ij patch by
 375 o_{ij} . Thus,

376

377
$$o_{ij} = \begin{cases} 2 & , i = H, j = H \\ 1 & , i = H, j = L \\ 1 & , i = L, j = H \\ 2 & , i = L, j = L \end{cases} \quad (\text{H2})$$

378

379 Let us define the set $\Omega = \{HH, HL, LL\}$, which includes the set of all patch types, noting that
 380 the type- HL patch is the same as the type- LH patch. The reproductive success of a quality- ρ

381 mothers with a quality- μ mother as social partner in a type- π patch (where π denotes the
 382 resources available in the patch, i.e. either ‘R’ or ‘P’) through offspring that remain
 383 philopatric is given by

384

$$385 \quad w_{\rho\mu,\pi}^{\phi}(x_{H\pi}, x_{L\pi}) = \frac{f_{\rho\mu,\pi}(1-d)}{(f_{\rho\mu,\pi} + f_{\mu\rho,\pi})(1-d) + (\sum_{\gamma \in \{R,P\}} p_{\gamma} \sum_{\mu\rho \in \Omega} p_{\mu\rho} (f_{\mu\rho,\gamma} + f_{\rho\mu,\gamma}))d(1-c)}. \quad (\text{H3})$$

386

387 The reproductive success of a quality- ρ mothers with a quality- μ mother as social partner in a
 388 type- π patch through offspring that disperse away from the natal patch and arrive at a type- ω
 389 patch with a quality- ε and a quality- ϱ individual is given by

390

$$391 \quad w_{\rho\mu,\pi \rightarrow \varepsilon\varrho,\omega}^{\delta}(x_{H\pi}, x_{L\pi}) = \frac{f_{\rho\mu,\pi}d(1-c)}{(f_{\varepsilon\varrho,\omega} + f_{\varrho\varepsilon,\omega})(1-d) + (\sum_{\gamma \in \{R,P\}} p_{\gamma} \sum_{\mu\rho \in \Omega} p_{\mu\rho} (f_{\mu\rho,\gamma} + f_{\rho\mu,\gamma}))d(1-c)}. \quad (\text{H4})$$

392

393 That is, the focal quality- ρ mother produces $f_{\rho\mu,\pi}$, a fraction d of which disperse, and where
 394 only a fraction $1 - c$ survive dispersal.

395

396 The reproductive success of a quality- ρ mother with a quality- μ mother as a social partner in
 397 a type- π patch through offspring that become quality- κ mothers with quality- λ mothers as
 398 social partners in a type- ψ patch is given by

399

$$400 \quad w_{\rho\mu,\pi \rightarrow \kappa\lambda,\psi} = w_{\rho\mu,\pi}^{\phi} p_{\pi \rightarrow \psi} p_{\kappa\lambda} o_{\kappa\lambda} + (\sum_{\gamma \in \{R,P\}} p_{\gamma} p_{\gamma \rightarrow \psi} \sum_{\varepsilon\varrho \in \Omega} p_{\varepsilon\varrho} w_{\rho\mu,\pi \rightarrow \varepsilon\varrho,\gamma}^{\delta}) p_{\kappa\lambda} o_{\kappa\lambda}. \quad (\text{H5})$$

401

402 That is, a quality- ρ focal mother with a quality- μ social partner in a type- π patch wins a

403 breeding spot in the local patch with probability $w_{\rho\mu,\pi}^{\phi}$. With probability $p_{\pi \rightarrow \psi}$ the type- π

404 patch becomes a type- ψ patch. The probability that the patch becomes a patch with a quality-
 405 κ and a quality- λ breeder is given by $p_{\kappa\lambda}$, in which case there are $o_{\kappa\lambda}$ quality- κ breeding spots
 406 available.

407

408 The focal quality- ρ breeder also derives fitness from offspring that disperse from the local
 409 patch. With probability p_γ the dispersed offspring arrive at a type- γ patch, which becomes a
 410 type- ψ patch with probability $p_{\gamma\rightarrow\psi}$. With probability $p_{\varepsilon\varrho}$ the type- γ patch has a quality- ε
 411 breeder and a quality- ϱ breeder, in which case the probability that the focal quality- ρ breeder
 412 wins a breeding spot through the dispersed offspring is given by $w_{\rho\mu,\pi\rightarrow\varepsilon\varrho,\gamma}^\delta$. Finally, the type-
 413 γ patches accommodate a quality- κ and a quality- λ breeder with probability $p_{\kappa\lambda}$, in which
 414 case there are $o_{\kappa\lambda}$ quality- κ breeding spots.

