Co-evolution of dispersal with behaviour favours social polymorphism

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Abstract

Dispersal determines gene flow among groups in a population and so plays a major role in many ecological and evolutionary processes, from biological invasions to species extinctions. Because patterns of gene flow shape kin structure, dispersal is also important to the evolution of social behaviours that influence reproduction and survival within groups. Conversely, dispersal patterns depend on kin structure and social behaviour. Dispersal and social behaviour therefore co-evolve but the nature and consequences of this interplay are not well understood. Here, we model this co-evolution and show that it readily leads to the emergence and maintenance of two broadly-defined social morphs: a sessile, benevolent morph expressed by individuals who tend to increase the fecundity of others within their group relative to their own; and a dispersive, self-serving morph expressed by individuals who tend to increase their own fecundity relative to others' within their group. This social polymorphism arises as a consequence of a positive linkage between the loci responsible for dispersal and social behaviour, leading to benevolent individuals preferentially interacting with relatives and self-serving individuals with non-relatives. We find that this positive linkage is favoured under a large spectrum of conditions, which suggests that an association between dispersal proclivity and other social traits should be common in nature. In line with this prediction, dispersing individuals across a wide range of organisms have been reported to differ in their social tendencies from non-dispersing individuals.

Introduction

Dispersal, the movement away from natal habitat to reproduce, is an important step in the life-history of most organisms (1, 2). At the population level, dispersal patterns shape kin structure which determines whether individuals interact and compete with relatives. This in turn influences the evolution of social behaviour such as helping or aggression (3, 4). At the same time, dispersal decisions are often influenced by kin and social interactions (5, 6, 7, 1, 8), resulting in the co-evolution among dispersal between groups and social behaviours within groups (e.g., 9, 10, 11, 12). However, the consequences of this co-evolution for within-species

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behavioural diversity (e.g., 13) remain elusive. Here, we model the co-evolution between unconditional dispersal and social behaviours, and show that it readily leads to a stable social polymorphism whereby individuals who disperse behave differently than non-dispersers.

To model social interactions within groups and dispersal between groups, we assume that the population is structured according to the standard island model (14, 5, 15), in which individuals belong to local groups of size N and interact socially only with other locals. As a baseline, we assume that individuals reproduce asexually and then die so that generations do not overlap. An offspring either remains in its natal population (with probability $1-d$), or disperses to another randomly chosen one (with probability d) at a cost c_{d}. Social interactions are modelled with a simple classical matrix game (16): individuals randomly pair up within their group and each independently chooses between two actions denoted B (with probability z) and M (with probability $1-z$). Depending on the action of each player, each reaps a material payoff (labelled R, S, T and P, Fig. 1a) that in turn linearly increases its fecundity. We assume that $T-S>0$, which means that an individual who plays B more often that its partner increases the partner's fecundity relative to its own, we therefore refer to action B as benevolent and conversely, M as self-serving (M.1 for details).

Results

First, we study mathematically the co-evolution of the probability d of dispersing with the probability z of adopting the benevolent action B when they are encoded by two linked loci that experience rare mutations with small quantitative effects (17) (M.2 for mathematical method). Initially monomorphic for both traits d and z, the population evolves gradually to converge towards an equilibrium for both traits. Whatever the initial population, dispersal always converges to an interior equilibrium d^* that depends on the cost of dispersal and group size, in agreement with previous results (5, 18) (Fig. 1b). There are four possible outcomes for the probability z of adopting the benevolent action B depending on payoffs (Fig. 1c): (1) when $R>T$ and $S>P$, it is always better to play B and so z evolves to one; (2) conversely, when $R<T$ and $S<P$, it is always better to play M so z evolves to zero; (3) when $R>T$ and $S<P$, it is better to play the same action, B or M, as the rest of the population, so z evolves to either one or zero, depending on the initial z in the population; and (4) when $R<T$ and $S>P$, it is better to play B in a M population and M in a B population, so z evolves to an interior equilibrium value $0<z^*<1$.

Once the population has converged to an interior equilibrium (d^*, z^*) for both dispersal and benevolence, the population either is maintained at this equilibrium by stabilising selection (i.e., the population is at a local ESS), or undergoes disruptive selection. Mathematical analysis reveals that disruptive selection occurs under a wide range of model parameters (Fig. 1d), and that it favours the emergence of two morphs: a more benevolent, sessile morph, and a more self-serving, dispersive morph (M.2 for details). To understand why selection favours these two morphs, consider an individual that expresses the more benevolent, sessile morph. Social behaviour and dispersal are genetically linked so its relatives are also more sessile, which in turn means that

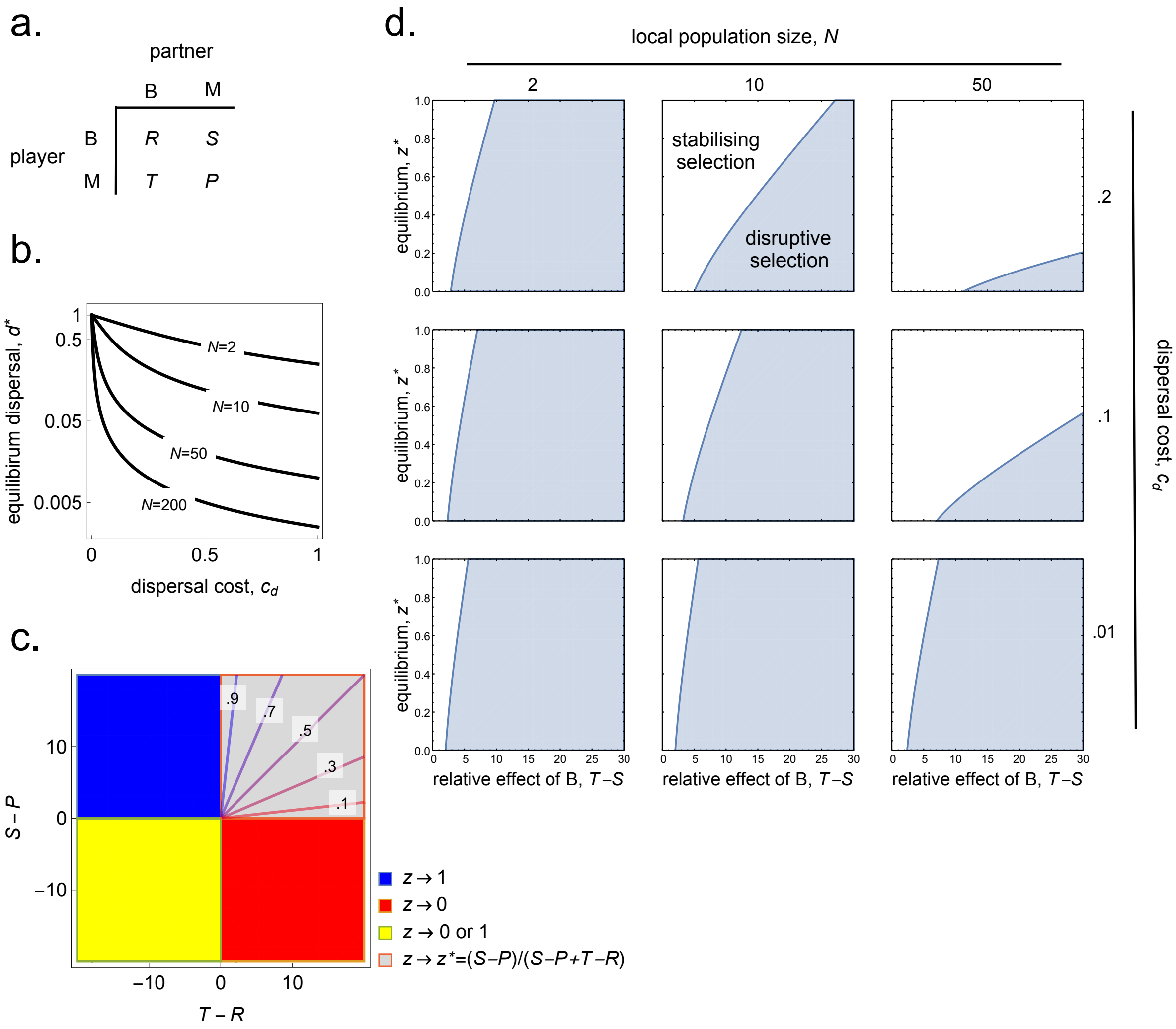

Figure 1: **Equilibrium and polymorphism when dispersal and social behaviour co-evolve.** **a.** Payoff to a player according to its behaviour and its partner's behaviour. **b.** Dispersal equilibrium d^* for different group sizes N. **c.** Outcomes for the probability z of adopting benevolent action B in terms of $T-R$ and $S-P$: (1) convergence to one (blue region); (2) convergence to zero (red region); (3) convergence to zero or one (yellow region); and (4) convergence to $0 < z^* = (S-P)/(S-P+T-R) < 1$ (grey region with z^* values shown by lines). **d.** Parameter region under which disruptive selection leads to polymorphism at the interior equilibrium (d^*, z^*) (shaded region, here shown with $T-R+S-P=1$). Disruptive selection is therefore favoured when groups are small, dispersal cost is low and benevolence has large effects (measured by $T-S$).

the recipients of its increased benevolence are more likely to be relatives. This positive interaction among kin then favours the invasion of the sessile, benevolent morph. Conversely, an individual expressing the more self-serving, dispersive morph is more likely to decrease the fitness of non-relatives, and this negative interaction among unrelated individuals favours the dispersive self-serving morph. When social behaviour and dispersal are genetically linked, polymorphism therefore arises due to the combined effects of dispersal on kin interaction and social behaviour on neighbours' fitness. In line with this, when only one trait, dispersal or benevolence, evolves and the other trait is fixed, the population remains monomorphic for a local ESS for all model parameters (M.2).