415

416 From equations (A2-A4), we can then define the 8×8 fitness matrix, denoted by \mathbf{w} , as

417

$$418 \quad \mathbf{w} = (w_{\rho\mu,\pi\rightarrow\kappa\lambda,\psi})_{8\times 8}. \quad (\text{H6})$$

419

420 From the fitness matrix, we find the reproductive value of each mother by calculating the left
 421 eigenvector associated with the eigenvalue one.

422

423 Relatedness

424

425 The relatedness coefficient depends on the previous state of the patch. The probability that a
 426 type- κ patch was a type- π patch is given by $p_{\pi\rightarrow\kappa}$. The probability that the type- π patch was a
 427 type- $\mu\rho$ is given by $p_{\mu\rho}$. The probability that two random offspring are both offspring of the

428 quality- ρ breeder is given by $(w_{\rho\mu,\pi}^\phi)^2$ and the probability that two random offspring are both
 429 offspring of the quality- μ breeder is given by $(w_{\mu\rho,\pi}^\phi)^2$, in both cases the relatedness
 430 coefficient is 1. The probability that both juveniles are offspring of different parents is given
 431 by $2w_{\rho\mu,\pi}^\phi w_{\mu\rho,\pi}^\phi$, in which case the relatedness coefficient is $r_{\mu\rho,\pi}$. The recursion equation that
 432 gives the relatedness coefficient between a quality- i and a quality- j breeder in a type- κ patch
 433 is given by

$$435 \quad r_{ij,\kappa} = \sum_{\pi \in \{R,L\}} p_{\pi \rightarrow \kappa} \left(\sum_{\mu \rho \in \Omega} p_{\mu\rho} \left((w_{\rho\mu,\pi}^\phi)^2 + (w_{\mu\rho,\pi}^\phi)^2 + 2w_{\rho\mu,\pi}^\phi w_{\mu\rho,\pi}^\phi r_{\mu\rho,\pi} \right) \right). \quad (\text{H7})$$

436
 437 This gives a system of recursion equations that can be solved for the relatedness coefficients
 438 in each patch.

439

440 Hamilton's rule

441

442 To define Hamilton's rule, it is useful to define reproductive value of a breeder through
 443 offspring that remain in the local patch (i.e. the philopatric component of reproductive value).

444 With probability $p_{\pi \rightarrow \omega}$ the focal type- π patch becomes a type- ω patch. With probability $w_{\rho\mu,\pi}^\phi$

445 an offspring of the focal breeder wins a breeding site. Finally, with probability $p_{\kappa\lambda}$ the focal

446 patch accommodates a quality- κ and a quality- λ breeder, in which case there are $o_{\kappa\lambda}$ quality- κ

447 breeding sites available, and in which case the focal breeder derives a reproductive value

448 $v_{\kappa\lambda,\omega}$. Collecting all these terms together, we obtain

449

$$450 \quad v_{\rho\mu,\pi}^\phi = \sum_{\omega \in \{R,P\}} p_{\pi \rightarrow \omega} \left(\sum_{\kappa \in \{H,L\}} \sum_{\lambda \in \{H,L\}} w_{\rho\mu,\pi}^\phi p_{\kappa\lambda} o_{\kappa\lambda} \right). \quad (\text{H8})$$

451

452 It is also useful to define the probability that a single offspring remains in the local patch and
 453 wins a breeding site, which is given by

454

$$455 \quad W_{\rho\mu,\pi}^{\phi}(x_{H\pi}, x_{L\pi}) = \frac{(1-d)}{(f_{\rho\mu,\pi} + f_{\mu\rho,\pi})(1-d) + (\sum_{\gamma \in \{R,P\}} p_{\gamma} \sum_{\mu\rho \in \Omega} p_{\mu\rho})d(1-c)}. \quad (\text{H9})$$

456

457 Hamilton's rule, is then given by

458

$$459 \quad -C_{ij,\kappa}V_{ij,\kappa} + B_{ij,\kappa}V_{ij,\kappa}r_{ij,\kappa} - (B_{ij,\kappa} - C_{ij,\kappa})W_{ij,\kappa}^{\phi} (v_{ij,\kappa}^{\phi} + v_{ji,\kappa}^{\phi}r_{ij,\kappa}) > 0. \quad (\text{H10})$$