To check our mathematical analyses and investigate the long-term effects of disruptive selection, we ran computer simulations under conditions that should lead to polymorphism (M.3 for details). As predicted, the population first converges to the interior equilibrium for dispersal d^* and the probability z^* to adopt benevolent action B, and splits into two morphs, a more benevolent, sessile morph, and a more self-serving, dispersive morph (Fig. 2a). Competition among the two morphs then creates a positive feedback that favours more extreme variants: benevolent individuals become increasingly benevolent and sessile to compensate for noxious interactions with self-serving individuals, while self-serving individuals become increasingly self-serving to take advantage of benevolence, and increasingly dispersive to avoid decreasing the fitness of relatives. The population eventually stabilises for two highly-differentiated genetic morphs, resulting in a strong association among dispersal and social behaviour (Fig. 2b).

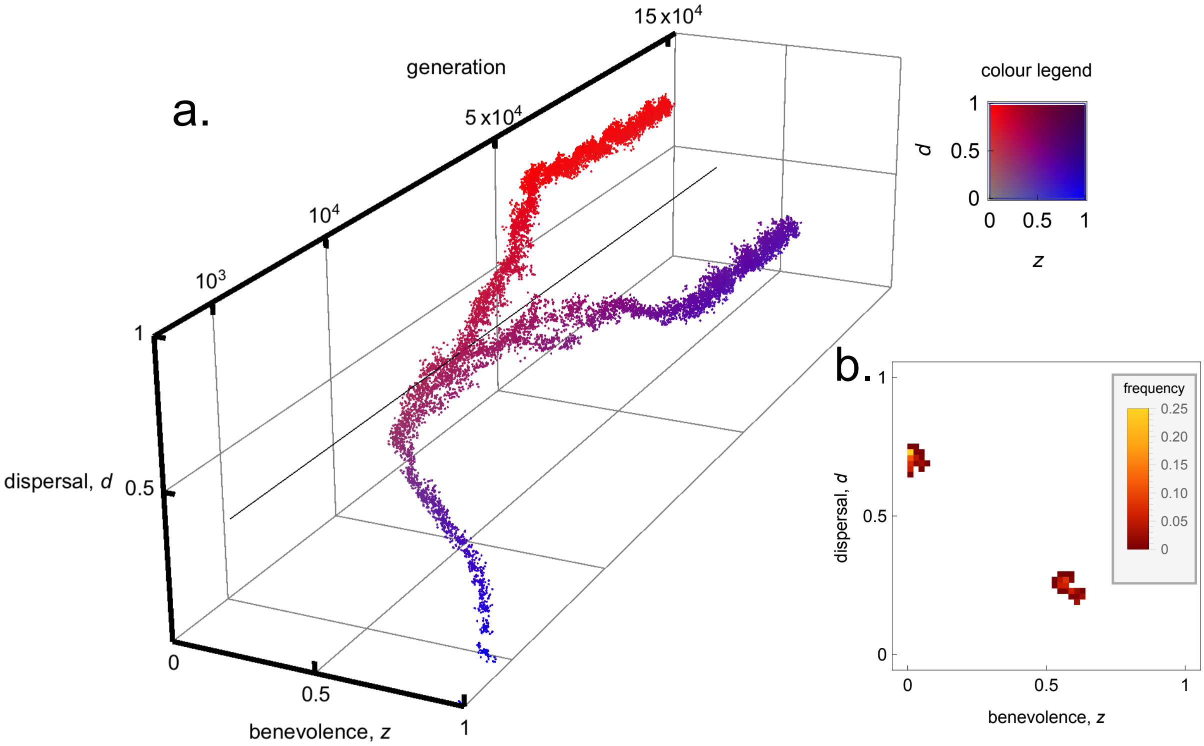

Figure 2: **The emergence and maintenance of social morphs when dispersal and social behaviour co-evolve.** **a.** Dispersal d and benevolence z in a simulated population of 10'000 individuals (trait values of 50 individuals randomly sampled every 500 generations, see colour legend for colouring scheme) and predicted interior equilibrium (solid black line, with $R = 50$, $S = 0$, $T = 100$, $P = -15$, $N = 8$, $c_\text{d} = 0.1$). **b.** Phenotypic distribution of whole population at generation 15×10^4 (same parameters as a.).

An important assumption made in the baseline model is that generations do not overlap. We relaxed this assumption by performing a mathematical analysis of dispersal and social behaviour co-evolution when generations overlap (M.4). This revealed that polymorphism is also often favoured in this scenario. In fact, in comparison to our baseline model, polymorphism is favoured for an even greater diversity of payoff variables, which means that a greater diversity of social behaviours may become associated with dispersal when generations overlap (M.4 for details).

We also determined the importance of genetic linkage in the emergence of highly-differentiated social morphs by studying the effects of various levels of recombination between the loci that control dispersal and social behaviour in simulations. These revealed that the emergence of distinct morphs depends on the level of recombination and that beyond a threshold, recombination prevents polymorphism and the population remains monomorphic (Fig. 3a). This is because recombination breaks the positive genetic linkage among the dispersal and social behaviour loci that is necessary for benevolent individuals to preferentially direct their benevolence towards relatives, and self-serving individuals to avoid harming their own.

Since disruptive selection promotes an association among dispersal and social behaviour, it should also promote a genetic architecture that makes this association heritable (19). We tested this by adding a third locus that controls recombination and let it evolve by introducing two alleles that mutate from one another, one recessive wild-type that codes for a recombination probability of $1/2$ and one dominant mutant that stops recombination (M.5 for details). Starting with a wild-type population at the predicted equilibrium (d^*, z^*) for dispersal and social behaviour, the mutant allele at the recombination modifier locus eventually invades so that recombination is shut down, which then permits the emergence of distinct morphs (Fig. 3b). Disruptive selection therefore leads to the genetic integration of dispersal and social behaviours to form a "supergene" (20), which allows benevolent individuals to preferentially interact with relatives, and self-serving individuals with non-relatives. This type of kin association through genetic and spatial assortment may constitute a first step towards more complicated conditional dispersal (21) or conditional social behaviours (9, 22), which allow individuals to fine tune their behaviours towards relatives.

Discussion

These analyses reveal that the co-evolution of dispersal and behaviour readily leads to a social polymorphism and dispersal syndrome. Two broad-brush predictions can be made from our results. The first is that associations between dispersal and social behaviour should be common. This prediction finds echo in multiple organisms ranging from protozoa to primates (8, 23, 24, 25, 26, 27, 28, 29, 30). For example, in the ciliate *Tetrahymena thermophila*, cooperative strains disperse at a lower rate than non-cooperative strains at intermediate population densities (30). Similarly, in prairie voles *Microtus pennsylvanicus*, individuals that disperse are more aggressive than those who do not (23).

The second prediction is that dispersal and social behaviour should be genetically linked when polymorphism is present. Data to test this prediction are scarce because few studies combine dispersal, behavioural and heritability assays. A notable exception is found in western bluebirds *Sialia mexicana*, for which a multi-generational pedigree analysis revealed that dispersal and social behaviour are genetically correlated such that dispersive males are more likely to produce aggressive offspring and non-dispersive males, non-aggressive

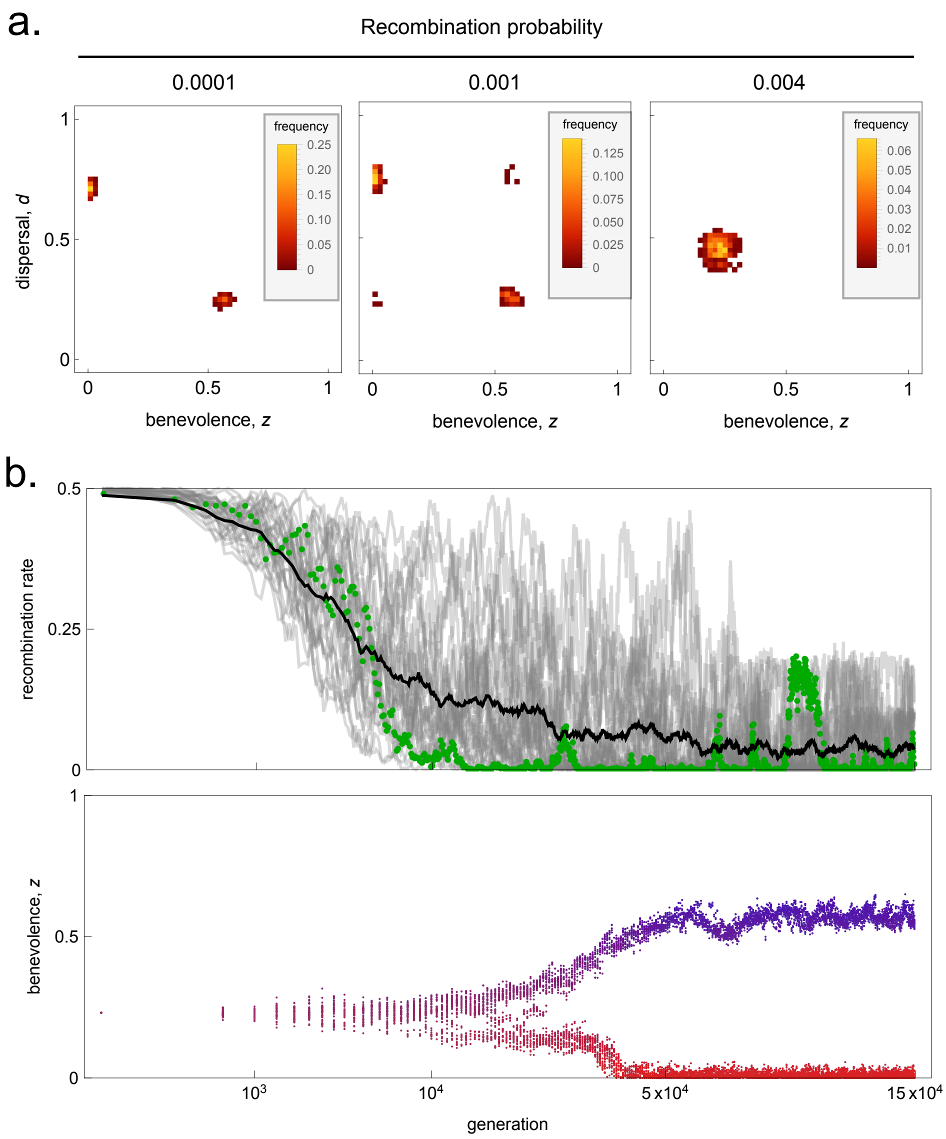

Figure 3: **The effect (a) and evolution (b) of genetic linkage between dispersal and social behaviour loci. a** Phenotypic distribution of whole population at generation 15×10^4 when recombination probability is fixed (value shown above graphs, other parameters same as in Fig 2a, M.5 for details). **b.** Upper panel: effective recombination rate in the population (number of recombination events/population size) every 100 generation when recombination evolves in a population of 10'000 individuals (for 30 replicates, each replicate is shown by a grey line, average recombination rate over replicates is shown in black). Lower panel: benevolence z of 50 individuals randomly sampled every 500 generations (coloured according to colour legend in Fig 2) for one replicate (shown in green in upper panel). Polymorphism arose in all 30 replicates.

offspring (31).

Eusocial species, who typically exhibit rich and variable patterns of dispersal and social behaviours, also provide a good model to test our predictions. Many ant species show a dispersal syndrome that associates dispersal with social organisation. Queens either disperse far away from their natal nest and form single-queen (monogyne) colonies, or disperse short distances and form multiple-queen (polygyne) colonies (32). In line with the predictions of our model, individuals from monogyne colonies typically exhibit high intra-specific aggression towards non-nestmates while individuals from polygyne colonies are much less aggressive (32). The genetic underpinning of social organisation has been uncovered in two ant species, *Solenopsis invicta* (33) and *Formica selysi* (34). Remarkably, in both cases, the social polymorphism and dispersal syndrome is controlled by a large non-recombining region that has independently arisen in each species, which suggests that integration of dispersal and social behaviour into a supergene like in our model can readily occur in nature.

Our simple model of course cannot explain all associations among dispersal and social behaviour which can be influenced by many other factors, e.g., (28, 35). Yet, the selection that associates dispersal and social behaviour that we revealed will act under most ecological settings because it only depends on kin structure which, due to limited dispersal, is ubiquitous in nature (36). While current data support the notion that individuals who disperse behave towards conspecifics in a way that is different to non-dispersers, further pedigree and genomic analyses will provide a better picture of how associations among dispersal and social behaviour are genetically constructed.

Materials and Methods

M.1 Matrix game

We use a pairwise matrix game (16) to model social interactions within groups. Here, we highlight some properties of this game and of the actions possible in this game. The payoff matrix (Fig 1a) entails that the average payoff to a focal player who adopts action B with probability z_1 against a partner who adopts this action with probability z_2 is

$$\pi(z_1, z_2) = Rz_1z_2 + Sz_1(1-z_2) + T(1-z_1)z_2 + P(1-z_1)(1-z_2). \tag{1}$$

We assume that the payoff that an individual receives increases its fecundity linearly, in which case the fecundity of the partner, relative to the fecundity of the focal player, can be written as

$$\frac{f_0 + \pi(z_2, z_1)}{f_0 + \pi(z_1, z_2)} = 1 + \frac{(T-S)(z_1 - z_2)}{f_0 + \pi(z_1, z_2)} \tag{2}$$

where f_0 is a baseline fecundity that ensures that fecundity is positive. Eq. (2) shows that when $T - S > 0$ and the the focal is more likely to express B than its partner ($z_1 - z_2 > 0$), this results in an increase of its partner's fecundity relative to its own (note, eq. (2) also entails $\partial[(f_0 + \pi(z_2, z_1)/(f_0 + \pi(z_1, z_2))]/\partial z_1|_{z_1=z_2} = (T - S)/\pi(z_2, z_2) > 0$ when $T - S > 0$). Conversely, when the focal is less likely to express B than its partner ($z_1 - z_2 < 0$), this results in a decrease of its partner's fecundity relative to its own. The quantity $T - S$ can therefore be thought of as the relative fecundity effect of action B.

We assume throughout that $T - S > 0$ so that expressing action B increases the fecundity of its recipients (for all $z_2 < 1$) relative to its actor, and we therefore call behaviour B "benevolent". Conversely, expressing M increases the fecundity of its actor relative to its recipient (for all $z_2 > 0$) , and we call behaviour M "self-serving". The condition that $T - S > 0$ includes well-known games. For instance, when $T > R > S > P$, B behaviour is equivalent to "Dove" in the Hawk-Dove game, or "Cooperate" in the Snow-Drift (or Volunteers' dilemma) game. When $T > R > P > S$, B is equivalent to "Cooperate" in the Prisoner's dilemma game. B behaviour therefore generally encompass cooperative and altruistic behaviours but not necessarily. Whether behaviour B is cooperative or altruistic *sensu* evolutionary biology depends on its fitness effects (15, 37), which themselves depend on population structure and life-cycle.

M.2 Evolutionary invasion analysis in the island model

M.2.1 Invasion and the average mutant growth rate

In general, the fate of a mutation that codes for a rare mutant phenotype $\mathbf{x}_\mathrm{m} = (z_\mathrm{m}, d_\mathrm{m})$ when the resident population has phenotype $\mathbf{x} = (z, d)$ can be deduced from the geometric growth rate $W(\mathbf{x}_\mathrm{m}, \mathbf{x})$ of that mutation. In a population of constant size, the geometric growth rate is given as the time-averaged mean cumulative growth over different replicates or sample paths of the invasion dynamics (38, 39). If the geometric growth rate is less or equal to one ($W(\mathbf{x}_\mathrm{m}, \mathbf{x}) \leq 1$), then the mutation will eventually go extinct in the population, otherwise it invades when rare (40, 41).

When the mutant and residents only differ by a small amount ($\|\mathbf{x}_\mathrm{m} - \mathbf{x}\| << 0$), the growth rate can be approximated by Taylor expanding $W(\mathbf{x}_\mathrm{m}, \mathbf{x})$ close to resident phenotype $\mathbf{x}$,

$$W(\mathbf{x}_\mathrm{m}, \mathbf{x}) \approx 1 + (\mathbf{x}_\mathrm{m} - \mathbf{x})^\mathrm{T}\mathbf{S}(\mathbf{x}) + (\mathbf{x}_\mathrm{m} - \mathbf{x})^\mathrm{T}\mathbf{H}(\mathbf{x})(\mathbf{x}_\mathrm{m} - \mathbf{x}), \tag{3}$$

where $\mathbf{S}(\mathbf{x})$ is a 2×1 vector and $\mathbf{H}(\mathbf{x})$ is a 2×2 matrix that respectively give the first- and second-order effects of selection. When mutations are rare with weak phenotypic effects, evolutionary dynamics can be decomposed into two time-scales (17), and $\mathbf{S}(\mathbf{x})$ and $\mathbf{H}(\mathbf{x})$ each capture a specific time-scale that we detail below for the infinite island model.

M.2.2 Directional selection in the infinite island model

On a fast time scale, the population evolves under directional selection, whereby selected new mutations rapidly sweep the population before a new mutation arises, so that the population “jumps" from one monomorphic state to another (17). The direction of evolution under directional selection is indicated by the selection gradient vector

$$\mathbf{S}(\mathbf{x}) = \begin{pmatrix} S_z(\mathbf{x}) \\ S_d(\mathbf{x}) \end{pmatrix} = \begin{pmatrix} \left.\dfrac{\partial W(\mathbf{x}_\mathrm{m}, \mathbf{x})}{\partial z_\mathrm{m}}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}} \\ \left.\dfrac{\partial W(\mathbf{x}_\mathrm{m}, \mathbf{x})}{\partial d_\mathrm{m}}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}} \end{pmatrix}. \tag{4}$$

In the infinite island model, the selection gradient on trait $u \in \{z, d\}$, which captures the directional coefficient of selection on trait u, has been shown (15, 12) to be equal to

$$S_u(\mathbf{x}) = \left.\frac{\partial w(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x})}{\partial u_1}\right|_{\substack{\mathbf{x}_1=\mathbf{x}\\ \mathbf{x}_{-1}=\mathbf{x}}} + (N-1)r_2(\mathbf{x},\mathbf{x}) \left.\frac{\partial w(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x})}{\partial u_2}\right|_{\substack{\mathbf{x}_1=\mathbf{x}\\ \mathbf{x}_{-1}=\mathbf{x}}}, \tag{5}$$

where $w(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x})$ is the individual fitness of a focal individual that we arbitrarily label as individual "1" (i.e., the expected number of adult offspring produced by individual "1"), when he has phenotype $\mathbf{x}_1 = (z_1, d_1)$, his $N-1$ neighbours have phenotypes $\mathbf{x}_{-1} = (\mathbf{x}_2, \dots, \mathbf{x}_N)$, and the resident has phenotype $\mathbf{x}$; and $r_l(\mathbf{x}_\mathrm{m}, \mathbf{x})$ is defined as the probability that $l-1$ randomly drawn (without replacement) neighbours of a mutant are also mutants (i.e., that they all belong to the same lineage). In a monomorphic population (so that $\mathbf{x}_\mathrm{m} = \mathbf{x}$), $r_l(\mathbf{x},\mathbf{x})$ reduces to the probability of sampling l individuals without replacement whose lineages are identical-by-descent, which is the standard l^{th}-order measure of relatedness for the island model (42). The selection gradient (eq. 5) is therefore the sum of the direct fitness effects of trait u and the pairwise relatedness ($r_2(\mathbf{x},\mathbf{x})$) weighted indirect fitness effects of trait u (note: $\mathbf{x}_{-1} = \mathbf{x}$ means $\mathbf{x}_2 = \mathbf{x}_3 = \ldots = \mathbf{x}_N = \mathbf{x}$) (15, 12).