460

461

Appendix I. Patch size

462

463 In the main text, I assumed that each patch has exactly two breeders, one high- and one low-
 464 quality breeder. Here, I consider that patch size can be greater than two, but I keep the
 465 proportion of high- and low-quality breeders in each patch constant, such that the number of
 466 high-quality and low-quality breeders is given by a , with $a = n/2$. This extension of the model
 467 does not change the calculation of reproductive values, as the increase in competition for
 468 breeder sites, owing to the increase in the number of breeders, is exactly compensated by the
 469 increase in the number of breeding sites available. However, this extension of the model does
 470 change the calculation of relatedness.

471

472 The probability that a type- κ patch was a type- π patch is given by $p_{\pi \rightarrow \kappa}$. The probability that
 473 two random offspring are both philopatric offspring is given by φ_{π} . The probability that two
 474 random offspring are both offspring of a focal quality- ρ breeder is given by

475 $f_{\rho\pi}/(af_{H\pi} + (1-a)f_{L\pi})$. If the two random philopatric offspring do not share the same

476 mother, then the coefficient of relatedness is given by r_{π} . The recursion equation that gives

477 the relatedness coefficient in a type- κ patch is then given by

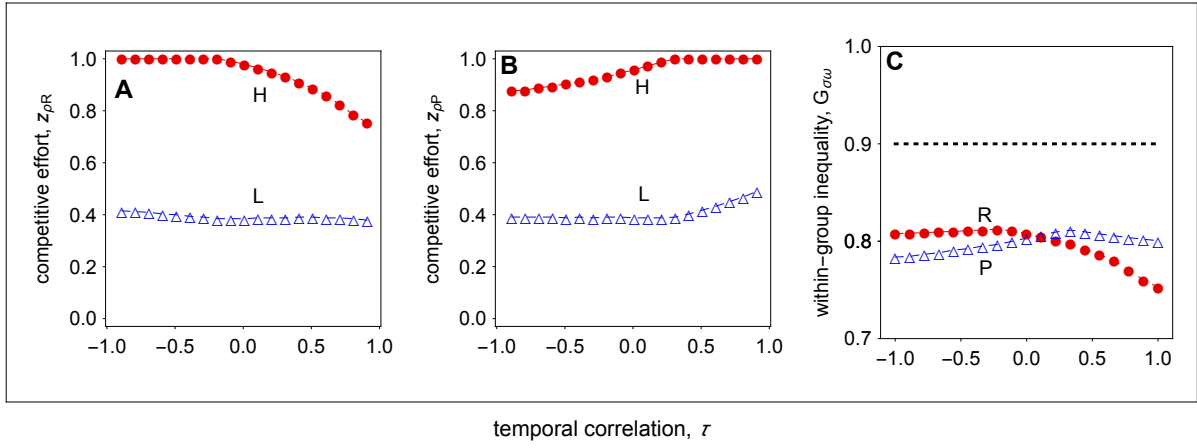
478

479
$$r_k' = \sum_{\pi \in \{R,L\}} p_{\pi \rightarrow \kappa} \varphi_{\pi} \left(\sum_{\rho \in \{H,L\}} a \left(\frac{f_{\rho\pi}}{af_{H\pi} + af_{L\pi}} \right)^2 + \left(1 - \sum_{\rho \in \{H,L\}} a \left(\frac{f_{\rho\pi}}{af_{H\pi} + af_{L\pi}} \right)^2 \right) r_{\pi} \right). \quad (11)$$

480

481 This gives a system of recursion equations that can be solved for the relatedness coefficients
 482 in each patch.

483



484

485 **Figure 11.** **A.** Competitive effort of high-quality and low-quality individuals as a function of
 486 the temporal correlation in resource-rich patches. **B.** Competitive effort of high-quality and
 487 low-quality individuals as a function of the temporal correlation in resource-poor patches. **C.**
 488 Coefficient of within-group inequality in resource-rich and resource-poor patches as a
 489 function of the temporal correlation. Parameter values: $n = 4$, $d = 0.1$, $c = 0.5$, $p = 0.5$, $q_{HR} =$
 490 $q_{HP} = 1.0$, $q_{LR} = q_{LP} = 0.1$, $\mu_R = 1.0$, $\mu_P = 0.1$.

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