In two-dimensional phenotypic space, $\mathbf{S}(\mathbf{x})$ points towards the direction of directional selection close to the resident, so adaptive dynamics will first settle for an equilibrium

$$\mathbf{x}^* = (z^*, d^*) \text{ such that } \mathbf{S}(\mathbf{x}^*) = 0, \tag{6}$$

when the equilibrium is an attractor of selection. The equilibrium is a local attractor, or a so-called convergence stable point (43), if the Jacobean matrix

$$\mathbf{J}(\mathbf{x}^*) = \begin{pmatrix} \left.\frac{\partial S_z(\mathbf{x})}{\partial z}\right|_{\mathbf{x}=\mathbf{x}^*} & \left.\frac{\partial S_z(\mathbf{x})}{\partial d}\right|_{\mathbf{x}=\mathbf{x}^*} \\ \left.\frac{\partial S_d(\mathbf{x})}{\partial z}\right|_{\mathbf{x}=\mathbf{x}^*} & \left.\frac{\partial S_d(\mathbf{x})}{\partial d}\right|_{\mathbf{x}=\mathbf{x}^*}, \end{pmatrix} \tag{7}$$

is negative-definite, or equivalently if it has eigenvalues with negative real parts (44, 12).

M.2.3 Stabilising/disruptive selection in the infinite island model

Once the population is at an equilibrium $\mathbf{x}^*$ that is convergence stable, the leading eigenvalue $\lambda(\mathbf{x}^*)$ of the Hessian matrix,

$$\mathbf{H}(\mathbf{x}^*) = \begin{pmatrix} h_{zz}(\mathbf{x}^*) & h_{zd}(\mathbf{x}^*) \\ h_{zd}(\mathbf{x}^*) & h_{dd}(\mathbf{x}^*) \end{pmatrix} = \begin{pmatrix} \left.\frac{\partial^2 W(\mathbf{x}_\mathrm{m}, \mathbf{x}^*)}{\partial z_\mathrm{m}^2}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}^*} & \left.\frac{\partial^2 W(\mathbf{x}_\mathrm{m}, \mathbf{x}^*)}{\partial z_\mathrm{m}\partial d_\mathrm{m}}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}^*} \\ \left.\frac{\partial^2 W(\mathbf{x}_\mathrm{m}, \mathbf{x}^*)}{\partial z_\mathrm{m}\partial d_\mathrm{m}}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}^*} & \left.\frac{\partial^2 W(\mathbf{x}_\mathrm{m}, \mathbf{x}^*)}{\partial d_\mathrm{m}^2}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}^*} \end{pmatrix}, \tag{8}$$

tells us whether selection is stabilising (when $\lambda(\mathbf{x}^*) \leq 0$ and all mutations close to the resident vanish) or disruptive (when $\lambda(\mathbf{x}^*) > 0$). Note that the Hessian necessarily has real eigenvalues because it is symmetric with real entries. In the infinite island model, it has been shown (12) that the $h_{uv}(\mathbf{x}^*)$ entry of the Hessian for $u \in \{z, d\}$ and $v \in \{z, d\}$, which is the quadratic coefficient of selection on traits u and v, can be decomposed as

$$h_{uv}(\mathbf{x}^*) = h_{\mathrm{w},uv}(\mathbf{x}^*) + h_{\mathrm{r},uv}(\mathbf{x}^*), \tag{9}$$

where

$$\begin{aligned} h_{\mathrm{w},uv}(\mathbf{x}^*) = & \left.\frac{\partial w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial u_1 \partial v_1}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} \\ & + (N-1) r_2(\mathbf{x}^*,\mathbf{x}^*) \left(\left.\frac{\partial^2 w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial u_2 \partial v_2}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} + \left.\frac{\partial^2 w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial u_1 \partial v_2}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} + \left.\frac{\partial^2 w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial u_2 \partial v_1}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} \right) \\ & + (N-1)(N-2) r_3(\mathbf{x}^*,\mathbf{x}^*) \left.\frac{\partial^2 w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial u_2 \partial v_3}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}}, \end{aligned} \tag{10}$$

captures the second-order fitness effects when the relatedness among mutants is the same as among residents (since $r_2(\mathbf{x}^*,\mathbf{x}^*)$ and $r_3(\mathbf{x}^*,\mathbf{x}^*)$ are evaluated when the population is monomorphic for the resident at equilibrium), and where

$$h_{\mathrm{r},uv}(\mathbf{x}^*) = (N-1) \left(\left.\frac{\partial w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial u_2}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} \left.\frac{\partial r(\mathbf{x}_\mathrm{m},\mathbf{x}^*)}{\partial v}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}^*} + \left.\frac{\partial w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial v_2}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} \left.\frac{\partial r(\mathbf{x}_\mathrm{m},\mathbf{x}^*)}{\partial u}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}^*} \right), \tag{11}$$

depends on the effects that the traits have on pairwise relatedness (i.e., on $\partial r(\mathbf{x}_\mathrm{m},\mathbf{x}^*)/\partial v$ and $\partial r(\mathbf{x}_\mathrm{m},\mathbf{x}^*)/\partial u$). For the models considered here, previous works (45, 46, 12) have shown that this effect can be expressed as

$$\begin{aligned} \left.\frac{\partial r(\mathbf{x}_\mathrm{m},\mathbf{x}^*)}{\partial v}\right|_{\mathbf{x}_\mathrm{m}=\mathbf{x}^*} = \frac{2r_2(\mathbf{x}^*,\mathbf{x}^*)}{1-m(\mathbf{x}^*)} \Bigg(& \big(1+(N-1)r_2(\mathbf{x}^*,\mathbf{x}^*)\big) \left.\frac{\partial w^\mathrm{P}(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial v_1}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} \\ & + \big(2r_2(\mathbf{x}^*,\mathbf{x}^*)+(N-2)r_3(\mathbf{x}^*,\mathbf{x}^*)\big)(N-1) \left.\frac{\partial w^\mathrm{P}(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial v_2}\right|_{\substack{\mathbf{x}_1=\mathbf{x}^* \\ \mathbf{x}_{-1}=\mathbf{x}^*}} \Bigg), \end{aligned} \tag{12}$$

where $m(\mathbf{x}^*)$ is the neutral backward probability of dispersal (i.e., the probability that a breeding spot is filled by an immigrant in a population monomorphic for the resident), and $w^\mathrm{P}(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x})$ is the expected number of offspring of individual 1 that remain in the focal island (i.e., its expected number of philopatric offspring).

The quadratic coefficient of selection on a single trait ($h_{zz}(\mathbf{x}^*)$ and $h_{dd}(\mathbf{x}^*)$) tell us about selection on that trait when it is evolving in isolation from the other. For instance, when $h_{zz}(\mathbf{x}^*) \leq 0$, selection on z is stabilising, but when $h_{zz}(\mathbf{x}^*) > 0$ selection is disruptive and z will diversify whether or not dispersal is also evolving. Meanwhile, the quadratic coefficient of selection on z and d, $h_{zd}(\mathbf{x}^*)$, captures the types of associations or correlations among z and d that are favoured by selection. It is therefore referred to as the correlational coefficient of selection (47). When $h_{zd}(\mathbf{x}^*)$ is positive, selection favours a positive correlation among both traits close to the resident and conversely, when it is negative, selection favours a negative correlation. It follows from standard linear algebra results (48), that if

$$h_{zd}(\mathbf{x}^*)^2 > h_{zz}(\mathbf{x}^*) h_{dd}(\mathbf{x}^*), \tag{13}$$

then the leading eigenvalue of $\mathbf{H}(\mathbf{x}^*)$ is positive ($\lambda(\mathbf{x}^*) > 0$), which in biological terms means that if the correlational coefficient of selection is strong relative to the quadratic coefficient of selection on both traits, it causes selection to be disruptive and polymorphism arises.

M.2.4 Fitness and genetic structure for baseline model

We now use eqs. (5)–(12) to derive the dynamics for the baseline model set out in the main text, in which generations do not overlap (i.e., Wright-Fisher life cycle). We first express the necessary components for our analysis in terms of z and d: the individual fitness function (of individual "1", $w(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x})$), and pairwise and three-way relatedness ($r_2(\mathbf{x},\mathbf{x})$ and $r_3(\mathbf{x},\mathbf{x})$). The fecundity of individual "1" is

$$f(\mathbf{x}_1, \mathbf{x}_{-1}) = f_0 + \sum_{j=2}^{N} \frac{\pi(z_1, z_j)}{N-1}, \tag{14}$$

where recall that f_0 is a baseline fecundity that ensures that fecundity is positive and the payoff function π is given in eq. (1). According to the life-cycle set out in the main text, the expected number of philopatric of individual "1" is

$$w^{\mathrm{P}}(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x}) = \frac{(1-d_1) f(\mathbf{x}_1, \mathbf{x}_{-1})}{\sum_{i=1}^{N}(1-d_i) f(\mathbf{x}_i, \mathbf{x}_{-i})/N + d(1-c_{\mathrm{d}}) f(\mathbf{x},\mathbf{x})}, \tag{15}$$

and the overall fitness of individual 1 is

$$w(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x}) = w^{\mathrm{P}}(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x}) + \frac{d_1(1-c_{\mathrm{d}}) f(\mathbf{x}_1, \mathbf{x}_{-1})}{(1-dc_{\mathrm{d}}) f(\mathbf{x},\mathbf{x})}. \tag{16}$$

We turn to pairwise and three-way relatedness that appear on the selection gradient (eq. 5) and Hessian matrix (eqs. 9-12). The neutral backward probability of dispersal, which recall is the probability that a breeding spot is filled by an immigrant in a monomorphic population, is given by

$$m(\mathbf{x}) = \frac{d(1-c_{\mathrm{d}})}{1-d+d(1-c_{\mathrm{d}})}, \tag{17}$$

the ratio of the number immigrant offspring to the total number of offspring in a group. Pairwise and three-way relatedness are found using $m(\mathbf{x})$ and standard identity-by-descent arguments (49, 15), giving

$$r_2(\mathbf{x},\mathbf{x}) = \frac{(1-m(\mathbf{x}))^2}{N-(N-1)(1-m(\mathbf{x}))^2}, \tag{18}$$

and

$$r_3(\mathbf{x},\mathbf{x}) = \frac{(1-m(\mathbf{x}))^3(1+3(N-1)r_2(\mathbf{x},\mathbf{x}))}{N^2-(N-1)(N-2)(1-m(\mathbf{x}))^3}. \tag{19}$$

We now have all that is necessary to infer on the adaptive dynamics of dispersal and benevolence using the selection gradient and Hessian matrix (eqs. 5–12).

M.2.5 Directional selection on dispersal

Equilibrium dispersal. We first look at the selection gradient on dispersal. Substituting eqs. (16) and eq. (18) into eq. (5) (with $u = d$) gives the selection gradient on dispersal,

$$S_d(\mathbf{x}) = \frac{1-c_{\mathrm{d}}}{1-c_{\mathrm{d}}d} \times \frac{l(d)}{h(d)}, \tag{20}$$

where

$$\begin{aligned} l(d) &= 1-(1+2c_{\mathrm{d}}N)d + c_{\mathrm{d}}(1+c_{\mathrm{d}})Nd^2, \\ h(d) &= 1-2\left(1-(1-c_{\mathrm{d}})N\right)d + \left(1-(1-c_{\mathrm{d}}^2)N\right)d^2 > 0. \end{aligned} \tag{21}$$

The equilibrium d^* for dispersal then solves $l(d^*) = 0$, which gives

$$d^* = \frac{1 + 2Nc_{\mathrm{d}} - \sqrt{1 + 4N(N-1)c_{\mathrm{d}}^2}}{2Nc_{\mathrm{d}}(1 + c_{\mathrm{d}})}, \tag{22}$$

in agreement with previous works on the evolution of dispersal $^{\text{e.g., eq. (14) of}}$ (45).

Convergence stability of equilibrium dispersal. The equilibrium eq. (22) is an attractor when dispersal is evolving in isolation from z if

$$\left.\frac{\partial S_d(\mathbf{x})}{\partial d}\right|_{\mathbf{x}=\mathbf{x}^*} = \frac{(1-c_{\mathrm{d}})l'(d^*)}{(1-c_{\mathrm{d}}d^*)^2 h(d^*)} < 0, \tag{23}$$

which is always the case because the derivative $l'(d) = -1-2c_{\mathrm{d}}(N(1-d)-d) < 0$ is always negative (since $N \geq 2$, $0 \leq c_{\mathrm{d}} < 1$ and $0 < d \leq 1$).

M.2.6 Directional selection on benevolence

Equilibrium benevolence. To look at the selection gradient on the probability z of adopting benevolent behaviour B, it is advantageous to use the following transformation for payoffs (50, 51, 52)

$$\begin{aligned} B &= T - P, \\ C &= P - S, \\ D &= R - S - T + P, \end{aligned} \tag{24}$$

which results in a payoff matrix with the form

$$\begin{pmatrix} B - C + D & -C \\ B & 0 \end{pmatrix}. \tag{25}$$

If transformation (24) can be used to study any symmetric game between two players, it is particularly useful for cooperative problems wherein a B-player gives benefit $B > 0$ to its partner at cost $-C < 0$, but if the partner is also B, there is a synergistic bonus $D > 0$ or discount $D < 0$ (eq. 25). Note that in terms of these new payoff variables, our assumption that action B is benevolent, $T - S > 0$, is $B + C > 0$. Substituting eqs. (16) and eq. (18) into eq. (5) (with $u = z$) gives the selection gradient,

$$S_z(\mathbf{x}) = \frac{(1 - r_2(\mathbf{x},\mathbf{x}))\,(Dz - C)}{f(\mathbf{x},\mathbf{x})}, \tag{26}$$

so that the equilibrium $\mathbf{x}^*$ which solves $S_z(\mathbf{x}^*) = 0$ is

$$z^* = \frac{C}{D}, \tag{27}$$

in agreement with previous works on the evolution of z alone (53) $^{\text{eq. (9) with } \kappa=0}$. Substituting the original payoff variables eq. (24) then gives the equilibrium value presented in Fig. 1c. Eq. (26) shows that dispersal has no effect on the convergence of z to an equilibrium here. This is because how limited dispersal influences convergence of z depends on the effects of dispersal on genetic relatedness, which favours benevolent behaviour, and on kin competition, which favours self-serving behaviour (54), and when local population size is constant (fixed N) and generations do not overlap, these effects cancel out regardless of payoffs (55).

Convergence stability of equilibrium benevolence. The equilibrium eq. (27) is an attractor point when z is evolving alone if

$$\left.\frac{\partial S_z(\mathbf{x})}{\partial z}\right|_{\mathbf{x}=\mathbf{x}^*} = \frac{(1-r_2(\mathbf{x},\mathbf{x}))\,D}{f(\mathbf{x}^*,\mathbf{x}^*)} < 0, \tag{28}$$

which occurs when $D<0$ (since $0<m(\mathbf{x})\leq 1$). So, in order for an internal equilibria to be an attractor, we must have $0<C/D<1$ and $D<0$, i.e., $R<T$ and $P>S$, which we will assume for the rest of this section.

M.2.7 Directional selection when dispersal and benevolence co-evolve

When both traits co-evolve, whether the point $\mathbf{x}^*=(z^*,d^*)$ is an attractor depends on the eigenvalues of the Jacobean matrix (eq. 7). Since both off-diagonal entries of the Jacobean are zero, i.e.,

$$\left.\frac{\partial S_d(\mathbf{x})}{\partial z}\right|_{\mathbf{x}=\mathbf{x}^*} = \left.\frac{\partial S_z(\mathbf{x})}{\partial d}\right|_{\mathbf{x}=\mathbf{x}^*} = 0, \tag{29}$$

the eigenvalues of the Jacobean are equal to the diagonal entries (eqs. 23 and 28), and so the conditions for

$$\mathbf{x}^* = (z^*,d^*) = \left(\frac{C}{D},\, \frac{1+2Nc_{\mathrm{d}}-\sqrt{1+4N(N-1)c_{\mathrm{d}}^2}}{2Nc_{\mathrm{d}}(1+c_{\mathrm{d}})}\right), \tag{30}$$

to be an attractor are the same as for z^* and d^* to be attractors when evolving in isolation from one another, which we have already derived. Thus, provided $0<C/D<1$ and $D<0$, the population will converge to $\mathbf{x}^*=(z^*,d^*)$ under directional selection. Note that these conditions preclude the existence of a convergence stable internal equilibrium for cooperative behaviour since it requires that the cost of cooperation is positive $-C>0$. The conditions for the other possible outcomes for the evolution of z (convergence to zero or one) are found similarly, by considering the selection gradient at $z=0$ and $z=1$.

M.2.8 Stabilising selection on dispersal and benevolence

Substituting eqs. (15), (16), (18) and (19) into eqs. (9)-eqs. (12) (with $u=v=d$), we find that we can express the quadratic coefficient of selection on dispersal at the equilibrium as a product

$$h_{dd}(\mathbf{x}^*) = -F_{dd}(\mathbf{x}^*)G_{dd}(\mathbf{x}^*) \tag{31}$$

where

$$\begin{aligned}
G_{dd}(\mathbf{x}^*) &= \frac{N^2\left(N+(N-1)(1-m(\mathbf{x}^*))^2\right)\left(N+(N-1)(1-m(\mathbf{x}^*))(2-m(\mathbf{x}^*))\right)}{N-(N-1)(1-m(\mathbf{x}^*))^2} > 0,\\
F_{dd}(\mathbf{x}^*) &= \frac{2(1-m(\mathbf{x}^*))^2 m(\mathbf{x}^*)}{N\left(N-(N-1)(1-m(\mathbf{x}^*))^2\right)\left(N^2-(N-1)(N-2)(1-m(\mathbf{x}^*))^3\right)(1-d^*)^2} > 0.
\end{aligned} \tag{32}$$

So, $h_{dd}(\mathbf{x}^*)<0$ is negative, and selection on dispersal when it is evolving alone is always stabilising (as previously found for this life-cycle (45)).

Similarly, substituting eqs. (15), (16), (18) and (19) into eqs. (9)-(12) (with $u=v=z$), the quadratic coefficient of selection on z at the equilibrium can be expressed as

$$h_{zz}(\mathbf{x}^*) = -F_{zz}(\mathbf{x}^*)\left(G_{zz}(\mathbf{x}^*)(B+C)^2 - K_{zz}(\mathbf{x}^*)Df(\mathbf{x}^*,\mathbf{x}^*)\right), \tag{33}$$

where

$$\begin{aligned} G_{zz}(\mathbf{x}^*) &= m(\mathbf{x}^*)(1-m(\mathbf{x}^*)) \geq 0 \\ K_{zz}(\mathbf{x}^*) &= N + (1-m(\mathbf{x}^*))(N+(N-2)(1-m(\mathbf{x}^*))) > 0 \\ F_{zz}(\mathbf{x}^*) &= \frac{2N(1-m(\mathbf{x}^*))^2 m(\mathbf{x}^*)}{\left(N-(N-1)(1-m(\mathbf{x}^*))^2\right)\left(N^2-(N-1)(N-2)(1-m(\mathbf{x}^*))^3\right) f(\mathbf{x}^*,\mathbf{x}^*)^2} \geq 0, \end{aligned} \tag{34}$$

Then, since we assume $D < 0$ here, $h_{zz}(\mathbf{x}^*) < 0$ is non-positive, and mutations that only change z will eventually vanish. So, selection on z when it is evolving alone is stabilising for all model parameters.

M.2.9 Disruptive selection on dispersal and benevolence when they co-evolve

Correlational coefficient of selection. When dispersal and benevolence co-evolve, selection at the equilibrium also depends on the correlational coefficient of selection, and by substituting eqs. (15), (16), (18) and (19) into eqs. (9)-eqs. (12) (with $u = z$ and $v = d$), we find that it can be expressed as

$$h_{zd}(\mathbf{x}^*) = -\sqrt{F_{dd}(\mathbf{x}^*)F_{zz}(\mathbf{x}^*)}\,G_{zd}(\mathbf{x}^*)(B+C), \tag{35}$$

where

$$\begin{aligned} G_{zd}(\mathbf{x}^*) = &-\frac{N^2-(N-1)(N-2)(1-m(\mathbf{x}^*))^3}{2d^*} + N(N-1)(1-m(\mathbf{x}^*))(2-m(\mathbf{x}^*)) \\ &+ \frac{N^3(1-(1-m(\mathbf{x}^*))^2)+N^2(1-m(\mathbf{x}^*))}{N-(N-1)(1-m(\mathbf{x}^*))^2} > 0, \end{aligned} \tag{36}$$

is positive (showing $G_{zd}(\mathbf{x}^*) > 0$ can be easily achieved with an algebraic computer program (56) once having substituted for the dispersal equilibrium eq. 22). Since we assume $B + C > 0$, eq. (35) shows that the correlational coefficient of selection is negative, $h_{zd}(\mathbf{x}^*) < 0$.

Disruptive selection. Substituting eqs. (31), (33) and (35) into eq. (13) shows that the correlational coefficient of selection will cause disruptive selection whenever

$$G_{zd}(\mathbf{x}^*)^2(B+C)^2 > G_{dd}(\mathbf{x}^*)\left(G_{zz}(\mathbf{x}^*)(B+C)^2 - K_{zz}Df(\mathbf{x}^*,\mathbf{x}^*)\right). \tag{37}$$

This can be re-arranged to

$$\frac{1}{K_{zz}(\mathbf{x}^*)}\left(G_{zz}(\mathbf{x}^*) - \frac{G_{zd}(\mathbf{x}^*)^2}{G_{dd}(\mathbf{x}^*)}\right) < \frac{D}{(B+C)^2}f(\mathbf{x}^*,\mathbf{x}^*), \tag{38}$$

so that the left hand side only depends on ecological variables: group size N and dispersal cost c_{d}. Meanwhile, the right hand-side $D/(B+C)^2 f(\mathbf{x}^*,\mathbf{x}^*)$ only depends on the properties of the game and can be re-arranged as

$$\frac{D}{(B+C)^2}f(\mathbf{x}^*,\mathbf{x}^*) = \frac{D}{(B+C)^2}\left(f_0 + (B+C)z^* - Dz^{*2}\right). \tag{39}$$

Substituting for the original payoff variables (eq. 24) into eq. (39), which is in turn substituted into eq. (38) then allows to produce Fig. 1d (with $T - R + S - P = 1$ and $f_0 = 1$).

In summary, the correlational coefficient of selection can cause polymorphism when z and dispersal coevolve. In order to gain more understanding about this result, let us consider a mutation that arises in a monomorphic population for the equilibrium $\mathbf{x}^*$ and that changes dispersal by $\Delta_d = d_\mathrm{m} - d^*$ and z by $\Delta_z = z_\mathrm{m} - z^*$. This mutation will invade whenever its growth rate is greater than one, i.e., whenever

$$W(\mathbf{x}_\mathrm{m}, \mathbf{x}^*) = 1 + \Delta_d^2 h_{dd}(\mathbf{x}^*) + \Delta_z^2 h_{zz}(\mathbf{x}^*) + \Delta_d \Delta_z h_{zd}(\mathbf{x}^*) > 1. \tag{40}$$

From eq. (35), the correlational coefficient of selection $h_{zd}(\mathbf{x}^*) < 0$ is negative. Then, since $h_{dd}(\mathbf{x}^*) < 0$ and $h_{zz}(\mathbf{x}^*) < 0$, eq. (40) shows that the only mutations that have a chance of invading are those that have opposite effects on dispersal and z, i.e., mutations with $\Delta_d \Delta_z < 0$. Thus, two types of mutation can invade the population, one type that increase z and decrease d and another type that decreases z and increases d. Further insights can be brought by looking at the correlational coefficient of selection when dispersal cost is low (i.e., when c_d is small),

$$h_{zd}(\mathbf{x}^*) = \underbrace{c_\mathrm{d}(1-c_\mathrm{d})\frac{B+C}{f(\mathbf{x}^*,\mathbf{x}^*)}}_{\frac{\partial w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial z_1 \partial d_1}|_{\mathbf{x}^*}} \quad \underbrace{-2c_\mathrm{d}}_{\frac{\partial r(\mathbf{x}_\mathrm{m},\mathbf{x}^*)}{\partial d}|_{\mathbf{x}^*}} \quad \times \quad \underbrace{\frac{B+C}{f(\mathbf{x}^*,\mathbf{x}^*)}}_{(N-1)\frac{\partial w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}^*)}{\partial z_1}|_{\mathbf{x}^*}} \quad + O(c_\mathrm{d}^2) = -c_\mathrm{d}(1+c_\mathrm{d})\frac{B+C}{f(\mathbf{x}^*,\mathbf{x}^*)} + O(c_\mathrm{d}^3), \tag{41}$$

which reveals that what causes the correlational coefficient of selection to be negative, is the combination of the effect of dispersal on pairwise relatedness ($\partial r(\mathbf{x}_\mathrm{m}, \mathbf{x}^*)/\partial d$) with the indirect fitness effects of social interactions ($\partial w(\mathbf{x}_1, \mathbf{x}_{-1}, \mathbf{x}^*)/\partial z_1$). The correlational coefficient of selection therefore favours mutations or morphs that ensure that its carriers either provide (1) more indirect benefits to their own kin; or (2) less indirect benefits to non-kin.

M.3 Computer simulations

We performed individual based simulations for a population composed of $N_\mathrm{d} = 1250$ groups, each populated by $N = 8$ haploid individuals, using Mathematica 11.0.1.0 (56). Starting with a population monomorphic for no dispersal $d = 0$ and full benevolence $z = 1$, we track the evolution of the multidimensional phenotypic distribution as small mutations continuously arise. Each individual $i = 1, \dots, 10000$ is characterised by a dispersal value d_i and a benevolence value z_i. At the beginning of a generation, we calculate the fecundity f_i of each individual according to its benevolence and that of its neighbours (eq. 14, with $f_0 = 1$, $R = 50$, $S = 0$, $T = 100$, $P = -15$). Then, we form the next generation of adults by sampling N individuals in each group with replacement, where each individual from the parental generation is weighted according to whether they belong to the group on which the breeding spot is filled or not. If an individual belongs to the same group in which a breeding spot is filled, then its weight is $f_i(1-d_i)$. If it belongs to another group, then its weight is $f_i d_i (1-c_\mathrm{d})/(N_\mathrm{d}-1)$ (with $c_\mathrm{d} = 0.1$). Once an individual is chosen to fill the breeding spot, each locus independently mutates with probability 0.01. If they do not mutate, then the offspring has the same phenotypic values as its parent. If they mutate, then we add to parental values a small perturbation that is sampled from a normal distribution with mean 0 and variance 0.005^2. The resulting phenotypic values are truncated to remain between 0 and 1. We repeated the procedure for 15×10^4 generations.

M.4 Analysis when generations overlap

We here study the adaptive dynamics of dispersal and benevolence when generations overlap. We assume that after reproduction, a random individual in each group dies and that offspring then compete for the single open breeding spot left vacant in each group at each generation.

M.4.1 Fitness and genetic structure

Following previous works (12), philopatric fitness and total individual fitness respectively now are

$$w^{\mathrm{P}}(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}) = \frac{N-1}{N} + \frac{1}{N}\frac{(1-d_1)f(\mathbf{x}_1,\mathbf{x}_{-1})}{\sum_{i=1}^{N}(1-d_i)f(\mathbf{x}_i,\mathbf{x}_{-i})/N + d(1-c_{\mathrm{d}})f(\mathbf{x},\mathbf{x})}, \tag{42}$$

and,

$$w(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}) = w^{\mathrm{P}}(\mathbf{x}_1,\mathbf{x}_{-1},\mathbf{x}) + \frac{1}{N}\frac{d_1(1-c_{\mathrm{d}})f(\mathbf{x}_1,\mathbf{x}_{-1})}{(1-dc_{\mathrm{d}})f(\mathbf{x},\mathbf{x})}. \tag{43}$$

Meanwhile, pairwise and three-way relatedness (12) are given by

$$r_2(\mathbf{x},\mathbf{x}) = \frac{1-m(\mathbf{x})}{1-(N-1)m(\mathbf{x})}, \tag{44}$$

and

$$r_3(\mathbf{x},\mathbf{x}) = \frac{2(1-m(\mathbf{x}))r_2(\mathbf{x},\mathbf{x})}{2+m(\mathbf{x})(N-2)}, \tag{45}$$

which completes the necessary expressions to derive the adaptive dynamics of dispersal and benevolence.

M.4.2 Directional selection on dispersal

Equilibrium probability of dispersal. Substituting eq. (43) and (44) into eq. (5) (with $u = d$) yields the selection gradient on dispersal,

$$S_d(\mathbf{x}) = \frac{(1-c_{\mathrm{d}})(1-d(1+c_{\mathrm{d}}N))}{N(1-c_{\mathrm{d}}d)(1-d(1-N(1-c_{\mathrm{d}})))}, \tag{46}$$

which shows that the equilibrium probability of dispersal (d^* such that $S_d(d^*) = 0$) is,

$$d^* = \frac{1}{1+c_{\mathrm{d}}N}, \tag{47}$$

(in agreement with previous work (12) $^{\text{eq. (26)}}$) which is greater than the equilibrium when generations do not overlap (eq. 22) because kin competition is greater when generations overlap (12).

Convergence stability of equilibrium probability of dispersal. If only dispersal is evolving, the equilibrium eq. (47) is a local attractor when

$$\left.\frac{\partial S_d(\mathbf{x})}{\partial d}\right|_{\mathbf{x}=\mathbf{x}^*} = -\frac{(1-c_{\mathrm{d}})(1+Nc_{\mathrm{d}})^3}{N^2(1+c_{\mathrm{d}}(N-1))} < 0, \tag{48}$$

which is always true.

M.4.3 Directional selection on benevolence

Equilibrium benevolence. Substituting eq. (43) and (44) into eq. (5) (with $u = z$), and evaluated at dispersal equilibrium $d^* = 1/(1 + c_\text{d}N)$ gives the selection gradient on the probability z of adopting benevolent behaviour B:

$$S_z(\mathbf{x}) = \frac{(1-c_\text{d})\big(Dz(1+c_\text{d}+Nc_\text{d})+Bc_\text{d}-C(1+Nc_\text{d})\big)}{N(1+c_\text{d}(N-1))f(\mathbf{x},\mathbf{x})}. \tag{49}$$

Solving the above for zero gives the equilibrium

$$z^* = \frac{C}{D} + \frac{B+C}{-D}\frac{c_\text{d}}{1+c_\text{d}(N+1)}. \tag{50}$$

Unlike when generations do not overlap (eq. 27), group size N and dispersal cost c_d now affect the equilibrium benevolence. This is because these variables determine dispersal (eq. 22), and when generations overlap, dispersal has greater effects on genetic relatedness than on kin competition (57). As a consequence, the indirect fitness benefits of z, as measured by $B + C > 0$, play a larger role on its evolution, and the equilibrium benevolence z^* is greater when generations overlap than when they do not (eq. 50 versus eq. 27).

Convergence stability of equilibrium benevolence. If only benevolence is evolving, equilibrium eq. (50) is a local attractor if

$$\left.\frac{\partial S_z(\mathbf{x})}{\partial z}\right|_{\mathbf{x}=\mathbf{x}^*} = D\frac{(1-c_\text{d})(1+c_\text{d}+Nc_\text{d})}{N(1+c_\text{d}(N-1))f(\mathbf{x}^*,\mathbf{x}^*)} < 0. \tag{51}$$

Therefore, the equilibrium for benevolence is internal ($0 < z^* < 1$) and an attractor when only benevolence is evolving if

$$C\left(N+\frac{1}{c_\text{d}}\right) < B < C\left(N+\frac{1}{c_\text{d}}\right) - D\frac{(1+c_\text{d}+Nc_\text{d})}{c_\text{d}}, \text{ and } D < 0. \tag{52}$$

Thus, unlike when generations do not overlap, a cooperative behaviour ($B > 0$, $-C < 0$) here can have a convergence stable internal equilibrium (with synergistic discount $D < 0$).

M.4.4 Directional selection when dispersal and benevolence co-evolve

When dispersal and benevolence co-evolve, whether the equilibrium

$$\mathbf{x}^* = (z^*, d^*) = \left(\frac{C}{D} + \frac{B+C}{-D}\frac{c_\text{d}}{1+c_\text{d}(N+1)}, \frac{1}{1+c_\text{d}N}\right), \tag{53}$$

is an attractor depends on the eigenvalues of the Jacobean (eq. 7). Because we find that one of the non-diagonal entry of this matrix is zero

$$\left.\frac{\partial S_d(\mathbf{x})}{\partial z}\right|_{\mathbf{x}=\mathbf{x}^*} = 0, \tag{54}$$

the eigenvalues are the diagonal entries that we have already calculated (eq. 48 and 51), and thus the conditions for the joint equilibrium eq. (53) to be internal and a local attractor are eq. (52), which we will henceforth assume to hold.

M.4.5 Stabilising selection on dispersal and benevolence

Once the population has converged to the equilibrium eq. (53), the quadratic coefficient of selection on dispersal is found by substituting eqs. (42)-(45) into the Hessian entry eqs. (9)-(12) (with $u = v = d$), which we can express as

$$h_{dd}(\mathbf{x}^*) = -F(\mathbf{x}^*)G_{dd}(\mathbf{x}^*), \tag{55}$$

where

$$\begin{aligned} F(\mathbf{x}^*) &= \frac{(1-c_\mathrm{d})(1+Nc_\mathrm{d})^2}{N(1+c_\mathrm{d})(1+(N-1)c_\mathrm{d})(1+(N+1)c_\mathrm{d})} > 0, \\ G_{dd}(\mathbf{x}^*) &= \frac{2(N+2c_\mathrm{d}(N-1))(1+Nc_\mathrm{d})(1+(N+1)c_\mathrm{d})}{N^2(1+(N-1)c_\mathrm{d})} > 0. \end{aligned} \tag{56}$$

Thus, $h_{dd}(\mathbf{x}^*) < 0$ is always negative and selection on dispersal alone is stabilising for all model parameters.

Similarly, the quadratic coefficient of selection on benevolence at the equilibrium eq. (53) is found by substituting eqs. (42)-(45) into the Hessian entry eqs. (9)-(12) (with $u = v = z$), and we find it can be written as

$$h_{zz}(\mathbf{x}^*) = F(\mathbf{x}^*)G_{zz}(\mathbf{x}^*)\frac{D}{f(\mathbf{x}^*,\mathbf{x}^*)}, \tag{57}$$

where

$$G_{zz} = \frac{2c_\mathrm{d}(1+(N+1)c_\mathrm{d})^2}{(1+Nc_\mathrm{d})^2} \geq 0. \tag{58}$$

So $h_{zz}(\mathbf{x}^*) \leq 0$ (since $D < 0$ at an internal attractor equilibrium – eq. 52), and selection on z alone is also stabilising for all model parameters.

M.4.6 Disruptive selection on dispersal and benevolence when they co-evolve

When dispersal and benevolence co-evolve, whether selection is disruptive depends on the correlational coefficient of selection, which is found by substituting eqs. (42)-(45) into the Hessian entry eqs. (9)-(12) (with $u = z$ and $v = d$), and which can be expressed as

$$h_{zd}(\mathbf{x}^*) = F(\mathbf{x}^*)G_{zd}(\mathbf{x}^*)\frac{B+C}{f(\mathbf{x}^*,\mathbf{x}^*)}, \tag{59}$$

where

$$G_{zd}(\mathbf{x}^*) = N^2c_\mathrm{d}(1+c_\mathrm{d}) - 2c_\mathrm{d}(2N-1) - 2. \tag{60}$$

Substituting eqs. (55), (57) and (59) into eq. (13) reveals after some re-arrangements that whenever

$$-\frac{G_{zd}^2(\mathbf{x}^*)}{G_{dd}(\mathbf{x}^*)G_{zz}(\mathbf{x}^*)} < \frac{D}{(B+C)^2}f(\mathbf{x}^*,\mathbf{x}^*) < 0, \tag{61}$$

the correlational coefficient of selection will cause selection to be disruptive. Unlike the left hand side of eq. (38), the left hand side of eq. (61) is always negative. This means that unlike when generations do not overlap, for any ecological parameters N and c_d, there exists a game that leads to disruptive selection when generations overlap. In addition, since cooperative games can have an internal convergence stable equilibrium when generations overlap (eq. 53), it is possible for such games to lead to polymorphism, which was not the case when generations do not overlap.

M.4.7 Selection when dispersal is cost-free

When dispersal is cost-free ($c_\mathrm{d} = 0$), analysis is much simplified. The population first converges to the equilibrium point

$$\mathbf{x}^* = (z^*, d^*) = \left(\frac{C}{D}, 1\right) \tag{62}$$

(provided $0 < C/D < 1$ and $D < 0$), at which there is no kin structure since dispersal is full ($d^* = 1$). In other words, the population is well-mixed and individuals interact at random. At this equilibrium, the Hessian matrix simply reads as,

$$\mathbf{H}(\mathbf{x}^*) = \begin{pmatrix} 0 & -\dfrac{2}{N^3}\dfrac{B+C}{f(\mathbf{x}^*,\mathbf{x}^*)} \\ -\dfrac{2}{N^3}\dfrac{B+C}{f(\mathbf{x}^*,\mathbf{x}^*)} & -\dfrac{2}{N^2} \end{pmatrix}, \tag{63}$$

and its dominant eigenvalue is,

$$\lambda(\mathbf{x}^*) = -\frac{1}{N^2} + \frac{\sqrt{4(B+C)^2/N^2 + f(\mathbf{x}^*,\mathbf{x}^*)^2}}{N^2 f(\mathbf{x}^*,\mathbf{x}^*)}. \tag{64}$$

Then, since

$$\lambda(\mathbf{x}^*) > 1 \iff \sqrt{4(B+C)^2/N^2 + f(\mathbf{x}^*,\mathbf{x}^*)^2} > f(\mathbf{x}^*,\mathbf{x}^*) \iff B+C \neq 0, \tag{65}$$

disruptive selection always occurs and leads to a polymorphism that creates kin structure: benevolent individuals that have z greater than $z^* = C/D$ also disperse less, allowing for relatedness among benevolent individuals to build up. In contrast, when dispersal is fixed at one ($d = 1$), the population will remain monomorphic for the convergence stable equilibrium z^* for linear games (58).

M.5 Computer simulations for recombination and recombination evolution

M.5.1 Fixed recombination

We incorporated recombination in our model by adding a stage of diploidy in the life-cycle of our population. After social interactions within groups, haploid individuals produce haploid gametes that disperse according to their genotype at the dispersal locus. Then, gametes randomly fuse within groups to make diploid individuals whose genome recombine according to a probability R, and that in turn produce a single haploid adult. In terms of simulations, this modified life-cycle entails that after calculating the fecundity f_i of each individual (as in M.3), each of the N breeding spots are filled by first sampling two haploid individuals from the parental generation according to the weighted sampling described in M.3 and fuse to make a diploid individual. Then, say a diploid individual has parent indexed i and j with genotypes (z_i, d_i) and (z_j, d_j) respectively. With a probability R, recombination occurs in this diploid, which produces two recombinant haploid genotypes, (z_i, d_j) and (z_j, d_i). With complementary probability $1-R$, recombination does not occur and the two haploid genotypes are the parental ones, (z_i, d_i) and (z_j, d_j). The breeding spot is filled by sampling one of the haploid genotypes at random (with equal probability). The rest of the simulation is as in M.3.

M.5.2 Recombination evolution

In order to model recombination evolution, we added a third quantitative locus that controls the recombination probability at the diploid stage. The genome of a haploid individual therefore carries three quantitative loci: (z, d, τ), where as before z encodes the probability of adopting B action, d the probability of dispersal at birth, and τ controls the probability of recombination among z and d loci. For simplicity, we assume that the τ locus is completely linked to the d locus. Two alleles segregate at the recombination locus τ: a wild-type R which codes for a recombination probability of $1/2$ and a dominant mutant r for zero recombination.

Diploid individuals are formed as in M.5.1. Then, say a diploid individual has parent indexed i and j with genotypes (z_i, d_i, τ_i) and (z_j, d_j, τ_j) respectively. Recombination in this individual occurs with a probability $1/2$ if $\tau_i = \tau_j = R$, or zero otherwise. If recombination occurs, the haplotypes produced are (z_i, d_j, τ_j) and (z_j, d_i, τ_i) since the τ locus is completely linked to the d locus. Mutation occurs at each locus independently with probability 0.01. Quantitative effects of mutation at the z and d loci are as in M.3, while mutations at the τ locus changes r to R and R to r. The rest of the simulation is as in M.3.

References

1. Clobert J, Baguette M, Benton TG, Bullock JM, Ducatez S (2012) *Dispersal Ecology and Evolution.* (Oxford University Press, Oxford).
2. Ronce O (2007) How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution. *Annu. Rev. Ecol. Evol. Syst.* 38(1):231–253.
3. Hamilton WD (1964) The genetical evolution of social behaviour. *J. Theor. Biol.* 7(1):1–52.
4. Frank S (1998) *Foundations of social evolution.* (Princeton University Press, Princeton).
5. Hamilton WD, May RM (1977) Dispersal in stable habitats. *Nature* 269(5629):578–581.
6. Cote J, Clobert J, Fitze PS (2007) Mother-offspring competition promotes colonization success. *Proc. Natl. Acad. Sci. U. S. A.* 104(23):9703–8.
7. Hoogland JL (2013) Prairie Dogs Disperse When All Close Kin Have Disappeared. *Science.* 339(6124):1205–1207.
8. Richardson KM, et al. (2016) Behaviour during handling predicts male natal dispersal distances in an establishing reintroduced hihi (*Notiomystis cincta*) population. *Anim. Conserv.* 20(2):135–143.
9. Lehmann L, Perrin N (2002) Altruism, dispersal, and phenotype-matching kin recognition. *Am. Nat.* 159(5):451–468.
10. Powers ST, Penn AS, Watson RA (2011) The concurrent evolution of cooperation and the population structures that support it. *Evolution.* 65(6):1527–1543.

11. Purcell J, Brelsford A, Avilés L (2012) Co-evolution between sociality and dispersal: The role of synergistic cooperative benefits. *J. Theor. Biol.* 312:44–54.
12. Mullon C, Keller L, Lehmann L (2016) Evolutionary Stability of Jointly Evolving Traits in Subdivided Populations. *Am. Nat.* 188(2):175–95.
13. Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447(7144):581–584.
14. Wright S (1931) Evolution in Mendelian populations. *Genetics* 16(3):290.
15. Rousset F (2004) *Genetic Structure and Selection in Subdivided Populations.* (Princeton University Press, Princeton, NJ).
16. Dugatkin LA (2008) *Principles of Animal Behavior, Second Edition.* (WW Norton New York).
17. Dercole F, Rinaldi S (2008) *Analysis of Evolutionary Processes: The Adaptive Dynamics Approach and Its Applications.* (Princeton University Press, Princeton).
18. Gandon S, Rousset F (1999) Evolution of stepping-stone dispersal rates. *Proc. R. Soc. London B Biol. Sci.* 266(1437):2507–2513.
19. Sinervo B, Svensson E (2002) Correlational selection and the evolution of genomic architecture. *Heredity (Edinb).* 89(5):329–338.
20. Schwander T, Libbrecht R, Keller L (2014) Supergenes and complex phenotypes. *Curr. Biol.* 24(7):R288–R294.
21. Hochberg ME, Rankin DJ, Taborsky M (2008) The coevolution of cooperation and dispersal in social groups and its implications for the emergence of multicellularity. *BMC Evol. Biol.* 8(1):238.
22. El Mouden C, Gardner A (2008) Nice natives and mean migrants: the evolution of dispersal-dependent social behaviour in viscous populations. *J. Evol. Biol.* 21(6):1480–91.
23. Myers J, Krebs C (1971) Genetic, behavioral, and reproductive attributes of dispersing field voles Microtus pennsylvanicus and Microtus ochrogaster. *Ecol. Monogr.* 41(1):53–78.
24. Ims RA (1990) Determinants of natal dispersal and space use in grey-sided voles, Clethrionomys rufocanus: a combined field and laboratory experiment. *Oikos* 57(1):106.
25. O'Riain MJ, Jarvis JU, Faulkes CG (1996) A dispersive morph in the naked mole-rat. *Nature* 380(6575):619–621.
26. Sinervo B, Clobert J (2003) Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science.* 300(5627):1949–1951.
27. Duckworth RA, Badyaev AV (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proc. Natl. Acad. Sci. U. S. A.* 104(38):15017–22.

28. Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philos. Trans. R. Soc. B Biol. Sci.* 365(1560):4065–4076.

29. Aguillon SM, Duckworth RA (2015) Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. *Behav. Ecol. Sociobiol.* 69(4):625–633.

30. Jacob S, et al. (2016) Cooperation-mediated plasticity in dispersal and colonization. *Evolution.* 70(10):2336–2345.

31. Duckworth RA, Kruuk LEB (2009) Evolution of genetic integration between dispersal and colonization ability in a bird. *Evolution.* 63(4):968–977.

32. Ross KG, Keller L (1995) Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. *Annu. Rev. Ecol. Syst.* 26(1):631–656.

33. Wang J, et al. (2013) A Y-like social chromosome causes alternative colony organization in fire ants. *Nature* 493(7434):664–8.

34. Purcell J, Brelsford A, Wurm Y, Perrin N, Chapuisat M (2014) Convergent Genetic Architecture Underlies Social Organization in Ants. *Curr. Biol.* 24(22):2728–2732.

35. Canestrelli D, Bisconti R, Carere C (2016) Bolder Takes All? The Behavioral Dimension of Biogeography. *Trends Ecol. Evol.* 31(1):35–43.

36. Bohonak AJ (1999) Dispersal, gene flow, and population structure. *Q. Rev. Biol.* 74(1):21–45.

37. Lehmann L, Keller L (2006) The evolution of cooperation and altruism - A general framework and a classification of models. *J. Evol. Biol.* 19(5):1365–1376.

38. Caswell H (2001) *Matrix population models: construction, analysis, and interpretation.* (Sinauer Associates, Inc, Saunderland).

39. Tuljapurkar S, Horvitz CC, Pascarella JB (2003) The many growth rates and elasticities of populations in random environments. *Am. Nat.* 162(4):489–502.

40. Karlin S, Taylor HM (1975) *A First Course in Stochastic Processes.* (Academic Press, San Diego).

41. Harris TE (2002) *The Theory of Branching Processes.* (Courier Corporation, Mineola).

42. Roze D, Rousset F (2008) Multilocus models in the infinite island model of population structure. *Theor. Popul. Biol.* 73(4):529–542.

43. Leimar O (2009) Multidimensional convergence stability. *Evol. Ecol. Res.* 11(2):191–208.

44. Brown SP, Taylor PD (2010) Joint evolution of multiple social traits: a kin selection analysis. *Proc. R. Soc. London B Biol. Sci.* 277(1680):415–422.

45. Ajar E (2003) Analysis of disruptive selection in subdivided populations. *BMC Evol. Biol.* 3(22):22.

46. Wakano JY, Lehmann L (2014) Evolutionary branching in deme-structured populations. *J. Theor. Biol.* 351:83–95.

47. Phillips PC, Arnold SJ (1989) Visualizing multivariate selection. *Evolution.* 43(6):1209–1222.

48. Horn RA, Johnson CR (1985) *Matrix Analysis.* (Cambridge University Press, Cambridge) Vol. 169, p. 561.

49. Karlin S (1968) Equilibrium behavior of population genetic models with non-random mating. *J. Appl. Probab.* 5(2):231–313.

50. Queller DC (1985) Kinship, reciprocity and synergism in the evolution of social behaviour. *Nature* 318(6044):366–367.

51. Queller DC (1992) Quantitative Genetics, Inclusive Fitness, and Group Selection. *Am. Nat.* 139(3):540–558.

52. Taylor P (2016) Hamilton's Rule in finite populations with synergistic interactions. *J. Theor. Biol.* 397:151–157.

53. Van Cleve J, Lehmann L (2013) Stochastic stability and the evolution of coordination in spatially structured populations. *Theor. Popul. Biol.* 89:75–87.

54. Queller DC (1992) Does population viscosity promote kin selection? *Trends Ecol. Evol.* 7(10):322–4.

55. Lehmann L (2008) The adaptive dynamics of niche constructing traits in spatially subdivided populations: evolving posthumous extended phenotypes. *Evolution.* 62(3):549–66.

56. Wolfram Research I (2014) *Mathematica.* (Wolfram Research, Inc., Champaign, Illinois, USA).

57. Taylor PD, Irwin AJ, Aug N (2007) Overlapping Generations Can Promote Altruistic Behavior. *Evolution.* 54(4):1135–1141.

58. Meszéna G, Kisdi É, Dieckmann U, Geritz SAH, Metz JAJ (2002) Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics. *Selection* 2(1-2):193–220.